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# MUTUAL BEHAVIORAL ADAPTATION OF PARTNERS IN DYADS IN TWO SPECIES OF PROSIMIANS

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*ABSTRACT:* The dynamics of mutual behavioural adaptation in the process of establishing social relationships in mouse lemurs (*Microcebs murinus*) and pygmy slow lorises (*Nycticebus pygmaeus*) was studied. Observations were made over a 3-hour period beginning when a male and a female were first placed together during the non breeding season. As well, the behaviour of stable pairs that had been together for more than one year was observed. Behaviour was recorded using the one/zero method with 5-sec intervals. Two stages of the development of social relationships, each with different functional values, were identified. The first stage involved mutual social investigation, the second the stabilization of the social relationship. Differences in the dynamics of social contacts between species members were due to their different social structures. The process of social adaptation of behaviour in dyads is discussed and quantitative and qualitative characteristics of breeding pairs and non breeding pairs are compared. It is suggested that a convenient strategy for improving breeding is to replace one of the partners with an experienced animal.

## INTRODUCTION

Zoos often face the problem of regulating the social behaviour of animals, especially in cases of a) pair formation for breeding, b) group formation, and c) the introduction of a new individual into a group. Attempts to pair monkeys are often problematic because the incompatibility of the prospective partners may result in a high level of aggression (Bernstein, 1969). The risk of trauma during pairing is considered to be lower in young animals than in adults (Bernstein & Draper 1964; Valery & Symms, 1966), so acquainting animals with each other at an early age is recommended (Bernstein 1969; Bernstein

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& Gordon, 1980; Erwin 1979).

The main difficulty in breeding primates in captivity is to find compatible mating partners. Because the social and sexual behaviour of primates is complicated, normal breeding often is possible only after establishing a harmonious relationship between the prospective partners. Pair formation can be further complicated by the idiosyncratic behaviour of individual animals and by pathological social and reproductive behaviour resulting from captivity. In these cases, changing partners is the main alterative. However, when maintaining genetic diversity is of primary concern, as in breeding threatened or endangered species, this is not always possible. The investigation of the pair formation process must be based on the idea of mutual behavioural adjustment of two individuals. Generally speaking we are interested in getting at the behavioural mechanisms of this process; the work reported here is our preliminary investigation of this problem.

When speaking about the social adjustment of the behaviour of two individuals, we mean that their coexistence is the result of changes in the social reactions of each individual. One may say that two individuals put in one area try to attain some sort of behavioural complementation in order to minimize their social discomfort. The physiological and psychological characteristics of this social discomfort depend on the characteristics of the social behaviour of the species, and may be illustrated by the social structure of the species in nature. During the process of mutual social behavioural adjustment every individual tries to control its partner's social behaviour by some changes in its own behaviour. The aim is to neutralize the partner's undesirable acts and to obtain more desirable ones. In this process an individual uses a behavioural strategy appropriate to its age, sex and the behavioural repertoire of its species.

In this study, behavioural adaptation during the development of social relationships was examined in the mouse lemur (*Microcebus murinus*) and the pygmy slow loris (*Nycticebus pygmaeus*). These species were selected because they display very different social structures in a natural environment (Petter,1962; Martin, 1972). Female mouse lemurs form a central population and the males, who remain at the periphery, come to the center only during the breeding season. Pygmy slow lorises presumably have individual territories and males enter the females' territories during breeding season; however, the pair may stay together for several weeks, or even months. Thus, one may assume that pygmy slow lorises are able to form more prolonged social relationships than mouse lemurs. It is likely that mutual behavioural

interactions are taking place resulting in the partners adapting to one another.

The present investigation was designed to: (1) compare the processes of behavioural adaptation in these two species with different social structures; (2) determine the behavioural strategies of males and females during the social interaction; and (3) discover which behavioural deviations might prevent animals from forming a breeding pair.

## METHOD

### *Subjects*

A total of 24 mouse lemurs (*Microcebus murinus*) and 14 lesser slow lorises (*Nycticebus pygmaeus*) from the Moscow Zoo were studied. In the Moscow Zoo, these two species have been maintained in various types of social relationships: (1) a male and female together over several years; (2) a male and female together during 2-3 breeding seasons; and (3) a male and female pairing for one breeding season only. The best breeding routine for mouse lemurs is the last, while the most successful routine for pygmy slow lorises is the second one.

