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DYNAMICS OF GROOMING AND GROOMING RECIPROCATION IN A GROUP OF CAPTIVE CHIMPANZEES (PAN TROGLODYTES)

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ABSTRACT

Grooming relationships between adult male chimpanzees are often reciprocal, i.e. individuals receive grooming from those they groom. Grooming may be reciprocated at the same time it is received (mutual grooming), or later within the same grooming session. Alternatively, it can be reciprocated at a much later stage, in another session. An analysis of individual grooming sessions at the dyadic level was used to investigate how chimpanzees reciprocate grooming within these sessions.

This study describes the grooming and reciprocation of grooming by male chimpanzees, living in a multi-male, multi-female group at the Edinburgh Zoo, Scotland. A method for the analysis of dyadic grooming relationships was based on the presence or absence of mutual and unilateral grooming in a session, which allows seven types of grooming session to be distinguished. Grooming session was defined empirically, and the duration of the bout criterion interval (BCI) depended on the presence or absence of oestrous females. For comparison, however, the same BCI was used throughout.

Without oestrous females, grooming was primarily reciprocated in sessions with mutual grooming and unilateral grooming by both participants. This kind of session proved highly cooperative and each male adjusted the duration of his unilateral grooming to that of mutual grooming, rather than to the duration of unilateral grooming by the other male. Mutual grooming was less important to dyads which had a strong grooming relationship. It is suggested that mutual grooming serves as an indication of the motivation to groom unilaterally. There was no indication that males reciprocated on the basis of TIT-FOR-TAT within these sessions, or between sessions in general.

Alternative hypotheses of mutual grooming were only partly confirmed in that some dyads used mutual grooming to reduce the (already very short) time they spent in grooming. However, mutual grooming did not arise from the accidental overlap in the grooming of two partners.

In the presence of oestrous females, grooming cooperation between the males broke down, and this was the result of heightened aggression as well as the presence of oestrous females itself. The balance in grooming given and received shifted in the direction of dominants

(i.e. dominants received more) under the influence of oestrous females, but in the opposite direction under the influence of aggression. Feeding had no effect on the reciprocity of grooming.

There was considerable dyadic variation. Some dyads groomed more when there were oestrous females, others groomed less. Some dyads had proportionally less mutual grooming with increasing numbers of oestrous females, others had more. There were generally no clear patterns of grooming reciprocation over longer time-spans than the session, but the overall degree of reciprocity of a dyad was frequently reached at the end of each day. Tracing the degree of reciprocation over a few weeks indicated that some dyads' grooming was governed by dominance, whereas that of others by cooperation.

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INTRODUCTION

THE RECIPROCATION OF GROOMING BY CHIMPANZEES

Ethologists are primarily interested in two kinds of question: 'How?' questions and 'Why?' questions (Orians, 1962, in Alcock, 1984). 'How?' questions require an explanation of the internal causes of behaviour, that is what, within the animal, causes the behaviour. For example, how do male birds sing? A possible answer would be that birds sing by forcing air from their lungs through a complex organ, the syrinx (proximate). 'Why?' questions, on the other hand, require an evolutionary explanation of the behaviour. For example, why do male birds sing? They sing to attract possible mates (ultimate). Thus, these two kinds of question complement, rather than contradict each other, and both add to an understanding of the behaviour under observation (Alcock, 1984).

The aim of studying the social behaviour of primates is to get an insight into its proximate and ultimate causes and, if appropriate, make comparisons with the behaviour of humans. Most primates live in groups and thus spend part of their time interacting with conspecifics. The size and composition of these groups are thought to have evolved in response to environmental factors, such as defensibility of resources, spatial and temporal distribution of food patches, and predation pressure (van Schaik & van Hooff, 1983; Wrangham, 1987).

For example, the distribution of food determines to a large extent the distribution of females, and the distribution of females determines the distribution of males (Wrangham, 1979). Furthermore, although an advantage of living in a large group is the increase in the likelihood a predator is detected, large groups result in more intra-group competition so that there will be an optimum group-size, in which predator detection and competition are weighed against each other (all other factors being equal). At the same time, living in a group means that each individual interacts with several other individuals, and will likewise be influenced by them.

The social behaviour of chimpanzees, Pan troglodytes, is interesting because of its complexity and fluidity: they live in multi-male, multi-female communities of around 50 individuals, and they are promiscuous. The males are philopatric: they stay within their area of birth. Females often migrate from one community to another, usually before they have reproduced. Males have a fluid dominance hierarchy and compete for females, whereas females have a more permanent dominance hierarchy and spend a lot of time feeding on their own or with their offspring (e.g. Nishida, 1979; Goodall, 1986a).

Social interactions in a chimpanzee community can be very complex indeed, and can take place at the dyadic, triadic, or polyadic level (i.e. involving two, three, or more individuals). Thus, while a chimpanzee may behave very differently towards different individuals, she can also behave differently to the same individual, depending on who else is present. For example, A may act subordinate to B when C is nearby, but dominant to B when D is nearby (see for example de Waal's (1989a) description of the relationships between the adult males in the captive Arnhem colony).

Reciprocal altruism, a form of cooperation where (unrelated) individuals take turns in being 'altruistic' toward each other, is also a kind of complex social interaction (Trivers, 1971). The evolution of altruistic behaviour can be understood if it is assumed that altruism is reciprocal. Thus, one individual may help another if he knows he will be helped in return. In fact, most patterns of 'altruistic' behaviour can, after detailed analysis, be shown to be essentially self-serving (Axelrod & Hamilton, 1981; Rothstein & Pierotti, 1988; Seyfarth & Cheney, 1988).

Since Trivers' (1971) article on the evolution of cooperation, there has been a growing interest in the dynamics of such cooperative relationships, leading to a formulation of the necessary conditions for cooperation in humans and other animals (Axelrod & Hamilton, 1981), based on the Prisoner's Dilemma Game (PDG), where two players can earn a reward depending on whether or not they cooperate. Possible outcomes of this game are mutual cooperation, mutual defection or unilateral defection, with their rewards as shown in Fig. i.1. The game is played several times in a row, thereby simulating a long-term relationship in which each player bases her future moves on the experience of previous moves (i.e. the Iterated Prisoner's Dilemma Game).

Axelrod (1990) found that TIT-FOR-TAT (TFT) was the most evolutionarily stable strategy (as defined by Maynard Smith, 1974) for playing this game successfully (but see Nowak & Sigmund, 1992): always start to cooperate on the first move and then do on the next move what the other player did on the last move. Thus, this is both a forgiving and a punishing strategy, and the most convincing evidence of its occurrence in real-life situations would be that defection is punished with defection, in an otherwise cooperative context. Furthermore, a condition of the PDG is that a time-lag exists between the defection by one individual, and the detection of that defection by the other. Without this time-lag, immediate retaliation would be possible, and the incentive to cheat and exploit the other's cooperative efforts (an essential aspect of the model) would disappear (Boyd, 1988).

