Group Responses to Specially Skilled Individuals in a Macaca fascicularis Group
Author(s): Eduard Stammbach
Source: *Behaviour*, Vol. 107, No. 3/4 (Dec., 1988), pp. 241-266
Published by: BRILL
Stable URL: http://www.jstor.org/stable/4534731
Accessed: 09/04/2009 15:08

GROUP RESPONSES TO SPECIALLY SKILLED INDIVIDUALS IN A MACACA FASCICULARIS GROUP

by

EDUARD STAMMBACH[1][2]
(Ethology and Wildlife Research, University of Zürich, Switzerland)

(With 4 Figures)
(Acc. 6-VII-1988)

Introduction

A great variety of methods are used to investigate the relation between primate social organization and ecology. They embrace gross correlational analyses of biologically relevant variables at one extreme (Clutton-Brock & Harvey, 1977) and detailed studies of individual learning abilities at the other. A first attempt to consider the contributions of individuals to a social group was provided by Hinde (1974); his concept, however, does not take into account the interaction of a social group with its environment. Nagel (1979) developed a new tool for obtaining data relevant to the topic. According to his conceptualization one should identify types of dyadic interactions and relationships as basic units of the social system and ask in addition how the dyad handles an environmental problem in a social manner. The link between social organization and ecology is thus made on a very basic level. Kummer (1978), in an extension of Hinde's social and Nagel's socioecological approaches, assumes that an individual shapes its relationships in such a way that it increases its chances of reproduction. Kummer suggests that each conspecific B of an individual A can, in various ways, increase or decrease the survival and thus the reproductive success of A. The effects of B on A depend (i) on B's qualities, on his skills, power and experience,

[1]) I thank Prof. H. Kummer for the support of this study and for his help in preparing the english manuscript. Karin Geering critically read the final manuscript. Special thanks are due to our animal caretakers, especially to Ruedi Wey, without their assistance, the study would have been impossible. The study was supported by the Swiss National Science Foundation, grants No. 3.359-0.82 and partly No. 3.242.85 to Prof. H. Kummer.

[2]) Present address: Wehntalerstr. 594b, CH-8046 Zürich, Switzerland.

(ii) on B's short- and long-term tendencies to perform acts that increase or decrease A's success in a given context and (iii) on B's availability. According to KUMMER, the value of a partner may be increased by (i) monitoring the state of the three factors, (ii) by selecting the best and most available of the potential partners accordingly and (iii) by altering the states of the factors of the chosen partner. The best partner that an individual might choose among the members of a group would be a skillful, powerful and experienced partner that is likely and inclined to improve his success and that is not "occupied" by a dominant group member. A crucial point of the approach of KUMMER is the necessity that monkeys should be able to evaluate their conspecifics.

In this study, I experimentally approach the ability of primates to monitor and use non-social skills of conspecifics. I do not attempt to identify the form of representation in which this knowledge about others is stored in the monkey's brains. But the flexibility of behavioural reactions according to eventual changes of individual characteristics indicates at least the minimum cognitive performance that is needed for explaining the observed phenomena: The more a monkey is capable of judging characteristics and qualities of others, the more we will expect him to adjust his behaviour accurately and quickly in order to benefit optimally from the capabilities of his conspecifics.

I chose the following procedure: In a first phase, I ascertained that all group members were able to attain some of their food by manipulating a popcorn dispensing apparatus, thus introducing the knowledge that lever pulling can produce food rewards into a group of longtailed macaques (*Macaca fascicularis*). Then a single individual that, because of its low dominance status, could not monopolize the apparatus, was trained in a more complex manipulation task. This task consisted of manipulating three levers in a correct sequence, whereupon food became available for himself and other group members. This specialist thus became the only producer of preferred food in the group. The main question of the study were: (i) Is it possible to establish low ranking animals as food producing specialists? (ii) Will other group members become aware of the special skills of that individual and will they adapt their behaviour accordingly in order to benefit from his skills? There is no a priori reason to assume that a low ranking specialist will be allowed to monopolize the apparatus just due to his exceptional skills. High ranking group members will at first try to get access to the food rewards and thus displace the specialist; they are expected to stop to chase the food producing specialist away from the preferred food site if they want to benefit from his activities. Furthermore, other group members should seek spatial proximity to the specialist as soon as he is approaching the food dispensing apparatus and try to join him so that they are present when the first food items are produced. (iii) Will there be any effects upon the dominance or social relationships in the group? Following KUMMER's (1978) hypothesis that animals may try to alter the tendency of others to improve their own success in a given situation, I expect that the food producer should be treated in a friendlier way than before. Interactions such as grooming should increase; aggressive acts should decrease. An increase should also be observed in providing alliances. If we consider proxemics as a further measure of social attention, we expect group members that benefit from the specialist to maintain spatial proximity to him even outside the experimental situation, thus indicating their closer association to the specialist as a consequence of the gained benefits.

Animals, material and methods

Animals.

The study colony consisted of 40 longtailed macaques (*Macaca fascicularis*) and was naturally composed. The animals stem from a large group from the Basle Zoo (Switzerland), where they had lived together since birth. They were separated from their native group and transferred to their new living quarters in summer 1981. Matrilineal kinship of the group is known. The group was permanently housed together in a 50 sqm indoor cage and a 1000 sqm outdoor enclosure and was fed three times per day with cereals, seasonal fruit and monkey pellets. Experimental animals were not deprived of food before experiments. Besides feeding times and during the night, the colony was allowed to interact freely for at least one and a half hour a day.

The experiments were carried out on subgroups of the colony. A subgroup was separated from the entire group for each experimental trial (p. 244). In each of three consecutive years (1983/4, 1984/5, 1985/6) one of three different subgroups was used (Table 1). The three subgroups were used in turn by three independent projects. No other projects were carried out simultaneously on one experimental subgroup. The subgroups consisted mainly of young males (subgroup 1), of young females (subgroup 2) and of adult females (subgroup 3), respectively. Mothers had their youngest offspring with them.

Apparatus.

The apparatus consisted of two parts: (i) The three levers that had to be manipulated in a correct sequence in order to release a food reward. Levers were arranged in a horizontal row, 30 cm from each other. (ii) A food dispensing mechanism that provided preferred food in three bowls. Three vertical levers 12 cm long were situated at a height that allowed a monkey to manipulate them in a sitting posture. A lever had to be pulled to an angle of 45° to release the food dispensing mechanism. Thus the movements that had to be performed were clearly visible to other group members. A correct manipulation by specialists consisted of pulling first the left, then the central, then the right lever. Every 20 seconds, a monkey had 10 seconds to make a correct manipulation. During these 10 seconds, a beeper indicated that the levers were activated. For the whole period, when the apparatus was ready for manipulation, a yellow xenon light blinked. The three food bowls were installed beneath the levers, the middle one directly under the levers and the

TABLE 1. Characteristics of subjects, subgroup composition

Sub-group	Name	Abbre-viation	Approx. age	Birth date	Sex	Offspring of	Dominance*) rank in subgroup
1	Ketut	KT	6	8. 9.1977	Male	Sakri	1
	Titin	TT	13	1970	Female	Sangi	2
	Salim	SL	4	5. 7.1979	Male	Sakri	3
	Ukui	UK	2	10. 7.1981	Male	Upit	4
	Malen	ML	3½	13. 3.1980	Male	Dana	5
	Junus	JN	3	29. 9.1980	Male	Titin	6
	Subali	SB	3	26.10.1980	Male	Sakri	7
2	Rini	RN	5	12. 8.1980	Female	Timor	1
	Tjat	TJ	3½	21. 3.1982	Female	Timor	2
	Topi	TP	9	7. 7.1976	Female	Timor	3
	Sanah	SN	6	8. 5.1979	Female	Dili	4
	Saja	SJ	2½	27. 2.1983	Female	Sanah	5
	Jumi	JM	5	27. 7.1980	Female	Upit	6
	Djambi	DJ	4½	5.1981	Female	Dana	7
	Sapi	SP	3½	8. 3.1982	Female	Sakri	8
3	Topi	TP	8	7. 7.1976	Female	Timor	1
	Toko	TK	2½	2. 5.1982	Male	Topi	2
	Dili	DL	9½	26. 5.1975	Female	Timor	3
	Djalan	DA	2½	11. 4.1982	Male	Dili	4
	Mayun	MY	8½	25. 4.1976	Female	Ambon	5
	Upit	UP	9½	28. 5.1975	Female	Ambon	6
	Titin	TT	14	1970	Female	Sangi	7
	Sakri	SK	11	15. 8.1973	Female	Dana	8
	Sapi	SP	2½	8. 3.1982	Female	Sakri	9

*) cf. Table 3.

other two on the left and on the right at a distance of 50 cm. Thus, if a monkey manipulated the levers correctly, he himself and at least two other monkeys could eat from the food reward which consisted of about a dozen pieces of fresh popcorn, a food cherished by the monkeys.