Pairs in the present study were housed in cages (1.5 x 1.5 x 2.0 m) equipped with two or three wooden nest-boxes and the necessary amount of branches and tree roots. The light/dark cycle was that of the Moscow latitude. In this facility, mouse lemurs fall into torpor in November and arouse in February. A similar cycle has been observed in other facilities in Europe ( Martin, 1972).

### *Procedure*

We observed pairs of animals on their very first encounters, new partners that had never seen each other before being placed together. We observed new pairings involving 12 male and 12 female mouse lemurs and 7 male and 7 female lesser slow lorises. Initial observations of new pairs lasted for 3 hours. After a year, during which there had been a breeding season, the formed pairs were observed again when we knew about the breeding success of each pair. These observations lasted for 1 hour. Following these observations we reformed pairs in such a way that non breeding partners were paired with breeding partners. The initial interaction of these new pairs was then observed, and in a year

we were able to determine their breeding success. The entire procedure for each species was as follows:

*Mouse lemurs*: 1988 - 12 pairs were formed and observed for 3 hours during their initial encounter. 1989 - The breeding success of all pairs formed the previous year was determined and the pairs were observed for one hour. Eight pairs had bred, four had not. We reformed the non breeding pairs with four of the breeding pairs, forming eight new pairs, with one member of each having previously bred. The initial encounters of the animals in these groups were then observed for 3 hours. 1990 year - We observed the eight pairs formed the previous year and determined their breeding success -- all pairs had offspring.

*Lesser slow lorises*: 1988 - Seven pairs were formed and observed for 3 hours during their initial encounter. 1989 - All pairs formed the previous year were observed for one hour and their breeding success determined; three pairs had not bred. Non breeding pairs were reformed with three breeding pairs, forming six new pairs that were observed on their initial encounters. 1990 - We observed the six pairs formed the previous year and determined their breeding success - only one pair did not breed.

Behaviour was recorded using the one/zero method with 5-sec intervals. All observations were carried out at night under red or green light. Experimental pairings occurred in cages similar to the home cages. To do this, during the day the wooden nest-boxes in which the animals were sleeping were moved from the home to the experimental cage. These wooden boxes (one with a male, the other with a female) were opened simultaneously in the evening, when the animals began to be active. All observations were made during the non breeding season.

Three categories of social behaviour were recorded: 1) social investigation - approaching the partner, sniffing and watching; 2) affiliative behaviour - grooming, long tactile contact, playing, etc.;and 3) aggressive behaviour - from ritualized aggressive displays to direct aggressive acts. Stages of pair formation were determined separately for each pair formed during 1988 and 1989 on the basis of analyses of curves of the dynamics of the partners' social activity. First, differences in reliability were determined for every pair and every form of activity, and then for the average data for breeding and non breeding pairs of both species, using a $\chi^2$ test.

## RESULTS

### *Mouse lemur data*

On the basis of qualitative and quantitative ($\chi^2$) analysis of the behaviour of the animals on their initial encounters, we divided the three-hour observation period into three stages. The average duration of each stage was as follows: stage 1 - 15 min; stage 2 - 35 min; stage 3 - 130 min.

The percentage of time spent in different behaviours during each stage of the 3-hour observation period for initial encounters in pairs of mouse lemurs is shown in Table 1. Several differences between animals in pairs that went on to breed and those that did not were observed. The data for males that went on to breed are shown in the top panel of the table. There was no aggressive behaviour at all, and

**Table 1. Percentage distribution of different types of behaviour during stages of the 3 hour observation period of initial encounters between members of pairs of mouse lemurs.**