There are examples of cooperation and reciprocal altruism in a variety of species (e.g. Packer, 1977; Packer & Pusey, 1982; Noë, 1990; Scheel & Packer, 1991), and even of the use of TFT (Wilkinson, 1984; refs in Axelrod and Dion, 1988; Milinski et al., 1990; Hart & Hart, 1992), although the validity of some of these reports has been questioned (e.g. Moore, 1984; Noë, 1990).

Not everyone agrees that the PDG is a good model of cooperative relationships. For example, the social organization within which cooperation occurs is not taken into account in the PDG (Noë, 1990), and it assumes that animals are likely to interact repeatedly with each other. However, some animals are very mobile, and may only meet once (Enquist & Leimar, 1993). Moreover, the rewards as formulated in the game do not always realistically reflect biological systems (e.g. the benefits of grooming and being groomed are much disputed, see Chapter IV), and there are several inconsistencies within the theory of reciprocal altruism (Rothstein & Pierotti, 1988).

In an attempt to clarify the issues Rothstein and Pierotti (1988) distinguished between four different kinds of 'altruism': (i) by-product beneficence, in which an egotistic act happens to be beneficial to other individuals; (ii) pseudo-reciprocity, in which the receiver of an altruistic act reciprocates with an egotistic act which is also beneficial to another (i.e. this latter act is by-product beneficence); (iii) reciprocal altruism, in which the receiver of an altruistic act reciprocates with an altruistic act; (iv) simultaneous cooperation, in which both individuals are altruistic at the same time, but the benefit of cooperation to both is higher than the sum of their individual gains would be, had they not cooperated. (In fact, this latter condition applies to reciprocal altruism as well, e.g. Noë, 1990). Additionally, the term 'reciprocity' is often used to denote a balance in acts given and received, and evidence of reciprocity is frequently used as evidence for reciprocal altruism (e.g. Connor, 1986; see MacCormack, 1976, for a discussion of the term 'reciprocity' as used in the anthropological literature).

The research of de Waal (1982, 1989b), de Waal & Luttrell (1988), and Hemelrijk & Ek (1991) has shown that chimpanzees exhibit several forms of reciprocal altruism. For example, de Waal's (1989b) work indicated that a chimpanzee is more likely to share her food with another if she has been groomed by the other before feeding, and less likely to share with another after having groomed that one before feeding. Furthermore de Waal (1982) suggested that chimpanzees 'trade' grooming for access to oestrous females, a phenomenon he termed 'sexual bargaining'. Hemelrijk and Ek (1991) found reciprocity for grooming in chimpanzees, showing that chimpanzees tended to groom those others more from whom they received more grooming (see also Simpson, 1973). However, it is not clear whether this grooming reciprocity was the result of reciprocal altruism (i.e. grooming in turns) or simultaneous cooperation (i.e. grooming simultaneously).

Reciprocation of grooming by grooming has also been found as reciprocal altruism in impala, Aepyceros melampus (Hart & Hart, 1992; Mooring & Hart, 1992), as mutualism (i.e. simultaneous cooperation) in lemurs, Lemur sp. (Barton, 1987), as reciprocity in bonnet macaques, Macaca radiata (Silk, 1982), and as reciprocal altruism in Japanese macaques, Macaca fuscata (Muroyama, 1991; see also Furuya, 1965).

The definition of reciprocity as used by Hemelrijk (1990a) applies strictly to the level of the group. In her work, reciprocity indicates that an individual gives more to someone from whom he receives more than to someone from whom less was received. According to her, there are two models for reciprocity at group level: the actor-reactor model, and the actor-receiver model. The difference between the two lies in the mental capacities necessary for an individual to keep track of social relationships within the group.

The first model states that actors give more to those that give them more, relative to what each gives to the others in the group. If in a group of three animals A , B and C, A gives most to B, B should give most to A. Thus, this model is based on reciprocation of preference rank: if B is second ranking in A's grooming hierarchy, then A should be second ranking in B's grooming hierarchy.

The second model takes the point of view of just one individual, who gives and receives. In this case, each individual gives more to those from whom more was received. Thus, if A received more from B than from C, he will give more back to B than to C, irrespective of what B and C gave to each other. In the first model an individual would be required to keep track of all the social relationships between his partners and the other members of the group, whereas the second model only requires an individual to keep track of his own relationships (Hemelrijk, 1990a).

In fact, an analysis of grooming at group level cannot reveal anything about the nature of reciprocity at the dyadic level, and the existence of reciprocity of grooming at group level does not necessarily mean that the chimpanzees compare their own grooming relationships to find out whom they should groom most, second most, and so on. For example, if they reciprocate grooming immediately when they receive it, they will not need to keep track of more than one grooming relationship at the same time. Such a reciprocation strategy is clearly not based on either the actor-reactor or the actor-receiver model, but it would result in significant reciprocity at group level.

This dissertation will primarily be concerned with the reciprocation of grooming by other grooming at the dyadic level. Grooming is easily observable, has a measurable duration, and it is usually completely clear how much of it is given and how much received. Chimpanzees reciprocate grooming both sequentially (i.e. A grooms B first, then B grooms A), and simultaneously (i.e. A and B groom each other at the same time), allowing for the possibility that reciprocal altruism and simultaneous cooperation are both operative, as well as that TFT is used as a strategy for the reciprocation of grooming.

The aim is to obtain insight into the strategies that chimpanzees use in the reciprocation of grooming, the roles of unilateral and mutual grooming in reciprocation, and the influence of the social context on the reciprocation of grooming.

Chapter I reviews the literature on grooming in chimpanzees and evaluates some of the conclusions drawn therein.

Chapter II gives an outline of the methods used in this project, and a general description of the chimpanzee group that was studied.

In Chapter III the foundation will be laid for the analysis of grooming at the dyadic level, and grooming sessions will be defined empirically.

In Chapter IV grooming between male chimpanzees will be analysed at the dyadic level, to see what (if any) strategies they use in the reciprocation of grooming, and to investigate the roles of unilateral and mutual grooming in the reciprocation of grooming. Is grooming an example of reciprocal altruism or mutual cooperation?

Chapter V tests two alternative hypothesis of the function or meaning of mutual grooming. Is mutual grooming a chance overlap in the grooming by two partners, or is it used by the chimpanzees to reduce the time they spend in grooming?

Chapter VI investigates the influence of food, aggression and oestrous females on grooming.

Chapter VII looks in more detail at particular dyads, in order to find patterns of reciprocation within grooming sessions.

Chapter VIII analyses in more detail the relationship between unilateral grooming, mutual grooming and interruptions in grooming within cooperative sessions.

Chapter IX draws conclusions, and gives suggestions for further research.