Experimental design.

Altogether five series of trials were carried out, each series with a different specialist, a monkey knowing to operate the apparatus successfully. The series, varying from 30 to 97 trials, will be referred to as replicates. In summer, the trials were carried out in the larger part of the outdoor enclosure (Fig. 1). In winter, the experiments took place in one half of the indoor cages (Fig. 2), while the rest of the group remained in the other half. Three of the replicates (p. 247) were carried out partly in the outdoor and partly in the indoor enclosures.

For the last five replicates (p. 247) and thus for the last five specialists two apparatus were available. Alternately, only one of the two was switched on with a maximum interval of 5 min. This was done for two reasons. (i) In the first three replicates and especially at the beginning of a replicate, i.e. when a specialist had to get accustomed to his role,

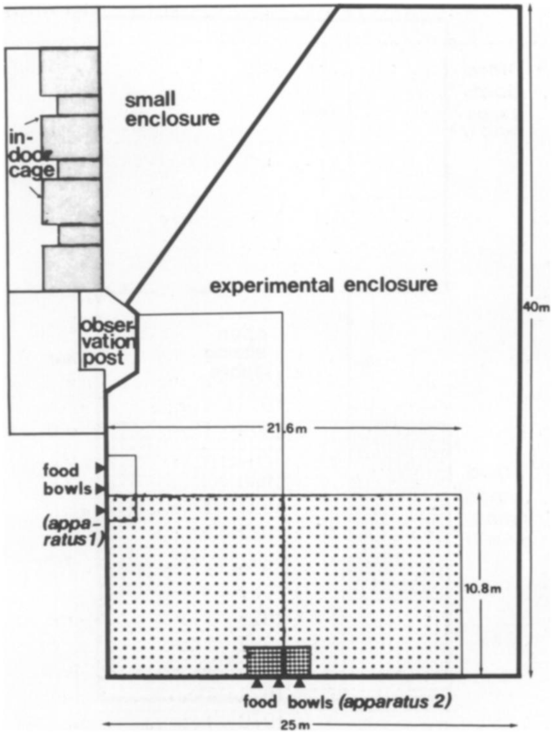


Fig. 1. Outdoor enclosure. The subdivision into the three areas is marked for 1 apparatus site only. Area 1 (food site) is tightly dotted, area 2 is sparsely dotted. Area 3, consisting of the rest of the experimental enclosure, is left white.

he often did not dare to approach the apparatus again after he had been chased away, since the chaser often remained near the apparatus. The availability of two apparatus sites improved the possibility to train and to establish the shyer female specialists. (ii) The manner with which other animals approached the apparatus relative to the position of the specialist could indicate whether they were aware of the skills of the specialist (p. 252). By alternately switching on one of the apparatus the animals were forced to approach the newly activated apparatus several times per trial and thus more such data could be collected in the last five replicates. In contrast, insufficient data are available for the first three replicates.

Meteorological and organizational reasons did not allow application of exactly the same conditions for all trials. A single outdoor trial lasted one hour and a half. In the first 45 minutes (feeding phase), the apparatus was switched on, which was indicated by the xenon light blinking, and successful lever manipulation was possible. In the second 45 minutes (social phase), the apparatus was switched off and social behaviour of the subgroup was observed. In winter, the social phase of the trials had to be reduced to 30 minutes.

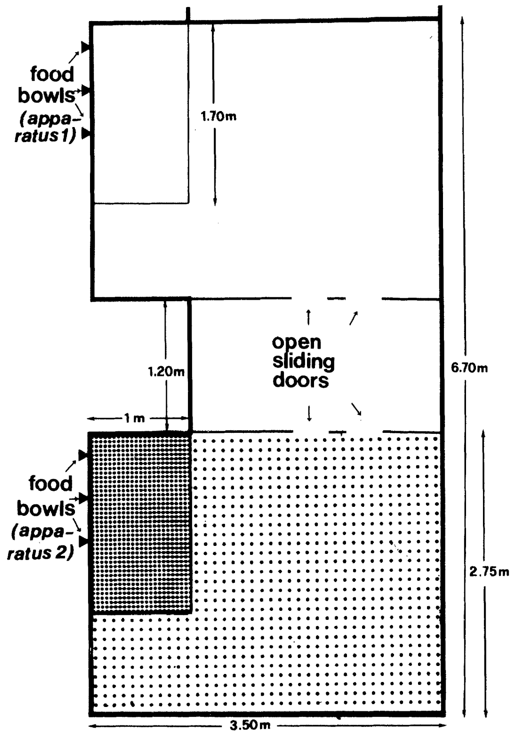


Fig. 2. Half of indoor enclosure. The subdivision into the three areas is marked for 1 apparatus site only. Area 1 (food site) is tightly dotted, area 2 is sparsely dotted. Area 3, consisting of the rest of the experimental enclosure, is left white.

Training.

Before the trials of the first replicate, each animal of the colony was pretrained individually to manage a simpler task where only one lever had to be pulled twice consecutively to get a food reward. Thus, at the beginning of the experiments, all monkeys had experienced that lever pulling can produce a food reward. This training was repeated regularly for animals of the colony that did not belong to the subgroup that actually was involved in the experiment at that time.

The training of a specialist took place within the subgroup: The subgroup was released into the experimental enclosure but only the prospective specialist was now rewarded, at first for each single pull on one of the levers. Since the food reward could be suppressed by switching off the food dispensing part of the apparatus, no other subgroup member than the specialist himself could perform a rewarded lever manipulation. However, it was rarely necessary to switch off the food dispenser. In a next phase, not one but three levers had to be pulled, regardless in which sequence, to get a reward. Then, the specialist was gradually accustomed to pull the levers in a given sequence: in a first step, he had to pull the left lever once. Then he had to perform two pullings at one or both of the other levers. In the last step of training, he got the reward only if he pulled the correct sequence left → middle → right. The other subgroup members thus could observe how the specialist learned.

Subgroups, replicates.

On subgroups 1 and 2, three replicates with three different specialists were carried out in sequence, in subgroup 3 only two (Table 2). Dominance relationships were obtained using the distribution of baring teeth grins (ANGST, 1974) as a subordination criterion. Specialists were chosen by two criteria. They had to be as low ranking as possible (p. xx) but nevertheless had to exhibit satisfactory lever pulling activity. Before each new replicate, during which only the lever pulling of the specialist was rewarded, a preparatory series of trials took place, in which all the animals of the subgroup were allowed to manipulate one single lever successfully again. This phase served both to dismiss the previous specialist as well as to bring all subgroup members to lever pulling again. The previous specialist was not rewarded at all for the first three trials of this preparatory series. This phase lasted until every subgroup member had pulled levers successfully at least twice.

TABLE 2. Replicates and specialists

Sub-group	Specialist	Number of trials	Total experimental time (hours)	Trial numbers	Observation period
1	Malen	47	35.0	14- 60	June 83-Sept 83
	Ukui	39	35.0	74-113	Oct 83-Jan 84
	Junus	70	52.0	134-203	Feb 84-June 84
2	Sanah	41	31.0	516-556	June 85-Sept 85
	Djambi	34	27.75	567-600	Oct 85-Nov 85
	Saja	55	41.0	607-661	Dec 85-Mar 86
3	Sakri	30	29.66	320-353	Sept 84-Oct 84
	Mayun	97	83.0	357-453	Nov 84-May 85

60 trials per specialist were planned, including the preparatory trials for all subgroup members. The schedule had to be corrected repeatedly for external reasons and was applied for the first replicate only. The effective numbers of trials are shown in Table 2. When the first two replicates with subgroup 1 were completed, it was apparent that up to 100 trials should have been carried out in order to fully produce the predicted effects.

Data registration and analysis.