| | Affiliative | Aggressive | Soc. Invest | Marking | Activity | Inactivity |
|---|---|---|---|---|---|---|
| *Pairs that became Successful Breeders* | | | | | | |
| Males | | | | | | |
| Stage 1 | 0.97 | 0 | 6.25 | 0 | 75.56 | 17.22 |
| Stage 2 | 1.48 | 0 | 1.94 | 0 | 47.22 | 49.35 |
| Stage 3 | 0.17 | 0 | 1.39 | 0.61 | 39.17 | 58.67 |
| Females | | | | | | |
| Stage 1 | 0.28 | 3.33 | 2.64 | 0 | 5.97 | 87.78 |
| Stage 2 | 0 | 4.85 | 0 | 0 | 3.89 | 90.26 |
| Stage 3 | 0 | 4.44 | 0.22 | 0 | 2.72 | 92.81 |
| *Pairs that did not Breed* | | | | | | |
| Males | | | | | | |
| Stage 1 | 0 | 0.14 | 5.56 | 0 | 56.25 | 38.05 |
| Stage 2 | 5.74 | 0 | 1.76 | 0 | 57.04 | 35.46 |
| Stage 3 | 0.61 | 0.17 | 0.33 | 0 | 34.72 | 64.17 |
| Females | | | | | | |
| Stage 1 | 3.06 | 1.11 | 3.19 | 0 | 20.42 | 72.22 |
| Stage 2 | 9.07 | 11.11 | 1.02 | 0 | 4.63 | 74.17 |
| Stage 3 | 0.50 | 1.22 | 0.11 | 0 | 4.72 | 93.44 |

affiliative behaviour increased to its highest level at stage 2, before it declined again. The level of social investigative activity was high at stage 1 and declined thereafter. Marking behaviour was observed only by breeding males, and it occurred only at stage 3. The data for the males that did not breed are shown in the lower part of Table 1. Some aggressive behaviour was observed at stage 1, and after declining to zero in stage 2, it increased to its highest level at stage 3. Affiliative behaviour was at its highest in stage 2, after which it declined. The level of social investigative activity decreased systematically from stage 1 to stage 3. The data for activity (walking and jumping) and inactivity (remaining stationary) were similar in breeding and non breeding males.

For the females that went on to breed (top of Table 1), affiliative behaviour occurred only during stage 1, while aggressive behaviour was present at all stages, being highest at stage 3. The level of social investigative activity was highest at stage 1, absent at stage 2, and observed once more at stage 3. The females that did not breed (bottom Table 1) showed affiliative behaviour at all stages, but the level was highest at stage 2. These females demonstrated aggressive behaviour which was also at its highest level at stage 2. The level of social investigative activity of these females decreased substantially from stage 1 to stage 3.

**Table 2. Percentage distribution of the kinds of behaviour that occur in response to the social investigative behaviour of the partner in mouse lemurs.**

| | Quiet | Soc. Invest. | Affiliative | Aggressive | Move Away |
|---|---|---|---|---|---|
| *Pairs that became Successful Breeders* | | | | | |
| Males | 0 | 12.50 | 12.50 | 12.50 | 62.50 |
| Females | 4.17 | 7.29 | 5.21 | 80.21 | 5.21 |
| *Pairs that did not Breed* | | | | | |
| Males | 9.09 | 18.18 | 54.54 | 0 | 18.18 |
| Females | 27.03 | 5.41 | 2.70 | 62.16 | 0 |

Table 2 shows the types of reactions that occurred in response to the social investigative activity of the partner. We see that in the pairs that later became successful breeders, the females responded more aggressively than those in non breeding pairs. In the breeding pairs the level of quiet reactions by the females was lower than in non breeding pairs; non breeding females never moved away from the males. Males

reacted aggressively to females only in pairs that later bred, and the level of affiliative behaviour was lower in breeding than in non breeding males. Males reacted quietly to the social activity of females only in non breeding pairs, while the males that later bred usually moved away from the females.

Data from stable partners, the pairs of mouse lemurs that had been kept together for over a year, are shown in Table 3. In the males, affiliative behaviour was present only in pairs that did not breed; aggressive behaviour and marking behaviour only in the breeding pairs. The only social behaviour displayed by the breeding females was marking, while the females in non breeding pairs showed a high level of affiliative behaviour. Females did not show any aggressive behaviour out of breeding season.