Figure i.1. Typical matrix of rewards for the iterated Prisoner's Dilemma Game (After Axelrod, 1990).

		Player I	
		Cooperate	Defect
Player II	Cooperate	R=3, R=3 Reward for mutual cooperation.	S=0, T=5 Sucker's Payoff, and Temptation to defect.
	Defect	T=5, S=0 Temptation to defect, and Sucker's payoff.	P=1, P=1 Punishment for mutual defection.

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CHAPTER I

SOCIAL GROOMING IN CHIMPANZEES: A CRITICAL REVIEW

Chimpanzees (Pan sp.), both in the wild and captivity, spend part of their time in social (or allo-) grooming (0-25% of observation time, e.g. Leger, 1977; Riss & Busse, 1977; Kraemer, 1979; Goodall, 1986a; Kawanaka, 1989). While there is a vast amount of literature on chimpanzees, fewer reports mention grooming and of the latter, only a fraction focuses to any extent on this behaviour, even though from early on the behaviour has been recognized as an important aspect of the social life of chimpanzees (e.g. Yerkes, 1933).

This review is written in an attempt to collect the currently available details of grooming in chimpanzees, in the hope that this will reveal aspects of the behaviour that still need to be elucidated. Most of the research has been dedicated to the common chimpanzee (Pan troglodytes), but there are also some reports on bonobos (Pan paniscus).

Definitions of grooming

Grooming has been defined in terms of motor patterns and function. For example, van Hooff (1974) defined it as "picking through the fur of another individual" (see also Leger, 1977; McGrew & Tutin, 1978; Bauer, 1979), and Ghiglieri (1984) stated that grooming serves "the apparent primary purpose of removing foreign particles, ectoparasites, or dead skin, etc." from the skin of the groomee. Wallis & Lemmon (1986) wrote that a "grooming bout involves the manual examination and cleansing of dirt, insects, etc., from another individual's hair and/or skin", combining motor pattern with function (see also Yerkes, 1943).

Despite slight disagreements on the definition of grooming, researchers have probably recorded almost exactly the same behaviour, even when it did not fully comply with their own definition. For example, Ghiglieri (1984) probably did not always observe the actual removal of foreign particles from the skin of the groomee, van Hooff (1974) probably did not always observe the "picking through the fur" he described, nor did McGrew and Tutin

(1978) always observe the "close inspection of the body surface" without hesitating to score, for example, the lazy combing of another chimpanzee's hair, without close visual inspection, as grooming too.

It is difficult to give an all encompassing definition of grooming. Thus, some authors have given longer and more general descriptions of the behaviour (e.g. Goodall, 1968b, 1986a; Yerkes, 1943). It occurs in many different contexts and is variable in its appearance, although the behavioural elements themselves may be stereotyped (Yerkes, 1943). Grooming is perhaps best characterised as the movement of at least a finger or lip of a chimpanzee through the hair or on the skin of another. Additionally, the tongue and teeth may be used and grooming spots may be sucked with the lips (pers.obs.). Usually at least one of them is sitting or lying down. While grooming occurs mostly in dyads, sometimes more than two individuals are involved, for example, when A grooms B, while B grooms C.

Measures of grooming and grooming 'unit'

Both frequency and duration measures have been used to quantify grooming behaviour, but it is not always clear how these are related to each other. For example, Simpson (1973) found that his frequency measure was not consistently correlated to his duration measure. Furthermore, frequencies and durations of grooming, obtained with time sampling techniques are not necessarily representative of true frequencies and durations. For example, Leger (1977) reported that instantaneous and one/zero sampling techniques produced scores which were only moderately correlated with hourly rate and mean bout duration (note, however, that he correlated true scores directly with one/zero and instantaneous scores, without first extracting more realistic values for rate and bout length, on the basis of some kind of definition of a bout, see below).

The following duration and frequency measures have been used:

A) Duration.

1. percentage of total observation time spent in grooming, i.e. true total duration, obtained by focal animal sampling and continuous recording (Goodall, 1968b; Pusey, 1983; Nishida, 1989).

2. the length of grooming sessions (Kano, 1980; Kuroda, 1980), or bouts, if separately defined (Nishida, 1988, see below), i.e. true bout duration on the basis of focal animal sampling and continuous recording.

B) Frequency.

1. the number of sessions per unit of observation time (Ghiglieri, 1984; Nishida, 1988; Sugiyama, 1988), i.e. true frequency obtained with focal animal sampling and continuous recording.

2. percentage of observation blocks in which grooming occurred (i.e. the 'rate' of grooming) on the basis of:

- instantaneous sampling (Merrick, 1977; King et al., 1980; de Waal & Luttrell, 1988).
- one-zero sampling (Gust, 1988).

The frequencies or rates, obtained with time sampling methods, may not be correlated with the true frequencies and rates of grooming (Leger, 1977; Kraemer, 1979b), but depend on the sample interval used and on the definition of a unit of grooming (Smith & Conolly, 1972, in Altmann, 1974; Martin & Bateson, 1986, also see below).

Grooming normally occurs in 'units' with a measurable duration, and these have variously been defined as 'sessions', 'sequences', or 'bouts'. A grooming bout is always defined with reference to the individual, as a period of grooming in which groomer-groomee roles do not change (Kano, 1980; Huffman, 1990), sometimes in combination with a criterion for the maximum allowed duration of interruptions in the bout (Nicolson, 1977 used a 1-min. criterion; Nishida, 1988 a 10 s. criterion).

A grooming sequence and session, however, are defined in terms of the dyad. A grooming sequence was defined as "a continuous period of social grooming between 2 chimpanzees, not interrupted by a pause of more than 10 s., nor by other grooming or other activities" (Nishida, 1988), and as "the period of grooming between two individuals during which there were rests of no more than 60 seconds" (Huffman, 1990).

A session has been defined as continuous grooming by two (or more) chimpanzees, either without specification of a time criterion to distinguish between sessions (Simpson, 1973; Kano, 1980; Ghiglieri, 1984), or with (Pusey, 1978, 5 min.; Goodall, 1986a, 2 min.; Nishida, 1988, 10 min.; Takahata, 1990b, 50 s.). Additionally, Goodall (1986a) gave a minimum duration for a grooming session. From these reports it becomes clear that criteria to distinguish between subsequent bouts, sequences, and sessions have been arbitrary, and that no two reports have explicitly used the same criterion. Comparison of the results of these reports is, therefore, difficult.

It is perhaps possible to establish the natural duration of grooming bouts, sequences and sessions and of the interruptions in them, on the basis of behavioural parameters, such as looking up, changes in body posture, in body parts groomed, or even in body parts used in grooming (e.g. right hand, left hand, lips). Additionally, the bout criterion interval could be determined, empirically, by log-survivorship analysis (see Chapter III).