During the feeding phase of trial, protocols were spoken on a tape recorder and then registered on an electronic data collector ZIRELCO-DATAPAD® . I protocoled successful and unsuccessful lever manipulations by every individual using Hansen frequencies (ALTMANN, 1974). The 20 sec intervals were signalled to the observer by the apparatus. The detailed sequences in which the levers were touched were not recorded; it would have demanded most of the attention of the observer. Instead, social interactions among individuals were recorded. Duration of continuous behaviour was estimated by the scan sampling method (ALTMANN, 1974), using 20 sec intervals. At the end of each interval the locations of all animals were recorded, using a subdivision of the enclosure into three areas. This subdivision was different for outdoor and indoor trials (Fig. 1 and Fig. 2). In the outdoor enclosure, area 1, measuring 1 × 3 m, enclosed the part nearer than 1 m to one of the food bowls of the active apparatus. In the indoor cage area 1 measured only

1.7 × 1 m due to fixed cage structures. A second, larger area was situated around the food bowls at a distance from which the animals usually observed the behaviour of other group members at the apparatus. In the outdoor enclosure, area 2 extended 10 m from the food sites. Since enclosure posts served as reference marks, the border of area 2 and 3 was set at 10.8 m distance from the center food bowl (see Fig. 1). This distance was chosen according to observations in the pilot experiments. It was chosen so that area 3 contained the animals which were not interested in the experiment and usually were engaged in other activities. In the indoor enclosure (Fig. 2), area 2 consists of the cage compatement where the apparatus was activated.

Protocols of the social phase of a trial were typed directly into the data collector. I recorded all social interactions among individuals. Durations of continuous behaviours could be determined precisely by recording the start and the end of bouts. Every 5 min the nearest neighbour of each individual was recorded. If no animal was present within a 7.2 m circle of the focal animal no neighbour was protocoled. The 7.2 m distance corresponded to the distance between enclosure posts. For each trial, the sequence in which the animals were selected was randomly determined.

Statistical analysis was performed by using the statistical analysis system SAS (SAS user's guide 1982a and b) for Kendall rank correlations and Wilcoxon rank sum tests.

Results

Activities of specialists.

The first juvenile male, Malen, was highly motivated for lever pulling and, towards the end of his replicate, he often stayed at the apparatus throughout a feeding phase. Malen hardly was displaced or threatened by other subgroup members. The other two juvenile male specialists, Ukui and Junus behaved similarly, but they were a bit more anxious than Malen. In contrast, three of the female specialists, Sakri, Sanah and Djambi ceased to operate the levers after a period of satisfactory activity. In the remaining two replicates with female specialists the latter overcame their initial shyness and showed satisfactory activity thereafter. The three males, Malen (ML), Ukui (UK) and Junus (JN) and the two females, Saja (SJ) and Mayun (MY) pulled levers regularly and at quite a high frequency. Females Sanah (SN), Djambi (DJ) and Sakri (SK), who "went on strike" before the end of the trial series as planned, had lower frequencies of manipulation. The most important precondition for successful completion of the experiments was fulfilled in five of the eight replicates: the subordinate specialists worked regularly in presence of other group members.

Measure of benefit from specialists.

Before dealing with the questions mentioned in the introductory section, we have to consider the way of measuring the amount of benefit that a group member gains from the specialist. At the end of each 20 sec interval I registered in which area of the enclosure each animal was staying, and thus could determine whether two animals were present simultaneously near the food bowls. If the lever was operated successfully food was present in the food bowls during that interval and the following one. Thus, the frequency with which an animal was present together with the specialist at the end of the interval when the lever pulling occurred or at the end of the following one, is a rough measure for the benefit that an animal gains from the specialist. These frequencies will be called frequencies of joint presence. One might object that a simpler measure would have been more accurate in measuring the amount of benefit, namely the total number of intervals when an animal was present alone as well as together with the specialist at the food site when food was available. But I chose the joint presence version that takes into account the simultaneous presence of the specialist because the measure has to reflect not the total quantity of food that is gathered by an animal but the quantity of food that a non-specialist gathered after having observed the specialist's manipulations. If an animal arrived at the food site after the specialist already had left it is less likely that he noticed that the specialist was responsible for the food now available. The opposite is most likely true if the specialist remains at the food site after having manipulated the levers. The joint presence measure thus estimates the benefit as perceived by the non-specialists.

Closest associations among specialists and non-specialists.

Table 3 contains two scores that illustrate the different amounts of benefit gained by group members from the specialist. The first score ("trials together") indicates in how many of the trials of a replicate a group member was present together with the specialist in one interval or more per trial and thus represents the regularity of access in the course of a replicate. The second score ("intervals together") shows in how many of the total number of intervals per replicate in which food was provided a group member was present at the food site together with the specialist. This score estimates the amount of food that was gained in presence of the specialist throughout a replicate. In the following I will refer to this %-score as sum of joint presence. The dyads in Table 3 are arranged according to their sums of joint presence. Most replicates suggest a bimodal distribution of scores, which means that some of the group members had regular and frequent access to food, while others seemed to be excluded. Both measures reveal almost the same rank order of

TABLE 3. Number of trials per replicate when the two dyad members were present together at the apparatus at least once in a trial and number of intervals per replicate when both were present

Group member	Specialist	Total number of trials per replicate	Number of trials together	% of trials together	% of intervals together
Ketut	Malen +	47	43	91.5	30.05
Salim	Malen +	47	43	91.5	24.57
Ukui	Malen +	47	36	76.6	8.81
Junus	Malen	47	39	82.9	6.73
Titin	Malen +	47	29	61.7	4.10
Subali	Malen	47	10	21.3	1.10
Ketut	Ukui +	39	27	69.2	11.78
Junus	Ukui	39	30	77.0	9.66
Malen	Ukui	39	28	71.8	9.24
Salim	Ukui +	39	22	56.4	4.85
Titin	Ukui +	39	15	38.5	4.85
Subali	Ukui	39	4	10.3	0.10
Ukui	Junus +	70	68	97.1	17.37
Malen	Junus +	70	50	71.4	11.71
Salim	Junus +	70	57	81.4	10.46
Ketut	Junus +	70	17	24.3	0.76
Titin	Junus +	70	17	24.8	0.75
Subali	Junus	70	6	8.6	0.17
Saja	Sanah	41	34	82.9	5.38
Rini	Sanah +	41	20	48.8	1.93
Tjat	Sanah +	41	20	48.8	1.21
Topi	Sanah +	41	5	12.2	0.60
Sapi	Sanah	41	2	4.8	0.04
Djambi	Sanah	41	1	2.4	0.02
Jumi	Sanah	41	1	2.4	0.02
Saja	Djambi +	34	24	68.6	5.09
Tjat	Djambi +	34	10	28.6	0.39
Sanah	Djambi +	34	5	14.3	0.37
Sapi	Djambi	34	4	11.4	0.37
Jumi	Djambi +	34	5	14.3	0.35
Rini	Djambi +	34	5	14.3	0.28
Topi	Djambi +	34	0	0	0
Tjat	Saja +	55	50	91.0	7.95
Rini	Saja +	55	49	89.1	7.13
Topi	Saja +	55	29	52.7	2.15
Sanah	Saja +	55	16	29.1	0.88
Sapi	Saja	55	5	9.0	0.33
Jumi	Saja	55	3	5.5	0.15
Djambi	Saja	55	1	1.8	0.01
Djalan	Sakri +	30	25	83.3	6.65
Sapi	Sakri	30	15	50	1.04
Toko	Sakri +	30	15	50	0.95

Topi	Sakri +	30	5	16.6	0.13
Upit	Sakri +	30	1	3.3	0.09
Mayun	Sakri +	30	2	6.7	0.07
Dili	Sakri +	30	2	6.7	0.06
Titin	Sakri +	30	0	0	0
Djalan	Mayun +	97	87	89.7	8.88
Toko	Mayun +	97	82	84.5	6.57
Topi	Mayun +	97	59	60.8	3.00
Dili	Mayun +	97	46	47.4	1.56
Upit	Mayun	97	11	11.3	0.24
Sapi	Mayun	97	8	8.2	0.31
Sakri	Mayun	97	8	8.2	0.30
Titin	Mayun	97	0	0	0

Dyads are arranged according to their sum of joint presence.
+ : group member ranks higher than specialist.

benefit gained by the non-specialists. The exclusion of some non-specialists may be due to two reasons. Either they were not tolerated by the specialist in that he left the food site when they approached, or they were displaced by higher ranking group members that themselves competed for maximal benefit with them. In the following I will not distinguish these two possibilities since (i) the aim of the study is to find out how an animal treats another one that benefits him with food and (ii) a detailed analysis of this question would require additional experiments that would have demanded the removal of high ranking animals from the group in order to allow low ranking group members to approach the food site.