**Table 3. Percentage distribution of different forms of activity during the 1-hour observations of stable pairs of mouse lemurs.**

| | Affiliative | Aggressive | Soc. Invest | Marking | Activity | Inactivity |
|---|---|---|---|---|---|---|
| *Pairs that became Successful Breeders* | | | | | | |
| Males | 0 | 0 | 1.39 | 21.11 | 21.94 | 55.56 |
| Females | 0 | 2.22 | 0 | 16.39 | 4.4 | 76.94 |
| *Pairs that did not Breed* | | | | | | |
| Males | 33.89 | 0 | 1.67 | 0 | 37.56 | 26.94 |
| Females | 34.17 | 0 | 0.28 | 0 | 5.55 | 60 |

*Pygmy slow loris data*

On the basis of qualitative and quantitative analysis of partners' behaviour for the pygmy slow lorises, the three-hour observation period was divided into two stages. The average duration of each stage was: stage1 - 45 min, stage 2 - 135 min. The percentage of time spent in different behaviours during each stage of the 3-hour observation period for initial encounters in pairs of slow lorises is shown in Table 4. For the animals that would later breed ( top panels of figure), the affiliative behaviour of both males and females increased from stage 1 to stage 2. Males were aggressive only at stage 1, while aggression in females increased from stage 1 to stage 2. Social investigative activity decreased in both males and females from stage 1 to stage 2. The females showed marking behaviour only at stage 2, but the males' marking behaviour was highest at stage 1 and decreased during stage 2.

**Table 4. Percentage distribution of different types of behaviour during stages of the 3-hour observation period of initial encounters between members of pairs of pygmy slow lorises.**

| | Affiliative | Aggressive | Soc. Invest | Marking | Activity | Inactivity |
|---|---|---|---|---|---|---|
| *Pairs that became Successful Breeders* | | | | | | |
| Males | | | | | | |
| Stage 1 | 2.87 | 0.69 | 3.94 | 1.34 | 41.39 | 49.77 |
| Stage 2 | 23.1 | 0 | 1.85 | 0.69 | 48.47 | 25.88 |
| Females | | | | | | |
| Stage 1 | 6.25 | 0.23 | 3.29 | 0 | 36.44 | 53.8 |
| Stage 2 | 20.42 | 0.56 | 1.34 | 0.23 | 20.83 | 56.62 |
| *Pairs that did not Breed* | | | | | | |
| Males | | | | | | |
| Stage 1 | 0 | 2.62 | 5.77 | 0.99 | 48.21 | 42.41 |
| Stage 2 | 0.06 | 1.08 | 3.15 | 0.7 | 34.04 | 60.96 |
| Females | | | | | | |
| Stage 1 | 0 | 2.9 | 0.09 | 0 | 10.86 | 86.14 |
| Stage 2 | 0 | 2.93 | 0.62 | 0 | 6.08 | 90.37 |

Males were equally active throughout the observation period, while the activity of females decreased during stage 2. Inactivity in females remained stable over time, while in males it decreased during stage 2.

For the partners of pairs that later did not breed (lower panels of table 4), we see that females in such pairs did not show any affiliative behaviour, and males showed affiliative behaviour only at stage 2. In general, the level of aggressive behaviour in the males was initially high and then declined, while for females it did not change greatly across stages. Females did not show marking behaviour, whereas males marked during both stages. Social investigative activity declined across stages, in males but increased for the females.

Table 5 compares the reaction to social investigative activity of partners in pair that would later breed with those that did not. Overall these responses did not differ for males, although only breeding males showed reciprocal social investigative and affiliative reactions. The behaviour of breeding and non breeding females differed to a greater extent. For pairs that did not breed, the females never moved away from the male, but in breeding pairs this reaction occurred frequently.

**Table 5. Percentage distribution of the kinds of behavior that occur in response to the social investigative behavior of the partner in pygmy slow lorises.**

| | Quiet | Soc. Invest. | Affiliative | Aggressive | Move Away |
|---|---|---|---|---|---|
| *Pairs that Bred Successfully* | | | | | |
| Males | 20.0 | 12.22 | 1.11 | 6.66 | 60.0 |
| Females | 27.82 | 2.60 | 15.65 | 13.04 | 40.86 |
| *Pairs that did not Breed* | | | | | |
| Males | 26.08 | 0 | 0 | 8.69 | 65.21 |
| Females | 34.37 | 2.43 | 0.69 | 62.50 | 0 |

**Table 6. Percentage distribution of different forms of activity during the 1-hour observations of stable pairs of pygmy slow lorises.**

| | Affiliative | Aggressive | Soc. Invest | Marking | Activity | Inactivity |
|---|---|---|---|---|---|---|
| *Pairs that Bred Successfully* | | | | | | |
| Males | 40.95 | 0 | 1.24 | 0.19 | 47.40 | 10.22 |
| Females | 39.71 | 0.59 | 0.19 | 0 | 4.75 | 54.75 |
| *Pairs that did not Breed* | | | | | | |
| Males | 16.00 | 0 | 1.69 | 0 | 5.86 | 75.65 |
| Females | 16.34 | 0 | 0.98 | 0 | 9.64 | 73.05 |

The level of affiliation was higher in breeding than in non breeding pairs, and aggression was more frequent in the females of non breeding pairs.