Table I.1 gives a hierarchical scheme of grooming, on the basis of Nishida (1988). There are four levels at which grooming may be recorded. At three of these levels both durations and frequencies could be of interest. However, depending on the exact definitions used to describe each level, there are restrictions on the sampling techniques that can be used.

Finally, according to Goodall (1986a), who used a minimum duration of grooming in her definition of a session, grooming of shorter than (an arbitrary) two min. duration often represents "token grooming", usually as part of greeting behaviour, dominant-subordinate sequences, or courtship and mating. This suggests that grooming frequencies and durations are context dependent, and it would be of interest to know how long these bouts of "token grooming" really last, and whether they indeed should be distinguished from other grooming.

In the following sections, the word 'session' is used to indicate a grooming 'unit', as defined by the particular author referred to.

Functions of grooming

Grooming may be hygienic, social or both. The hygienic function of allogrooming in chimpanzees can be deduced from observations of the removal of particles from the partner's hair and skin (Goodall, 1968b; Thiel, 1989; Ghiglieri, 1984; Nishida, 1988). Additionally, selfgrooming often involves the removal of mud, insects, body fluids etc. from an individual's own hair or skin (Goodall, 1986a).

Hutchings & Barash (1976) attempted to test the hygienic hypothesis of primate grooming by comparing the body parts groomed in selfgrooming with those groomed in allogrooming. They distinguished between body parts accessible and inaccessible to the selfgroomer, and found that allogrooming was concentrated on areas of the body, inaccessible to the selfgroomer. This, they argued, provided indirect evidence for a hygienical function of grooming, and similar results were obtained by Barton (1983, 1985) for primates in general, and by Ghiglieri (1984) and Thiel (1989) for chimpanzees.

However, these results can also be explained by the notion that body parts which were inaccessible to the selfgroomer, were just more accessible to the allogroomer than body parts which were accessible to the selfgroomer. Furthermore, the distinction between accessible and inaccessible is one of degree, and chimpanzees can reach almost all parts of their own bodies, if they want to, even though sometimes with one finger only.

Chimpanzees can be host to many different internal and external parasites (Myers & Kuntz, 1972), but there is no evidence that grooming reduces the chance of infestation by any of them. The case mentioned by Nishida (1988), of an orphaned chimpanzee lacking a "smooth coat of fur" for at least 5 months, due to the absence of grooming by the mother, and the apparently adaptive behaviour of the chimpanzee louse (Pedicularis schaefi) to become immobile when exposed to light, making it extra difficult to detect for a groomer (Kuhn, 1968, in Goodall, 1986a), are the only pieces of direct evidence for a hygienic function of grooming in chimpanzees.

The proposed social functions of grooming are manifold, and include affiliation (van Hooff, 1974; Goodall, 1968b, 1986a; Nishida & Hiraiwa-Hasegawa, 1987), stress alleviation (Sugiyama, 1969; Simpson, 1973; Goodall, 1986a), appeasement (Ghiglieri, 1984; de Waal, 1989a), and social manipulation and trade, where grooming is exchanged for food, support, or sex (Nishida, 1983b, 1988; Goodall, 1986a; de Waal & Luttrell, 1988; de Waal, 1989a; but see Hemelrijk, 1990a; Hemelrijk & Ek, 1991). Additionally, grooming may serve as a declaration of the commitment the groomer has to a relationship (Simpson, 1991). I will deal with the specifics of these hypothesized functions in later sections.

Dynamics of grooming

a.Initiation of grooming

A grooming session is often preceded by an approach of one or both partners, either of whom may then start to groom, or present some part of her body (usually the head, neck, rump, or bottom; Goodall, 1968b; van Hooff, 1974) to be groomed by the other, by making it easily accessible to the other. There is no clear correlation between approach and the start of actual grooming (Simpson, 1973), and sometimes both individuals start to groom at the same time (Goodall, 1965; pers.obs.). The approaching individual may lipsmack or teethclap (Nishida, 1970; Ghiglieri, 1984), the meaning or function of which is unknown. Chimpanzees can request grooming by vigorously scratching themselves or, as was the case with a two year old chimpanzee, by placing another's hand on his own body (Tomasello et al., 1989).

When a solicitation for grooming by scratching or presenting is ignored, the solicitor may increase the intensity of her attempts to initiate a grooming session by whimpering (especially by infants), touching the other's hand or arm or positioning her body between the two partners of an on-going grooming session (Goodall, 1968b). Regularly, however, two individuals that have been within reach of each other for some time will suddenly start a grooming session without any obvious cues, and sometimes two individuals that are separated by as much as 20 m. approach each other simultaneously and unhesitatingly in order to groom (pers.ob.). Partner choice for grooming is dependent on age, sex, rank and oestrous condition of the individuals involved (Goodall, 1968b; Simpson, 1973), as well as on the social context and individual preference.

However, there are no published data for chimpanzees on the distribution of the different ways of initiating grooming over age-sex classes, nor have there been comparisons of the effectiveness of different grooming invitations.

b. The Grooming episode

Chimpanzees may use their fingers, nails, lips, tongue and teeth in grooming (Yerkes, 1943; pers.obs.). The lips may be applied directly to the skin of the partner, or particles removed with the fingers may be brought to the mouth. There may be close visual inspection of the other's hair and skin (Goodall, 1968b; van Hooff, 1974; McGrew & Tutin, 1978; Ghiglieri, 1984) or a slow combing of the hair combined with only occasional glances at the parts being groomed (Goodall, 1986a). The groomee "permits the partner to change the position of its limbs or head and it usually then maintains this position at least for a short time even if it seems occasionally somewhat awkward and uncomfortable" (van Hooff, 1974), or the groomer may move around the groomee, thereby obtaining access to other body parts (pers. obs.).

Once a grooming session has started, both partners seem to like it. However, approach to be groomed was more frequent than approach to groom, in young chimpanzees, suggesting that being groomed was preferred over grooming (Mason et al., 1962; see also Falk, 1958).

That chimpanzees like to be groomed can also be judged by the way in which groomers are allowed to manipulate the groomees' body parts, and from the relaxed posture of the groomee (Ghiglieri, 1984). However, Ghiglieri (1984) observed grooming almost exclusively when the animals were resting, and probably quite relaxed anyway.

A groomer will often lipsmack or teethclap (Köhler, 1935; Yerkes, 1943; Nishida, 1970). It has been suggested that these sounds are used to attract the attention of other individuals and create new enthusiasm for grooming (Goodall, 1986a), but no quantified reports have been published.

During a grooming episode, a groomee may continually present new body parts (Ghiglieri, 1984), scratch those areas that she wants to be groomed (Goodall, 1968b), or indicate where she wants to be groomed by guiding the fingers of the groomer to the required place (Hayes, 1951; pers.obs.). This latter phenomenon, however, refers to chimpanzees that had extensive contact with human beings, and has not been reported for wild chimpanzees.