Displacing and chasing the specialist.

The highest ranking group members usually try to monopolize the source if a limited source of preferred food is available in a monkey group. This happened in these experiments too, at least in the first trials of a replicate. As soon as a specialist operated the levers correctly, a high ranking group member would approach and displace or chase him away from the apparatus. Of course, no further food reward was available until the specialist returned to the apparatus and pulled the levers again. In order to facilitate this, high ranking animals should learn to approach cautiously and not to chase the specialist. However, not all the dominant non-specialists initially displaced and chased the specialist.

To test this hypothesis, I determined for each trial (i) in how many 20 sec intervals the specialist left the 1 m area around the apparatus; this number gives an estimated maximum number of intervals, in which the specialist could have left the apparatus because he was displaced or chased. (ii) How many of the leavings were preceded by displacements of chases? A displacement was protocoled when another animal entered the 1 m area situated around the apparatus and the specialist left within 2 sec afterwards. Chasing was recorded when the specialist was threatened or chased by others while he stayed in the nearest zone around the apparatus and left it within 2 sec. Cases in which more than one group member displaced or chased the specialist were scored for each of them.

Table 4 contains the Kendall τ for the correlation between the proportion of leavings induced by displacement or chasing in a trial and the ordinal number of the trials. In case of reduction of the proportion across subsequent trials, a negative correlation should appear. In 14 of 55 dyads displacings were significantly reduced in course of the replicates. In only one the actor was lower ranking than the specialist. Chasing was reduced in 15 dyads of the 36 in which the specialist was lower ranking (= 41.6%). No significant positive correlation was found.

Following and passing the specialist.

For the last five replicates two apparatus were available. Alternately, only one of the two was switched on. Thus, both specialists and non-specialists had to move from one apparatus to the other several times. How a non-specialist reacts to the movements of the specialist may give a hint on what he already knows about the specialist's role. An ignorant non-specialist should approach the apparatus only after a successful lever manipulation by the specialist, responding to the visible food only. Informed monkeys should approach the apparatus already when the specialist starts to approach it, they should follow or even pass him. Three stages of the learning process can be distinguished: (i) Another animal approaches after the specialist already manipulated the levers successfully. (ii) Other animals follow the specialist while he approaches the apparatus in order to pull levers or (iii) they even pass and arrive before him at the apparatus, and wait for his lever pulling.

I defined two measures that reflect these patterns of behaviour. If the specialist approached the apparatus, which means that he walked or ran at least 1 m in the direction of the active apparatus while he was within area 2 of the enclosure, (i) following was protocoled if a non-specialist moved behind the specialist and in the same direction for at least 1 m

TABLE 4. Kendall τ correlations between number of displacements and chasings from the apparatus per presence of the specialist and trial numbers

Group member	Specialist	Displacing	Chasing
Ketut	Malen +	-0.31**	-0.36**
Salim	Malen +	-0.29**	-0.21*
Ukui	Malen +	ns	—
Junus	Malen	ns	ns
Titin	Malen +	ns	ns
Subali	Malen	—	—
Ketut	Ukui +	-0.52**	-0.42**
Junus	Ukui	—	—
Malen	Ukui	-0.25*	—
Salim	Ukui +	ns	-0.33**
Titin	Ukui +	ns	—
Subali	Ukui	—	—
Ukui	Junus +	ns	ns
Malen	Junus +	—	—
Salim	Junus +	ns	ns
Ketut	Junus +	-0.20*	ns
Titin	Junus +	ns	-0.23*
Subali	Junus	—	—
Djalan	Sakri +	-0.45**	—
Sapi	Sakri	—	—
Toko	Sakri +	ns	ns
Topi	Sakri +	ns	ns
Upit	Sakri +	—	ns
Mayun	Sakri +	ns	ns
Dili	Sakri +	ns	ns
Titin	Sakri +	—	—
Saja	Sanah	ns	—
Rini	Sanah +	-0.53**	-0.38**
Tjat	Sanah +	-0.36**	-0.51**
Topi	Sanah +	-0.26*	-0.33**
Sapi	Sanah	—	—
Djambi	Sanah	—	—
Jumi	Sanah	—	—
Saja	Djambi +	ns	ns
Tjat	Djambi +	ns	-0.48**
Sanah	Djambi +	ns	ns
Sapi	Djambi	—	—
Jumi	Djambi +	ns	—
Rini	Djambi +	ns	ns
Topi	Djambi +	—	ns
Tjat	Saja +	-0.30**	-0.40**
Rini	Saja +	ns	-0.50**
Topi	Saja +	-0.27**	-0.23**
Sanah	Saja +	—	—
Sapi	Saja	—	—
Jumi	Saja	—	—
Djambi	Saja	—	—
Djalan	Mayun +	-0.40**	-0.22**
Toko	Mayun +	-0.32**	-0.25**
Topi	Mayun +	ns	ns
Dili	Mayun +	-0.22**	-0.32**
Upit	Mayun	—	—
Sapi	Mayun	—	—
Sakri	Mayun	—	—
Titin	Mayun	—	—

Dyads are arranged according to their sum of joint presence. +: group member ranks higher than specialist, —: insufficient amount of data, ns: not significant, *: significant at 5% level, **: significant at 1% level.

within area 2 of the enclosure before the specialist entered area 1. (ii) Passing was recorded if a non-specialist after having followed arrived first at the food site before the approaching specialist. Passing was protocoled even if the specialist immediately left the apparatus again. The frequencies of both types of behaviour were divided by the total number of approaches to the apparatus performed by the specialist. If an animal learned about the skills of the specialist, both proportions should increase in course of the trial series. Passing was rare in the much smaller indoor

TABLE 5. Kendall τ correlations between number of followings and passings of others per number of approaches of the apparatus by the specialist and trial numbers

Group member	Specialist	Following	Passing	Group member	Specialist	Following	Passing
Saja	Sanah	0.37**	0.33**	Djalan	Sakri +	0.59**	0.33*
Rini	Sanah +	ns	ns	Sapi	Sakri	ns	0.40**
Tjat	Sanah +	ns	—	Toko	Sakri +	0.39**	0.33*
Topi	Sanah +	—	—	Topi	Sakri +	—	ns
Sapi	Sanah	ns	—	Upit	Sakri +	ns	—
Djambi	Sanah	—	—	Mayun	Sakri +	ns	—
Jumi	Sanah	—	—	Dili	Sakri +	ns	—
Saja	Djambi +	ns	ns	Titin	Sakri +	—	—
Tjat	Djambi +	ns	—	Djalan	Mayun +	ns	ns
Sanah	Djambi +	ns	—	Toko	Mayun +	0.16*	ns
Sapi	Djambi	ns	ns	Topi	Mayun +	0.20**	ns
Jumi	Djambi +	—	—	Dili	Mayun +	ns	ns
Rini	Djambi +	ns	—	Upit	Mayun	ns	—
Topi	Djambi +	—	—	Sapi	Mayun	ns	—
Tjat	Saja +	0.27**	ns	Sakri	Mayun	ns	—
Rini	Saja +	0.36**	—	Titin	Mayun	—	—
Topi	Saja +	ns	—				
Sanah	Saja +	ns	—				
Sapi	Saja	—	—				
Jumi	Saja	—	—				
Djambi	Saja	—	—				

Dyads are arranged according to their sums of joint presence. +: group member ranks higher than specialist, —: insufficient amount of data, ns: not significant, *: significant at 5% level, **: significant at 1% level.

cage and insufficient data are available on indoor trials (specialists Saja and Mayun).

Within each specialist's trial series I looked for positive correlations (Kendall's τ) among the proportions and the trial numbers. Table 5 shows that for following significant positive correlations were found in 7 dyads and for passing in 4 dyads of a total of 37 dyads that could be tested. No significant negative correlations were found. Of course we cannot conclude from a non significant correlation that the respective dyad partner of the specialist was unable to assess the specialist's skills. He may have been prevented from following and passing by a higher ranking group member that had priority of access to the food bowls. The significant correlations are found in dyads with high sums of joint presences in which non-specialist partners had frequent access to the apparatus site and thus frequent opportunity to follow or pass.