Table 6 presents the data from the one-hour observation periods of pairs of slow lorises that had been together for more than a year. Males of both breeding and non breeding pairs did not demonstrate aggressive or marking behaviour. Affiliative behaviour was more frequent in breeding than in non breeding males. In females, aggressive behaviour was observed only in breeding pairs and then very infrequently. Affiliative behaviour was higher in breeding than in non breeding females. Activity levels were similar in both groups, but levels of inactivity were higher in the non breeding than in breeding females.

## DISCUSSION

### *Adaptation of social behaviour in species with different social structures*

The way in which behaviour changed during the initial 3-hour observation period was divided into three stages for mouse lemurs (Table 1) and two stages for pygmy slow lorises (Table 4). This division was reliable according to a $\chi^2$ criterion. The functional meaning of the first two stages is similar for both species. At stage 1 there is a high level of social investigative activity. Stage 2 can be considered the stage of mutual behavioural adaptation. During this stage the level of aggression in pairs of mouse lemurs and the level of affiliative behaviour in pairs of pygmy slow lorises increases. In the slow lorises the social behaviour of partners does not change much once stage 2 has begun and the pair can be considered to be formed. However, for the mouse lemur, stage 3 is the most important for eventual breeding success. Here the activity of the males and females is separated spatially in the cage and also according to the time of day. There are very few social contacts (except the high level of female aggression) and usually one can see only one animal active in the cage (male or female) while the other one is either in the nest-box or sitting motionless in a corner. The main differences in the behaviour of mouse lemur partners that eventually form breeding and non breeding pairs are: a) affiliative behaviour is seen at all stages for females that do not go on to breed, but is observed only at stage 1 for breeding females; and b) males that later breed do not display any aggressive behaviour at all during the first three hours with their female partners.

From analysis of the reaction to social investigative activity by the partner in these two species, the mouse lemurs appear to have lower thresholds for reacting to the social influence of their partners; they react immediately to social investigative activity. For the pygmy slow lorises, responses to the partner's investigative activity are calmer (less intense). With respect to the behaviour of pairs that would later go on to successfully breed, a high level of affiliative behaviour was observed in the slow lorises, while for the mouse lemurs social interactions were almost nonexistent, consisting only of single instances of interactions between the males in females.

The data from the 10 one-hour observations of the stable pairs (animals that had remained together for one year) of both non breeding and breeding mouse lemurs (Table 3) indicate: a) both males and females of the breeding pairs showed marking behaviour, while non

breeding animals did not; and b) non breeding males and females engaged in affiliative behaviour, whereas members of breeding pairs did not. For the pygmy slow lorises (Table 6), partners in both groups showed affiliative behaviour, although it was higher in the breeding pairs. We suggest that male and female mouse lemurs act independently of one another, with the female taking the main role in this process. We think that there are two social subsystems in this species - one for the male and one for the female, and if they do not combine the animals breed successfully (Vakhrusheva & Meshik, 1989). This assumption agrees with data from field investigations of mouse lemurs ( Martin, 1972; Petter, 1962). On the contrary, for breeding success in pygmy slow lorises prolonged affiliative interactions are necessary, as confirmed by others (e.g. Zimmerman, 1989). However, in some cases, keeping a pair of pygmy slow lorises together for a long time may prevent them from breeding because their social interactions become stereotyped, showing a high level of affiliative behaviour (Welker & Welker, 1989).

We suggest that the mutual behavioural adaptation of two individuals is reached by maintaining behavioural asymmetry between partners, with each individual playing its social role. The social role depends on the sex, age, and social status of the individual. The process of social adjustment differs in pairs of prosimians with different social structures. So in slow lorises, the males and females form pairs by engaging in high levels of affiliative behaviour in order to establish their social relationship. There is no such affiliation in mouse lemurs for whom the process of mutual social adaptation involves the partners remaining separated in space and time of day.