Grooming may be unilateral (A grooms B, B does not groom A), or mutual (A and B groom each other at the same time; Sparks, 1967). Sparks (1967) used the term "reciprocal" grooming to refer to grooming in turns. However, as mutual grooming and grooming in turns are both reciprocal forms of grooming, the term "sequential" can better be used for turn taking in grooming. Mutual and sequential grooming are then both forms of reciprocal grooming.

Mutual grooming is common in chimpanzees (Goodall, 1986a; Nishida, 1988), but rare in bonobos (Ihobe, 1992). Generally no distinction has been made between mutual and unilateral grooming, on the assumption that the former results from a chance overlap in the grooming of two partners, rather than having a meaning or function of its own. Alternatively, mutual grooming could be the result of attempts by the groomers to reduce the actual time spent grooming, thereby leaving more of it free for other activities, such as feeding (cf. Dunbar & Sharman, 1984).

Grooming parties may contain up to 10 grooming animals, and a grooming session may last for up to 2.5 hours, although normally a session lasts for less than one hour (Goodall, 1968b). Groomer-groomee roles may switch up to 40 times during a session (Ghiglieri, 1984). In long sessions, grooming may be alternatingly intensive and lazy (Goodall, 1965), and a male's median grooming duration is specific for that male, rather than for the particular interaction (Simpson, 1973). Again, there are no published data on groomer-groomee role changes, or on the intensity of grooming, and their relation to independent variables, such as age, sex, and social status.

Grooming is an extremely variable behavioural pattern, ranging from a mere scanning of the partner's fur, through a scratching and picking at bits of skin, to a surgical extraction of splinters and the caring for wounds (Yerkes, 1933, 1943; Miles, 1963). It has been observed in the context of cannibalism, and on the dead body of an infant; as leaf-grooming, where an individual picks up a leaf and appears to make grooming movements directed at its surface, thereby perhaps communicating a willingness to groom others (Goodall, 1977, 1986a; Nishida, 1980); as dental grooming, where one individual was observed to use sticks to groom another's teeth on several occasions, in captivity. This, and the observations of an individual wiping clean parts of another's body with some leaves, are the only examples of tool-use in social grooming (McGrew & Tutin, 1972, 1973; Goodall, 1986a).

In bonobo grooming sessions there may be up to 10 groomer-groomee role reversals (Kano, 1980), and bonobos probably spend more time grooming each other's faces than chimpanzees (de Waal, 1988), but the general grooming techniques are the same in both species of chimpanzee (Badrian & Badrian, 1984).

c.Termination of grooming

There is almost no information about the causes and circumstances of a grooming session ending. A session usually ends by non-reciprocation (Goodall, 1968b; Ghiglieri, 1984), when the partner leaves, goes to sleep, starts to feed, or groom herself. Sometimes, a session ends when another individual interferes by presenting for grooming or inviting play. In captivity, sessions are frequently interrupted by provisioning (pers. obs.).

Grooming and age

Frequencies and durations of grooming vary with the ages of the individuals involved. This section reviews the grooming of post-weaning individuals only. The development of grooming in infants and mother-offspring grooming will be discussed separately.

Generally, older chimpanzees give and receive more grooming than younger ones (Goodall, 1968b; Merrick, 1977). The time spent in grooming changes only little during adolescence, but young adolescent males spend less time grooming adult males than do older adolescent males (Pusey, 1990). Grooming time increases from late adolescence (7-9 years) to adulthood (Kraemer et al., 1982; note that adolescence in captive chimpanzees comes at an earlier age than in wild ones), and there is a positive correlation between grooming time and age for adult males (Simpson, 1973; Bygott, 1974, 1979). Furthermore, older adult males are groomed more than younger adult males, and groom each other more than they groom younger ones (Simpson, 1973). In old age, females spend less time in grooming, but both males and females show an increase in their grooming time with young adult and prime males (Huffman, 1990). A relationship between grooming and age might also exist for bonobos (Kuroda, 1980).

Thus, the relationship between grooming and age has been studied relatively well. Some of the changes in grooming time reflect changes in association patterns, when chimpanzees begin to spend less time with their mothers and become socially integrated into the community as a whole. For females this also means spending more time alone and, later on, with their own offspring. For males it means becoming accepted by the adult males, and attaining a position in their dominance hierarchy (for a more extensive discussion, see Pusey, 1990).

The changes in grooming patterns of maturing male chimpanzees are consistent with the 'commitment principle' (Simpson, 1991), which predicts that grooming is used to declare a partner's value to a relationship. For example, adolescent males primarily groom adult males, but are not yet groomed by them. They have to groom themselves into the dominance hierarchy. Only when they have become part of this hierarchy will they start to be of value to adult males (e.g. as allies), who then begin to groom them back.

Grooming and sex

Grooming occurs between members of the same or opposite sex. Generally, males groom more frequently than females (Nishida, 1970), although mothers with older offspring (i.e. juvenile, adolescent or mature) spend about as much of their time in grooming as adult males (Goodall, 1968b, note that these data are based on observations in camp, see section on grooming in the feeding context). Adult males also groom other adult males more often than they groom adult females and than adult females groom each other (Goodall, 1965; Sugiyama, 1969; Nishida, 1979; Ghiglieri, 1984; de Waal, 1986; Takahata, 1990a).

Grooming sessions between males tend to go on for longer than between females (Ghiglieri, 1984; Goodall, 1986a). However, at Bossou, there was a higher frequency of male-female grooming than of male-male and female-female grooming (Sugiyama, 1988). Sugiyama suggests that this chimpanzee community may be female-bonded instead of non-female-bonded (Wrangham 1979, 1980) as other chimpanzee communities studied thus far (see Wrangham et al., 1992 for a detailed comparison between different chimpanzee communities).

There are indications that between early adolescent (6-8 years) and early adult (10-12 years) stages, females spend more time in grooming than males, and mothers more than females without offspring (Kraemer et al., 1982, see her Fig.3).

Adult females mainly groom within the family, i.e. with their offspring (Goodall, 1986a. For bonobos: Badrian & Badrian, 1984) and outside the family they groom adult females more frequently than they groom adult males (Ghiglieri, 1984). At Mahale, however, adult females groomed adult males more frequently than they groomed either adult and sub-adult females or juveniles and infants (Nishida, 1979). These contrasting reports can be reconciled by looking at Goodall (1968b).

Goodall divided adult females into mothers with infants and mothers with older offspring (juvenile, adolescent, mature). From her Table 35 (pp. 266-267) it can be seen that mothers with infants spent more time grooming adult females than mothers with older offspring did (58% vs. 10% of total time spent grooming). Furthermore, mothers with older offspring groomed adult males more than they groomed adult females. As Nishida's (1979) data are based on interactions involving 5 adult males, 10 adult and subadult females, 2 juveniles and 1 infant, the majority of his 'adult and subadult' females probably falls in Goodall's 'mother with offspring' class (he observed only one infant, and most adult females are mothers). Thus, mothers with older offspring at Mahale, like at Gombe and Kibale (Ghiglieri, 1984), groomed adult males more than they groomed either females or immatures.