We may conclude that some of the animals not only were able to perform the more simpler task of holding back their aggressive tendencies in order to get an increasing amount of benefit from the specialist, but that there was also an element of anticipation. Some animals obviously could associate the approaching of the apparatus by the specialist with the later provisioning of the food reward in which they could participate.

The following objection may be made: As mentioned earlier, a flashing light and a beeper indicated the activation of an apparatus. Thus the animals might have approached an apparatus merely reacting to these signals, and the following or passing occurred just because of the simultaneous approach of both the specialist and his partner towards a newly activated apparatus. This objection can be rejected though. When the alternative apparatus was switched on the specialists seldom approached it immediately. In at most 4% of the cases they arrived at the apparatus site in first 20 sec interval after the alternative apparatus was switched on. In about one third of the cases, the specialists arrived in the second interval. The peak for non-specialists appears in the third or in the fourth interval after the alternate apparatus was switched on. Therefore followings and passings of others really were reactions to the movements of the specialist. Furthermore, followings and passings were set into relation with the total number of approaches performed by the specialist and the changes of these proportions were analysed. Since due to the previous training procedure all the animals were very familiar with the apparatus it is improbable that these improvements of following or even passing were due to improved learning of the flashing light as a conditioned stimulus. We have to conclude that the animals learned that both conditions for food delivery had to be fulfilled, namely that (i) the apparatus had to be switched on and (ii) the actual specialist had to be present at the apparatus.

Changes in social interactions.

Until now I have described changes in the behaviour of the specialists and their partners while the apparatus was active. It should be easy for a monkey to learn to behave accurately in order to benefit from the food rewards that are provided by the specialist. The less he chases or displaces a specialist and the sooner he approaches the apparatus with the lever pulling specialist, the larger food reward he obtains. It would be less easy to explain if animals began to treat a specialist differently in the course of trials even at times when no immediate increase of a food reward results from their action. In order to test this, the trials were carried out in two phases. In the food phase of a trial the apparatus was switched on and the specialist usually manipulated the levers. In the subsequent social phase of each trial, the apparatus was out of action and thus no immediate food reward could reinforce changes of behaviour.

The dominance status of the specialist was not affected. During the social phase, measures of social relationships were recorded, namely (i) the spatial proximity of the animals serving as a measure of association among individuals and (ii) interaction data like grooming behaviour directed towards the social partner, aggressive behaviour and forming alliances in aggressive episodes. The nearest neighbour of each animal of the subgroup was protocoled every five minutes. The exact duration of each grooming bout was recorded. For aggressive behaviour and alliances the exact frequencies are available. Since the duration of the trials and trial phases were not equal for every replicate, the scores and durations, were converted to rates and proportions per hour, respectively, for each trial.

A sufficient degree of certainty about experimentally induced increases or decreases of neighbourship scores and behaviour scores requires three conditions in a specialist-non-specialist dyad:

(i) The group member must indeed have gained a satisfactory amount of benefit from the specialist. We can expect that animals that reached the highest scores on sums of joint presence should most likely change their behaviour directed towards the specialist as a reaction to the obtained benefits.

(ii) The changes in social measures should coincide in time with the experimentally determined specialization of individuals. For this purpose, I performed a first analysis using a Wilcoxon rank sum test for each of the 55 specialist-non-specialist dyads. I compared the neighbourship scores and behaviour frequencies in the social phase of all trials during which the dyad member referred to as the specialist was indeed established as specialist (specialist trials) with the scores and frequencies of all trials when other individuals of the group were the specialists (control trials). The analysis thus considers changes that are correlated with the experimental conditions set by the experimenter, i.e. which one of the animals is allowed to perform successful lever manipulations, and does not take into account the actual activity and eventual benefits from the specialists as the next, additional analysis will do. It will locate significant influences of experimental conditions regardless of whether they are true dyadic effects among the specialist and a group member or complex triadic effects of the experimental condition. The Wilcoxon rank sum analysis thus is expected to reveal experimentally induced effects in dyads that do not correspond to our hypothesis. Therefore, we also should attempt to assess which of these significant effects can be attributed to mainly dyadic effects and try to exclude those affected by triadic processes. This will be done by the next procedure.

(iii) The changes of social measures should correlate with the amount of benefit gained per trial due to the specialist. For this second analysis, all specialist and control trials of a dyad were pooled. A Kendall τ correlation across trials per dyad between grooming and neighbourhood on one hand and joint presence on the other was calculated. Joint presence was zero by definition during the control trials, since the measure represents the amount of benefit gained from the specialist. Frequencies of sitting together at the food site without taking into account who operated the levers, however, would measure the mutual tolerance of two dyad members, strongly influenced by triadic effects. Furthermore, the analysis of displacing/chasing and of following/passing already suggested that non-specialists are aware that the specialist is associated with food production. I believe it is justified to assume that a non-specialist is aware that the lever manipulating specialist is responsible for food production and that merely sitting together at the food site is an unnecessarily crude criterion to estimate the gained benefit from the specialist. The Kendall τ measures the synchrony in the development of grooming and neighbourship and of profitable joint presence. It is not sensitive to delayed effects of profiting on the affiliation measures but in contrast to the Wilcoxon tests avoids false conclusions based on triadic effects. Thus, each statistical procedure has its weakness, which is why both are performed.

Before dealing with the results of the analyses, I would like to stress that the aim of this part of the analysis is not to detect all possible changes in social behaviour that might have been caused by the experimentally induced specialization, but to denote only the changes that are most probably due to experimental conditions. Table 6 summarizes the results for neighbourship scores and grooming frequencies. For each dyad the grooming given to the specialist as well as the grooming received from the specialist are analysed. The Wilcoxon rank sum tests reveal that, in 14 dyads, neighbourship scores were significantly higher during the specialist trials and significantly lower in 8 dyads. In 13 of the dyads even

TABLE 6. Scores of Wilcoxon rank sum tests and Kendall τ correlation coefficients measuring the relation between status of specialists and neighbourship scores and grooming rates

Data		Neighbourships		Grooming given to specialist		Grooming received from specialist	
Group member	Specialist	Wilcoxon rank test	Kendall τ coeff.	Wilcoxon rank test	Kendall τ coeff.	Wilcoxon rank test	Kendall τ coeff.
Ketut	Malen +	ns	ns	ns	ns	ns	ns
Salim	Malen +	-0.02	-0.18*	ns	ns	ns	ns
Ukui	Malen +	0.02	ns	ns	ns	ns	ns
Junus	Malen	ns	ns	ns	ns	ns	ns
Titin	Malen +	ns	ns	ns	ns	ns	ns
Subali	Malen	ns	ns	ns	ns	ns	ns
Ketut	Ukui +	ns	ns	ns	ns	ns	ns
Junus	Ukui	ns	ns	ns	ns	ns	ns
Malen	Ukui	0.02	0.17*	ns	ns	ns	ns
Salim	Ukui +	ns	ns	ns	ns	ns	ns
Titin	Ukui +	-0.02	-0.16*	ns	ns	ns	ns
Subali	Ukui	ns	ns	ns	ns	ns	ns
Ukui	Junus +	0.01	0.20**	0.02	0.23**	ns	ns
Malen	Junus +	ns	ns	ns	ns	ns	ns
Salim	Junus +	ns	ns	ns	ns	ns	ns
Ketut	Junus +	-0.02	ns	ns	ns	ns	ns
Titin	Junus +	0.02	ns	ns	ns	ns	ns
Subali	Junus	ns	ns	ns	ns	ns	ns
Saja	Sanah	ns	ns	-0.04	-0.14*	-0.02	-0.16*
Rini	Sanah +	ns	ns	ns	ns	ns	ns
Tjat	Sanah +	0.03	ns	ns	ns	ns	ns
Topi	Sanah +	0.01	0.18*	0.01	0.31**	ns	0.26**
Sapi	Sanah	-0.01	ns	-0.01	ns	ns	ns
Djambi	Sanah	-0.02	ns	ns	ns	ns	ns
Jumi	Sanah	ns	ns	0.05	ns	0.02	ns
Saja	Djambi +	0.01	0.31**	ns	ns	ns	ns
Tjat	Djambi +	0.04	ns	ns	ns	ns	ns
Sanah	Djambi +	-0.01	ns	ns	ns	ns	ns
Sapi	Djambi	ns	ns	ns	ns	ns	ns
Jumi	Djambi +	-0.01	ns	ns	ns	ns	ns
Rini	Djambi +	ns	ns	ns	ns	ns	ns
Topi	Djambi +	ns	ns	ns	ns	ns	ns
Tjat	Saja +	0.01	0.25**	0.04	0.17*	ns	ns
Rini	Saja +	0.01	0.27**	0.01	0.27**	0.01	0.19**
Topi	Saja +	0.01	0.19**	ns	0.17*	ns	ns
Sanah	Saja +	ns	ns	0.01	0.19**	ns	ns
Sapi	Saja	ns	ns	ns	0.21**	ns	ns
Jumi	Saja	ns	ns	ns	ns	-0.03	ns
Djambi	Saja	ns	ns	ns	ns	ns	ns
Djalan	Sakri +	0.01	0.20*	0.01	0.28**	ns	ns
Sapi	Sakri	ns	ns	ns	ns	ns	0.15*