When comparing marking behaviour in breeding and non breeding pairs of lorises and mouse lemurs, we suggest that marking for both species involves an androgenic marking mechanism. In mouse lemurs, where the females are normally aggressive toward the males, marking was high in both partners of stable breeding pairs (Table 3), while in pairs of slow lorises only breeding males engaged in marking (Table 6). For non breeding stable pairs of both species marking was never observed. Although the the probability of an androgenic mechanism being involved is consistent with the data from the initial encounters (pair formation) in slow lorises, marking was not observed in either male or female mouse lemurs at that time. It is unclear why the males did not mark at this time, perhaps being placed with another animal was too stressful, or perhaps the females' activity inhibits the male.

*Behavioural strategies of males and females*

*Males.* The main difference between the social investigatory behaviour of males and females in mouse lemurs and lorises was the high level of the males' social activity. The social behaviour of males of both species was very similar during stage 1. Later, the level of affiliative behaviour of the lorises became higher.

*Females.* The level of social activity in females was lower than that of males, and it was the females that determined the process of pair formation in both mouse lemurs and pygmy slow lorises. Mouse lemur females were aggressive toward the males, and breeding was successful when the male was tolerant. In the lorises, the affiliative reactions of the female stimulated further affiliative interactions with the partner.

*Deviations in social behaviour which prevent a pair from breeding*

We suggest the following causes of initial behavioural incompatibility in pairs of pygmy slow lorises resulting in their inability to breed: (a) the social passivity of the females that did not breed compared with those that did, and (b) a somewhat higher level of aggression by the males that did not breed toward their partners. Both of these were evident at stage 1, soon after the animals were first put together. At stage 2 the non breeding pairs showed a very low level of social investigatory behaviour. Perhaps if the female is socially passive, she does not stimulate the male's social activity. In mouse lemurs, on the other hand, it seems that the high level of aggressive behaviour in females and the high level of social activity in males at stage 1, stimulated the partners to become breeding pairs. At stage 2, females in these pairs were socially active and aggressive, but at stage 3 they became as passive as the males.

The social behaviour of partners of both species that were kept together for more than a year and did not breed was similar. Loris pairs showed low levels of affiliative behaviour, relatively high levels of aggression, and low levels of social investigative activity. Mouse lemurs pairs showed high levels of affiliative behaviour and general social activity. Strictly speaking mouse lemurs do not form pairs because the partner's activity is differentiated in space and time, and it is this behavioural "incompatibility" that guarantees their breeding success.

*Methods of social behavioural correction*

The main cause of incompatibility between males and females is the inadequate social behaviour of one or both partners during the process of pair formation. The methods for correcting this must be worked out on the basis of the following causes: (1) social passiveness of lesser slow loris females; (2) low levels of aggressiveness of mouse lemur females; (3) low levels of general social activity and relatively high level of aggression in slow loris males; and (4) low levels of general social activity and relatively high level of affiliative behaviour in mouse lemurs males. In general, the main cause of behavioural incompatibility of partners is the absence of appropriate species-specific social behaviour by one partner. As a method of behavioural correction, we replaced the partners of non breeding animals with ones that were well-experienced in social and sexual behaviour. This method is based on the idea that partners mutually control each other's social behaviour. The presence of an experienced partner "refreshes"correct reactions with the help of affiliative and equivalent acts and it acts negatively on "incorrect" behaviour displayed by the non breeding animal.

From the results described above, the following four conclusions merge.

1. Pair formation is based on the mutual social adaptation of partners. The main purpose of social adaptation is to mould complementary, co-adaptive behaviour.

2. The process of social adaptation during pair formation can be divided into two stages, each one with its own functional significance: stage 1 - social investigation, stage 2 - behavioural adaptation.

3. In pygmy slow lorises and mouse lemurs the first stage is less important than the second, when differences based on the social structure of the species appear.

4. In mouse lemurs the probability of reproductive success is based on the low level of social activity of partners and on the absence of a social structure that we typically think of as a pair. In pygmy slow lorises reproductive success is based on a high level of affiliative behaviour between the partners which provides a real pair formation.

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