Furuichi (1989) attempted to explain his own contrasting results by noting that Kano (1980) and Kuroda (1980) either had not excluded mother-son grooming from their male-female category, or had not taken account of sex-ratios in their study populations. However, Furuichi's (1989) results are also in contrast with those of Kano (1986; in Sugiyama, 1988), after the latter were corrected for sex-ratio. Even then, it is not clear how Furuichi's comment explains his low occurrence of female-female grooming and high occurrence of male-male grooming, which are both independent of mother-son grooming.

In bonobos male-female grooming occurs more often and lasts for longer than female-female grooming, and male-male grooming occurs least (Kano, 1980; Kuroda, 1980; Badrian & Badrian, 1984; Nishida & Hiraiwa-Hasegawa, 1987; Sugiyama, 1988; cf. Ihobe, 1992). However, Furuichi (1989) found that female-female grooming occurred least often, and de Waal (1988) found that it occurred most often in a captive colony.

Most studies, however, do agree as to the lower frequency of male-male grooming in bonobos compared to chance expectation (based on the sex-ratio) and compared to chimpanzees, and these inter-specific differences correspond to other contrasts between bonobos and chimpanzees. For example, chimpanzees commonly form all-male groups, whereas bonobos do so much less frequently (Nishida & Hiraiwa-Hasegawa, 1987). Also, female bonobos tend to be more sociable than female chimpanzees (Badrian & Badrian, 1984).

Grooming and rank

Chimpanzees groom higher ranking individuals more often and longer than lower ranking individuals (Crawford, 1942a, b, and Nowlis, 1941, cited in Mason, 1970; Okano et al., 1973; Goodall, 1986a; Takahata, 1990b), and between males, the higher the rank of the partner, the longer a male will groom him (Simpson, 1973). The higher a male's status, the less long he grooms, and the longer his partners groom him, and a male usually grooms a partner with higher status more than he is groomed by him, at Gombe. However, the alpha male groomed others long (Simpson, 1973).

At Gombe, adult males (excluding the alpha male) groomed shorter with increasing status (Simpson, 1973). At Mahale, the top ranking male groomed and was groomed most often, and also groomed about twice as long as he was groomed (Nishida, 1970, 1979; Takahata, 1990b; Kawanaka, 1990). For captive females at Arnhem, there was a positive correlation between the frequency of grooming a specific (female) partner and the dominance status of that partner (Hemelrijk, 1990a). Low rankers rarely failed to reciprocate grooming and rarely terminated a session directly, at Kibale (Ghiglieri, 1984).

In post-reunion behavioural sequences at Gombe, displaying males who were involved in social grooming after their display, were involved more frequently, but for shorter periods of time than non-displayers (Bauer, 1979). In other words, as high ranking males generally seem to display more frequently than low ranking males (Goodall, 1986a), it may be concluded that high rankers at a reunion are involved in more frequent grooming bouts of shorter durations than low rankers (note that Bauer did not define a bout of grooming).

Grooming and Female Oestrus

The oestrous condition of a female has a significant effect on her involvement in grooming, so much so that an early study found that most heterosexual grooming consisted of an oestrous female and a mature male (Sugiyama, 1969). Females in oestrus are groomed more by males than are anoestrous females, both in captivity and in the wild (Goodall, 1965;

Merrick, 1977; Wallis & Lemmon, 1986; Pusey, 1990; Takahata, 1990a; Hemelrijk et al., 1992). Merrick (1977) found that oestrous females in captivity did not reciprocate the grooming they received from a male, but in the wild oestrous females give and receive more grooming than anoestrous females (Pusey, 1978, 1990; Takahata, 1990a).

In contrast, there was no clear relationship between grooming and the oestrous condition of females, at Mahale (Kawanaka, 1989). Contrasting evidence comes also from McGinnis (1973), who found that, at Gombe, grooming between the sexes occurred in a smaller percentage of approaches during female oestrus. It is not certain that Pusey's (1979, 1990) and McGinnis' (1973) reports really contradict each other, as different measures of grooming have been used. Particularly in the latter report, it is unclear how the percentages of approaches leading to grooming relate to the total time of heterosexual grooming. In other words, although the percentage of approaches leading to grooming was found to be lower when oestrous females were involved, the grooming sessions that occurred may have been longer, so that in fact anoestrous females were groomed less than oestrous females.

Grooming sessions between the males of the Arnhem colony lasted much longer when an oestrous female was present (de Waal, 1982). Merrick (1977) found that, in contrast to adult males, anoestrous females in captivity are not influenced in their grooming behaviour by the presence of other, oestrous females.

Males that are involved in a restricted mating pattern (i.e. they try to monopolize an oestrous female either by directing aggression at her or other members of the community, or by taking her on a consortship) tend to groom oestrous females more than do other males (Tutin, 1979), and female chimpanzees tend to mate with males that have shown high frequencies of grooming (Hemelrijk et al., 1992). Consortships themselves have also high frequencies of, especially, male to female grooming (Tutin & McGinnis, 1981). Grooming has also been observed before initiation of courtship by a male, during courtship (Tutin & McGinnis, 1981) and after copulation, and lasts shorter than 2 or 3 minutes in these contexts, and usually only a few seconds (Goodall, 1965; Takahata, 1990a).

After a female has given birth, there is an increase in the frequency with which she is groomed, both in captivity (Merrick, 1977) and in the wild (Goodall, 1986a) but the grooming frequency drops again during the first month.

Female bonobos in oestrus are also more likely to be involved in grooming than anoestrous females (Kuroda, 1980), but grooming was not observed in the context of courtship and copulation (Kano, 1980).

Development of Grooming in the Infant

The literature on the ontogeny of grooming is sparse and anecdotal. A female chimpanzee, Viki, raised as a human child, was first observed to 'groom' at 8 weeks, when she started to make picking movements at a bedspread (Hayes, 1951). Others have found grooming to start at 2 or 3 months (Goodall, 1986a), 17 weeks (Nicolson, 1977), and 25 weeks (Plooij, 1984) in the wild, and 39 weeks in captivity (Yerkes, 1943). By 11 months an infant at Gombe was first observed to present for grooming to its mother (Plooij, 1984).

Viki achieved coordination of mouth and fingers at 6 months and at 12-18 months she was first heard to make sounds while grooming (lipsmacking). She began to "search for grooming spots" (Hayes, 1951) on others at 18 months, at which age wild infants at Gombe were proficient in adult grooming techniques (Goodall, 1967, 1986a), although grooming at this age remained an infrequent event at Mahale (Nishida, 1988). Viki started to selfgroom at 2 years, like Gombe infants (Goodall, 1968b), but in contrast to infants at Mahale, who all groomed themselves at one year (Nishida, 1988). Viki started to search for self-groom-spots at 3 years.