Toko	Sakri +	ns	ns	ns	ns	ns	ns
Topi	Sakri +	ns	ns	0.01	ns	0.01	ns
Upit	Sakri +	ns	ns	ns	0.21*	ns	ns
Mayun	Sakri +	ns	ns	ns	ns	ns	ns
Dili	Sakri +	ns	ns	0.01	ns	0.01	ns
Titin	Sakri +	ns	ns	ns	ns	ns	ns
Djalan	Mayun +	0.01	0.34**	0.01	0.28**	ns	ns
Toko	Mayun +	0.01	0.29**	0.02	0.25**	ns	ns
Topi	Mayun +	ns	-0.15*	0.04	ns	-0.01	-0.15*
Dili	Mayun +	ns	0.19**	0.01	0.25**	-0.01	ns
Upit	Mayun	ns	ns	ns	ns	ns	ns
Sapi	Mayun	ns	ns	ns	ns	ns	ns
Sakri	Mayun	ns	ns	ns	ns	ns	ns
Titin	Mayun	-0.01	ns	ns	ns	0.01	ns

For Wilcoxon tests the significance probabilities are given. A negative probability indicates a lower neighbourship score or grooming rate during the specialist phase. Dyads are arranged according to the sum of joint presence. +: group member ranks higher than specialist, ns: not significant, *: sigificant at 5% level, **: significant at 1% level.

the amount of grooming given to the specialist by the non-specialist was higher. Grooming was lower in 2 of the dyads. Systematic changes in grooming by the specialist occurred in 9 dyads; grooming was higher in 4 but lower in 5 dyads. For threatening, chasing and providing alliances it appears that an insufficient amount of data was available. Significant positive Kendall τ correlations between joint presence and neighbourship scores were found in 11 dyads, negative ones in 3 dyads. Correlations between joint presence and grooming given to the specialist are significantly positive in 12 dyads and significantly negative in 1 dyad. Correlations between joint presence and grooming received from the specialist are significantly positive in 3 dyads and significantly negative in 2 dyads. No Kendall τ correlations were calculated for the remaining measures, since the Wilcoxon rank sum tests had already shown that data are insufficient.

Table 6 indicates that in seven dyads between a specialist and a non-specialist, namely Ukui-Junus, Topi-Sanah, Rini-Saja, Tjat-Saja, Djalan-Sakri, Djalan-Mayun and Toko-Mayun, both kinds of statistical analyses show significant increases in both affiliation measures. In the dyad Rini-Saja not only the grooming frequencies directed towards the specialist Saja increased, but her grooming of Rini as well. In six of these seven specialist-non-specialist dyads, which reacted both most strongly to the change from specialist to control phases (Wilcoxon rank sum tests) and to differences in their daily scores of joint presence (Kendall τ cor-

TABLE 7. Mean neighbourship scores per hour and mean grooming rates in minutes per hour for trials carried out with a subgroup when a specialist was established versus when he was not

Data Group member	Specialist	Neighbourship*) scores Phase		Grooming**) Phase	
		Control	Specialist	Control	Specialist
Ukui	Junus	3.04	5.12	1.12 min	3.60 min
Tjat	Saja	1.26	2.54	0.03 min	0.50 min
Rini	Saja	0.98	3.00	0.13 min	0.58 min
Djalan	Sakri	0.42	0.95	0.03 min	0.77 min
Djalan	Mayun	0.21	1.91	0.0 min	1.02 min
Toko	Mayun	0.05	1.03	0.0 min	0.44 min

*) Maximal score per hour: 13. **) Maximal rate per hour: 60 min.

relations), the non-specialists ranked among the two non-specialists who profited the most of all other subgroup members (cf. Table 3). Topi, who increased grooming and proximity to Sanah, is the only exception. Some of the non-specialists that benefitted most from specialists in the respective subgroups did not increase their affiliative behaviour towards the specialist. Possibly, this would have happened if the experiments had been carried out over a long period of time. However, the aim of this study is to reveal evidence that monkeys are able to monitor skills of others and not to show that gaining benefit from a partner results in an increase in affiliative behaviour.

Table 7 outlines the relative moderate extent of the changes of neighbourship scores and grooming. Figs 3 and 4 show the detailed course of rates and scores. For the dyad Ukui-Junus (Figs 3a and 4a) no data are available for trials 15 to 20 and 90 to 128. For statistical analyses these trials were treated as missing data points. Especially the behaviour of Djalan is most interesting. First he began to increase his friendly interactions with Sakri, the first of the specialists established in his subgroup. When Mayun became specialist, he switched and began to "flatter" Mayun. Figs 3d and e and 4e and f show how Djalan's grooming and neighbouring depended on the specialist status of both Sakri and Mayun. The Figures provide an additional insight. Djalan continued his special treatment of Sakri even after she had been dismissed as specialist. Obviously he needed several trials before he realized that the animal with the specialist's role had changed. In summary we may conclude that in