Infant chimpanzees have a strong inborn drive to groom (Yerkes, 1933; Hayes, 1951; Falk, 1958; Goodall, 1986a). Chimpanzees that had been isolated from other chimpanzees as adolescents learned how to groom but lacked coordination and patterning of the separate elements (manipulation, visual inspection). They became fairly normal groomers, however, when after several years they were mixed with normal, wild caught adults again. This recovery did not take place in chimpanzees that experienced other adults much later for the very first time, as early adults (Davenport, 1979).

A clear distinction should be made between the inborn drive to groom, and the development of typical grooming, which depends on the social environment for its normal course (Yerkes, 1943; Mason et al., 1962). The fact that chimpanzees, isolated as adolescents, lack coordination and patterning of grooming implies that the development of grooming to the adult pattern is not yet complete in individuals of this age group (or is lost after isolation), which is in sharp contrast to the reports of infants attaining adult grooming techniques as early as 18 months. However, nowhere are terms such as 'patterning', 'coordination' and 'adult pattern' defined, and there is probably considerable variation in the authors' understanding of these terms. Thus, for example, Davenport (1979) probably does not refer to the same 'adult pattern' as Goodall (1967, 1986a).

The frequency and duration of grooming increases during infancy at Gombe (Clark, 1977; Goodall, 1967, 1968b), but not in captivity (Bloomsmith, 1989), and it remains a rare event until the infant is at least 3 years old (Yerkes, 1933, 1943; Nishida, 1988). In captivity there was an increase in the time spent in selfgrooming, while social grooming remained low until late adolescence (Kraemer et al., 1982). Grooming in infancy was exclusively directed at the mother, and sometimes at siblings, until the 5th year of life at Mahale(Nishida, 1988).

Mother-offspring grooming

a. A comparison between Gombe and Mahale.

As there are relatively good, quantified data available on mother-offspring grooming at Gombe (Goodall, 1968b; Clark, 1977) and Mahale (Nishida, 1988), a detailed comparison will be made between the findings from these two sites.

-At Gombe (Goodall, 1968b, her figs. 32&33), the frequency of sessions decreased from approximately 0.29/h in the first six months of life, to 0.13/h at age 1-4.5 years and then increased to about 0.68/h when the offspring was 9-13 years old.

-At Gombe, the frequency with which the mother groomed her offspring decreased from 0.29/h to 0.08/h during the first 4.5 years of life, then increased to about 0.42/h for 9-13 year olds.

-At Gombe, the frequency with which the offspring groomed their mother increased over the complete age range, from about zero in the first six month to 0.25/h at age 9-13 years.

-At Gombe, the percentage of grooming bouts that lasted less than one minute decreased gradually from more than 70% of all bouts at age 0.5-1.0 to less than 25% at age 8-15 for both mother and offspring. By that time more than 60% of offspring's grooming bouts lasted longer than 10 minutes and about 40% of mother's grooming as well (see also Goodall, 1967). Goodall (1968b) does not give details of the percentage of their total time that mothers and offspring were involved in grooming during these stages of the offspring's life.

-From Clark's (1977) fig.2 (after regrouping of her data, see below) it can be derived that, at Gombe, with increasing age of the offspring from 1-4.5 years to 4.5-7 years old, percentage of time that the mother groomed her offspring remained about the same (3.0% and 2.9% respectively) whereas percentage of total time that offspring groomed the mother increased (from 2.3% to 3.8% respectively).

-At Mahale, Nishida (1988) found no correlation between the age of the offspring and the percentage of total time they groomed the mother or were groomed by the mother over an age range of 1 month to 29 years. This is in contrast to Goodall's data for Gombe, which imply that infant's grooming time increased with age (as both frequency and duration increased with age) and Clark's data for two age-classes, which confirmed this tendency for Gombe chimpanzees.

-Nishida (1988) did not find a significant positive correlation between age of offspring and the length of grooming bouts either, at Mahale (but see below).

In order to allow a more detailed comparison between Goodall's (Gombe), Clark's (Gombe) and Nishida's (Mahale) data, both Clark's and Nishida's data were regrouped into Goodall's age classes of offspring (0-0.5; 0.5-1; 1-4.5; 4.5-7; 7-9; 9-13 years). These correspond roughly to her more recent classification (Goodall, 1986a). Average values were then calculated for each age-class with respect to several variables of grooming. The results of this procedure are listed in Tables 1.II, 1.III, and 1.IV.

There are opposite trends in the frequency distribution (males and females taken together) over the age-classes at Gombe and Mahale (Table 1.II). At Gombe, the frequency of grooming decreased until weaning, remained about constant until early adolescence and then increased again. At Mahale, there was an increase in the first year, then no change until weaning, and a decrease after early adolescence. This incompatibility could have resulted from the following:

-differences in definition of bout and session between Goodall and Clark on the one hand, and Nishida on the other.

-Goodall calculated frequency by dividing the total number of observed grooming sessions by the total time the mother and her offspring were observed together, whereas Nishida divided by the total observation time of the mother. Clark used the same method as Goodall, but her subjects were with their mothers almost all the time anyway.

Comparison of the same Gombe (Goodall, Clark) figures (offspring-mother grooming, Table 1.II), with Mahale (Nishida) bouts/h (offspring-mother grooming; Table 1.IV) instead of the sessions/h, reveals that, at Mahale, there was an increase in the bouts/h of offspring's grooming with increasing age to about the 7th year of life in females and the 9th year of life in males, after which the frequency decreased again. Gombe data show an increase in frequency over the whole range of age-classes. Note that the different tail-off frequencies for males and females, which Nishida's data reveal correspond to the earlier ages at which females started to groom in his study.

Finally, regrouping of Nishida's data also reveals interesting changes in the total minutes per observation hour (of the mother) that offspring spent in grooming with increasing age (Table 1.III). For both males and females, total time of grooming increased until age 9, then decreased slightly in the last age-class. Grooming by the mother fluctuated between age-classes but did not follow such a clear pattern.

Taking Nishida's (Mahale) scores for females and males together and putting them next to those of Clark (whose study objects fall in two age-classes only) shows that over these two age-classes there was a similar trend in total grooming time at Gombe and Mahale (Table 1.III). In fact, the values for mothers are similar between the two study sites. However, there is a marked difference between offspring's grooming, infants at Mahale spending on average less than half as much time in grooming than infants at Gombe. In other words, the differences between mother's grooming and infant's grooming at Mahale are much larger than at Gombe, in these age-classes.