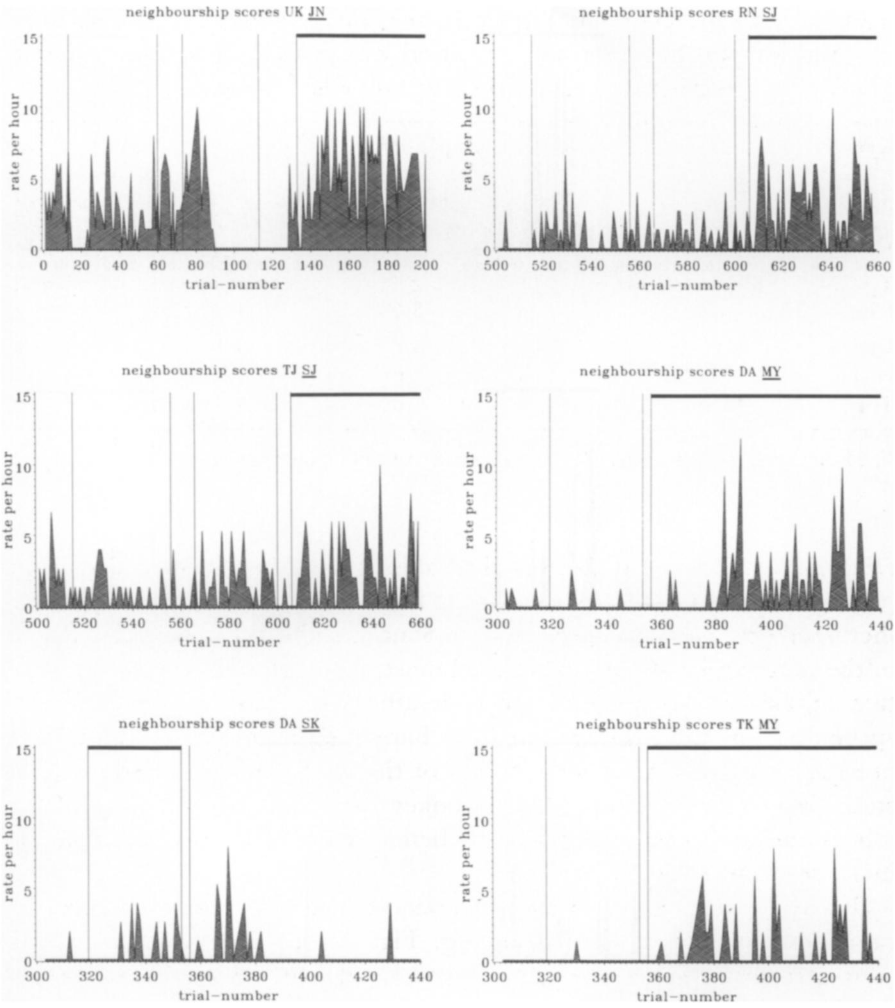
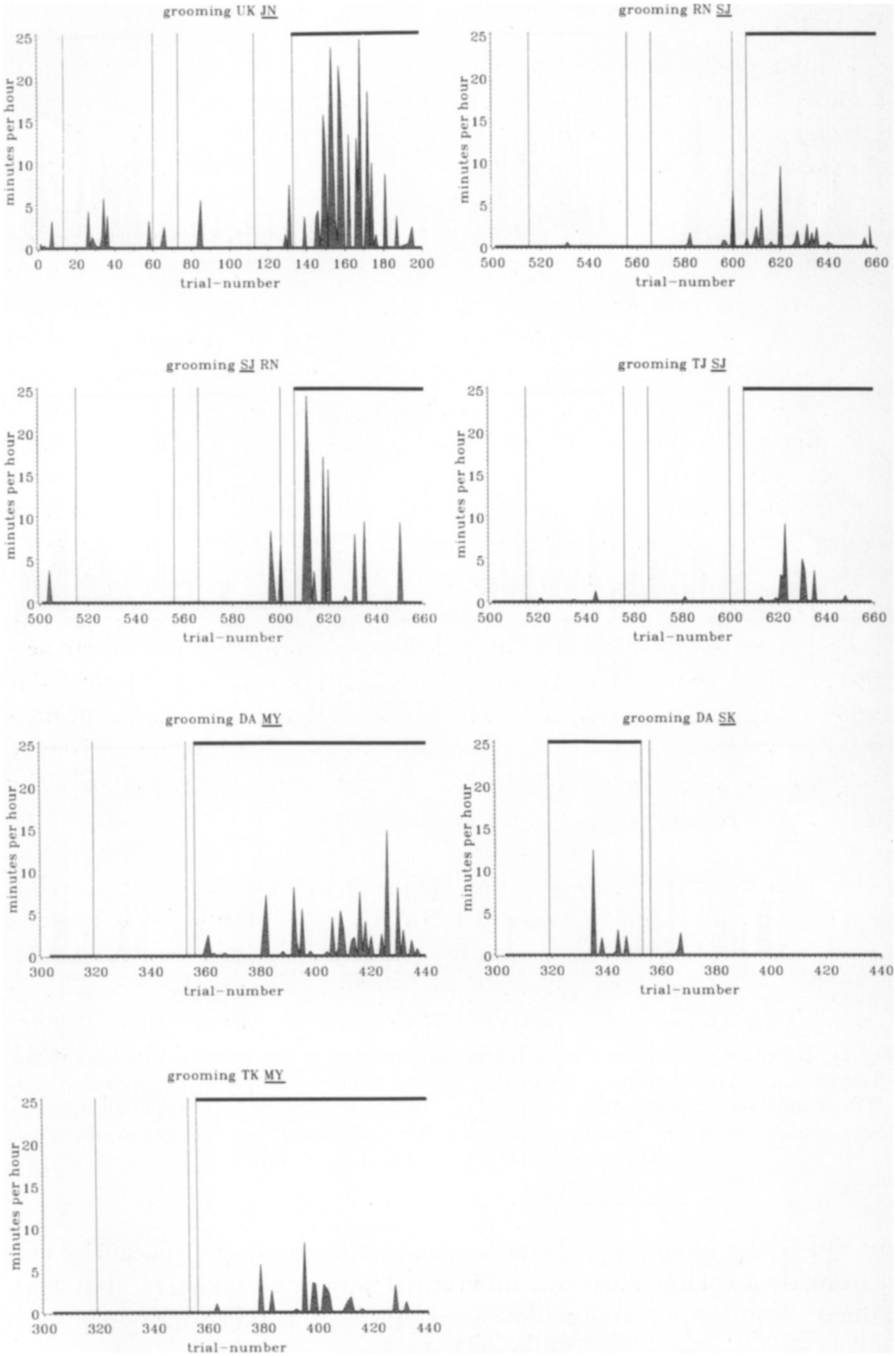


Fig. 3. Neighbourship scores in each trial as observed in the dyads where significant changes in social interactions happened in reaction to the experimental conditions. Vertical lines indicate the beginning or the end of a replicate. A black horizontal bar indicates the specialist's replicate. Names of specialists are underlined. No data are available for Uk-Jn for trials 15 to 20 and 90 to 128.

six dyads the changes in behavioural treatment of the specialists are reasonably explained by the differential amount of benefit that was gained: A macaque who profits from the feeding skills of another one indeed may increase his affiliation behaviour.


grooming UK JN
grooming RN SJ
grooming SJ RN
grooming TJ SJ
grooming DA MY
grooming DA SK
grooming TK MY
minutes per hour
trial-number

Discussion

The main questions of this study were: (i) Is it possible to establish low ranking group members as specialized food producers? (ii) Are other members able to adapt their behaviour in order to gain benefits? (iii) Do changes also occur even in social contexts outside the feeding phase of the trials?

(i) All animals trained as specialists succeeded in operating the apparatus regularly and non-specialists ceased to pull levers on their own. The latter simply might be explained by extinction: lever manipulations of non-specialists dropped because they were not rewarded for their incorrect manipulations. However, as soon as they were rewarded again at a one-lever apparatus in the preparatory trial, when the specialist of a former replicate was dismissed, they started successful manipulations almost immediately.

(ii) The next analysis showed that non-specialists that benefitted from one of the specialists could learn to refrain from displacing and chasing him during the course of a replicate. This finding suggests that non-specialists learned that the specialist's presence at the feeding site was necessary for subsequent food release. It is possible to explain their performance in terms of association learning: the monkeys' knowledge might be of the form "Apparatus plus specialist means release of popcorn". Furthermore, the study provides evidence that non-specialists are able to anticipate the specialist's later actions or effects, as suggested by the increase of following and passing that can be shown for some of the dyads.

(iii) The most interesting finding is that besides these short-term adaptations, the specialists were treated differently in purely social contexts outside the experimental situation by some of their partners, as a consequence of their activity at the apparatus. In none of the 55 specialist-non-specialist dyads were all affiliative scores reduced, but in seven of them a significant increase in both affiliative measures occurred. In six of the seven dyads the non-specialist was among the two group members who

---

Fig. 4. Grooming rates per hour given to the specialist in each trial as observed in the dyads where significant changes in social interactions happened in reaction to the experimental conditions. Vertical lines indicate the beginning or the end of a replicate. A black horizontal bar indicates the specialist's replicate. Names of specialists are underlined. No data are available for Uk-Jn for trials 15 to 20 and 90 to 128.

gained the most from the specialist. This makes it very improbable that other reasons than gaining benefit from the specialist induced the increase of sociopositive interaction. One could interpret the increase of neighbourships as an extended anticipation of the specialist's role, generalized from the feeding to the social phases of the trials, as if his partners assumed that the specialist had other skills in other contexts as well and thus maintained proximity favourable for these other benefits. Increased grooming however cannot be interpreted as simple anticipation of such benefits and suggests that non-specialists associated the positive experience of getting food rewards with the specialized individual who therefore was treated differently even outside the feeding phases. To my knowledge, this is the first study to present evidence for this. In conclusion: Monkeys are able to assess exceptional and useful capabilities of others.

KUMMER (1978) proposed that a member of a primate group should choose his partners according to their optimal qualities and skills. This study shows by experiment that monkeys are indeed able to monitor skills, or at least their effects, of other group members. In earlier studies (STAMMBACH, 1978; STAMMBACH & KUMMER, 1982) we searched for determinant factors that direct group structuring in hamadryas baboons. It appeared, first, that high ranking animals were preferred social partners, in accordance with the model of SEYFARTH (1977). Choice experiments, where the animals could approach their preferred partner without actively being influenced by them or potential competitors, revealed, however, that partners were also selected according to aqualities other than rank. The reasons for this attractiveness remained unknown. In this study foraging skill appears as one possible, dominance-independent aspect of attractiveness that changed social interactions. Models of social structure and especially of grooming (see *e.g.* SEYFARTH, 1977, 1980; SEYFARTH, CHENEY & HINDE, 1978) should therefore no longer be restricted to dominance rank and aspects of kin relationships (KURLAND, 1977; SILK *et al.*, 1981). We have to expect that monkeys choose their social partners carefully according to further characteristics.

Summary

The aim of this study was to investigate the capability of monkeys to assess special characteristics in conspecifics. In a first phase I ascertained that all members of a colony of longtailed macaques (*Macaca fascicularis*) were able to attain food by manipulating a one lever apparatus, thus introducing the "tradition" of lever pulling. Then, experiments were carried out on subgroups of the colony where only one of the lower ranking

subgroup members was trained to succeed in a more complex task where three levers had to be pulled in a correct sequence. Eight specialists were established in sequence. These specialists became food producers for themselves and for the other group members. Each trial of a specialist's series was carried out in two phases. In the first, the food phase, the food dispensing apparatus was active and responses of other subgroup members to the food producing specialist were observed. In the second, the social phase, the apparatus remained inactive and observations focused on social interactions of the subgroup. As expected, primarily high ranking subgroup members attempted to participate in the food rewards gained by the specialist. It is shown that high ranking animals began to hold back their initial chasing of the specialist from the food site in course of the trials and were soon tolerated to sit near the subordinate food producer. Furthermore, some of the non-specialists began to follow or even to pass the specialist when he was approaching the apparatus to manipulate the levers. These non-specialists thus indicated that they were able to anticipate later actions. In seven out of 55 specialist-non-specialist relationships all predicted changes in social interactions occurred. In the majority of the dyads in which a change in social affiliation was registered an increase of grooming or spatial proximity was positively correlated with the amount of benefit gained from the specialist. In the social phase of the trials the non-specialists gave more grooming to the food producers and maintained spatial proximity even in this second phase. To conclude: At least some of the group members became aware of the skills of the specialists and adapted their behaviour accordingly as if to maximize benefits from their skills.

Previous studies had already suggested that monkeys know about social position, social relationships and kinship of group members. This study adds a new aspect of knowledge, namely knowledge on capabilities and skills of others. Differential knowledge allows monkeys to select partners optimally according to their skills and social position.

References

Altmann, J. (1974). Observational study of behavior: Sampling methods. — Behaviour 49, p. 227-267.

Angst, W. (1974). Das Ausdrucksverhalten der Javaneraffen. — Adv. in Ethology Vol. 15. Paul Parey, Berlin Hamburg.

Clutton-Brock, T. H. & Harvey, T. H. (1977). Primate ecology and social organization. — J. Zool. London 183, p. 1-39.

Hinde, R. (1974). Interactions, relationships and social structure in non-human primates. — Symp. 5th Cong. Int. Primat. Soc., Nagoya Japan, p. 13-24.

Kummer, H. (1978). On the value of social relationships to nonhuman primates: A heuristic scheme. — Soc. Sc. Inf. 17, p. 687-705.

Kurland, J. A. (1977). Kin selection in the japanese monkey. — Contr. Prim. Vol. 12, Karger, Basel, p. 145.

Nagel, U. (1979). On describing primate groups as systems: the concept of ecosocial behavior. — In: Primate ecology and human origins: Ecological influences on social organization (I. S. Bernstein & E. O. Smith, eds). Garland Press, New York & London, p. 313-339.

SAS User's Guide (1982a). Basics. — SAS Institute Inc., Cary, North Carolina, p. 921.

—— (1982b). Statistics. — SAS Institute Inc., Cary, North Carolina, p. 584.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. — J. Theor. Biol. 65, p. 671-698.

—— (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. — Anim. Behav., p. 28: 798-813.

——, Cheney, D. L. & Hinde, R. (1978). Some principles relating social interactions and social structure among primates. — In: Recent advances in primatology, (D. J. Chivers & J. Herbert, eds). Academic Press, London, p. 39-51.

SILK, J. B. (1982). Altruism among female *Macaca radiata:* Explanations and analysis of patterns of grooming and coalition formation. — Behaviour 79, p. 162-188.
STAMMBACH, E. (1978). On social differentiation in groups of captive female hamadryas baboons. — Behaviour 67, p. 322-338.
——— & KUMMER, H. (1982). Individual contributions to a dyadic interaction: an analysis of baboon grooming. — Anim. Behav. 30, p. 964-971.

Zusammenfassung

Diese Studie über kognitive Fähigkeiten von Primaten untersucht, ob Javaneraffen (*Macaca fascicularis*) Eigenschaften und insbesondere spezielle Fähigkeiten von anderen Artgenossen einschätzen können und ihr Verhalten so anzupassen wissen, dass sie von deren Fähigkeiten profitieren. Bevor die eigentlichen Experimente durchgeführt wurden, trainierte ich alle Tiere einer Javaneraffen-Kolonie darauf hin, sich an einer einfachen Apparatur durch Bedienung eines Hebels Futter zu beschaffen. Damit war allen Koloniemitgliedern das Prinzip "Hebelziehen" bekannt. Die Experimente wurden daraufhin an Untergruppen der Kolonie durchgeführt. In acht Versuchsserien wurde jeweils ein tiefrangiges Untergruppenmitglied an einer komplexeren Apparatur trainiert, drei Hebel in einer korrekten Sequenz zu ziehen, worauf die Apparatur eine grössere Futterbelohnung ausschüttete, von der nicht nur diese Individuum, sondern auch andere Gruppenmitglieder fressen konnten. Das speziell trainierte Individuum wurde damit zum Futterlieferanten für sich und seine Gruppenmitglieder. Jeder Einzelversuch wurde in zwei Phasen durchgeführt. In einer ersten, der Futterphase, war der Futter liefernde Apparat eingeschaltet und die Reaktionen der anderen Gruppenmitglieder auf den Futter produzierenden Spezialisten wurden beobachtet. In der zweiten, der Sozialphase, war der Apparat ausgeschaltet und die Beobachtungen richteten sich auf das soziale Verhalten der anderen Gruppenmitglieder gegenüber dem Spezialisten.

Wie zu erwarten war, versuchten vor allem hochrangige Untergruppenmitglieder an dem vom Spezialisten produzierten Futter teilzuhaben. Diese hochrangigen Tiere jagten vorerst den Spezialisten von der Apparatur weg, um zum Futter zu kommen, lernten aber im Verlauf der Versuche ihr Jagen zu reduzieren und gar ganz aufzuhören. Einige der Nichtspezialisten begannen überdies, dem Spezialisten zu folgen oder ihn gar zu überholen, sobald dieser sich der Apparatur näherte. Dies ist ein Hinweis, dass diese Nichtspezialisten künftige Handlungen des Spezialisten voraussehen können.

In sieben von 55 Spezialist-Nichtspezialist-Dyaden konnten zudem in der Sozialphase der Versuche Aenderungen in den sozialen Interaktionen festgestellt werden, von denen sechs mit grosser Sicherheit auf die spezielle Position des Futterproduzenten zurückzuführen sind. Sechs Nichtspezialisten, die in ihrer jeweiligen Untergruppe am meisten vom Spezialisten profitierten, liessen diesem vermehrt soziale Hautpflege zukommen und hielten sich zudem auch während der Sozialphase häufiger in seiner Nähe auf, wie mit der Methode der nächsten Nachbarschaften gezeigt werden konnte. Daraus ist zu schliessen, dass mindestens ein Teil der Untergruppenmitglieder das Können des Spezialisten erkannte, passten sie doch ihr Verhalten in einer Art und Weise an, dass sie ihren Nutzen maximieren konnten.

Andere Studien hatten bereits darauf hingewiesen, dass Affen über Wissen über soziale Position, soziale Beziehungen und Verwandtschaftsverhältnisse verfügen. Die vorliegende Studie fügt einen neuen Aspekt des Wissens hinzu, nämlich das Wissen über Fähigkeiten und Können anderer. Das differenzierte Wissen über potentielle Partner erlaubt es einem Affen, seine Partner bezüglich Fähigkeiten und sozialer Position optimal auszuwählen.