This difference can not be accounted for by methodological discrepancies: definitions of session and bout are irrelevant here (since the figures express total time), mutual grooming has been included in the figures, and differences in the use of total observation time (either of the mother or of mother and offspring being together) have no effect on the ratio of figures of the two age-classes at both sites. Thus, these figures probably reflect a genuine difference between Gombe and Mahale, and the differences may be related to possible differences in age at weaning, or other social factors.

In summary, the regrouping of Nishida's data brought to light some relationships which had not been found with the correlation techniques he had used. The results of this grouping into age-classes indicates that chimpanzee development takes place in actual stages, in the sense that progression from one developmental stage to the next brings about changes, whereas between these periods of change there are periods of relative stability (see also Pusey, 1990). Each individual goes through similar stages, but the age at which it goes into the next phase and the duration of each phase is different for each individual. Therefore, it is more elucidating to group individuals of similar stages (age-classes) together and calculate mean values for each age-class, instead of using each individual as a separate data point (see Kraemer et al., 1982).

General description of mother-offspring grooming

Male chimpanzees maintain a life-long grooming relationship with their mothers (Goodall, 1986a; Kawanaka, 1989). In the wild, mothers start to groom their infants on the first or second day after parturition and continue to do so regularly, although there are individual differences at this early stage (Nicolson, 1977), some mothers grooming their newborns very intensively, while others only groom them sporadically (Yerkes & Tomilin, 1935). The frequency with which the infant is groomed increases in the first few weeks of life

(Goodall, 1968b, 1986a). During the first few months, both duration and frequency of grooming remain constant (Nicolson, 1977).

Mothers in captivity groom their infants more intently than mothers in the wild (Budd et al., 1943, in Goodall, 1968b; Lemmon, 1968; Rogers & Davenport, 1970, both in Nicolson, 1977), but there remains great individual variation in the intensity (i.e. duration and thoroughness) of mother to offspring grooming (Yerkes, 1943).

At Gombe, with increasing age of the infant (0-4.5 years), grooming frequency decreases, while the duration of sessions increases (Goodall, 1968b), and total time spent in grooming decreases from 11% in the first months to 5% just before weaning. At this stage it is still almost exclusively the mother who does the grooming.

As mentioned previously, the infant starts to groom its mother at 25-30 weeks and the frequency and duration of its bouts increase with age (Goodall, 1968b; Nishida, 1988). At Gombe, grooming duration increases from less than 2% in the first three years of life, to 2-11% in the fourth year (Clark, 1977). The length of grooming bouts of pre-weaning infants averaged 2.5 minutes at Gombe (Clark, 1977) whereas at Mahale, bouts seldom exceeded 2 minutes before the 7th year of life (Nishida, 1988). This difference could be due to the different criteria used by these investigators to distinguish between separate bouts of grooming. There is also an increase in the percentage of grooming sessions in which mother and infant groom mutually (Goodall, 1968b).

During the final year of suckling and in the months following the end of suckling, bout frequency of mother-infant grooming remained constant, but average bout length of offspring's grooming after weaning was about 2.5 times higher than before weaning at Gombe (derived from Clark, 1977). There are no Mahale data available on the frequency of mother-offspring grooming around the time of weaning, but the increase in bout length was smaller.

However, total grooming time at Mahale (per observation hour) for mother-offspring and offspring-mother grooming increased to, respectively, 1.3 and 10 times its original value (from Nishida's (1988) Table VI), whereas at Gombe, total time increased only about 1.8 times in both cases (Clark, 1977, from her fig.2, excluding Flo/Flint, because of the unusually early presence of a younger sibling), with peak values just at the time that suckling ended. In captivity, there were no changes at all in grooming during the final weaning phase (Horvat & Kraemer, 1982). The actual number of grooming bouts per hour after weaning ranged from 0.6 to 2.4 at Gombe (N=6; Clark, 1977) and from 0.5 to 1.4 (N=4, Nishida, 1988) at Mahale.

Again, it should be stressed that the bout criterion is probably different in these studies. Additionally, Nishida's criterion for weaning was the resumption of oestrus in the mother, while Clark used termination of suckling as her criterion. Furthermore, Clark's frequencies refer to the number of contact bouts that involved grooming and/or suckling, while Nishida did not give details of the time when suckling ended. Thus, the difference between Gombe and Mahale in the increase in total time of infant's grooming during and after weaning could be an artefact.

The length of grooming bouts decreases with the birth of a sibling or in the year after the end of suckling (Clark, 1977), with the infant starting to build his own nest and contact with the mother becoming less frequent (Clark, 1977; McGrew, pers.comm.). Mutual grooming increased in frequency (Goodall, 1968b; Clark, 1977) and duration (Nishida, 1988) with the age of the offspring (from year 4), especially during the final year of suckling and seemed to decrease with the birth of a sibling.

At this stage, most grooming between mother and offspring occurs after the offspring approaches, but mothers also approach for grooming, doing so more often to sons than to daughters (Clark, 1977; Pusey, 1978). Pusey (1978), studying the Gombe chimpanzees, found no general change with age in the percentage of time offspring spent in grooming with the mother, for individuals between 4-15 years of age, but Goodall (1968b) reported an increase in frequency of grooming and a decrease in the percentage of bouts lasting shorter than one minute. She also found a gradual increase with age in the percentage of grooming sessions in which grooming between mother and offspring was mutual.

Although Pusey (1990) noted that grooming between mothers and their adolescent offspring was usually mutual at Gombe, at Mahale "virtual reciprocity", which was attained at about 11 years of age, was not based on mutual grooming only, but primarily on unilateral or sequential grooming (Nishida's (1988) Table III, IV).

Mothers with more offspring devote a higher percentage of their total grooming time to grooming their offspring than mothers with fewer offspring. (Nishida's (1988) Table II), and immigrant mothers with one infant spent more time grooming their offspring than residents with one infant. The immigrant mothers probably had more time, as a result of lower levels of association with resident group members (Nishida, 1988).

For bonobos, Kano (1988) reported that the frequency of grooming sessions is highest between adult females and juveniles, probably representing mother-offspring grooming. He also found that these sessions were mostly unilateral (grooming by the female) and lasted much shorter on average than sessions between mature individuals.

Grooming in a peaceful context: affinity

Although grooming is generally accepted to be the expression of affinity between the grooming partners, there is only one quantified report of this (van Hooff, 1974). Grooming occurs usually in a peaceful context, or in a greeting context and it is important in maintaining relationships within the community (Goodall, 1965, 1968b; Badrian & Badrian, 1984, for bonobos). The behaviour is sometimes used as an index of friendly or affinitive relationships (e.g. Sugiyama, 1988), and could be an indication of commitment to a relationship (Simpson, 1991).

It is probable that grooming by chimpanzees is the expression of at least an ultimate affinitive relationship, because grooming between (male) members of neighbouring communities has not been reported, and because it ceases completely with the outbreak of fierce hostilities (Goodall, 1986a). However, grooming occurs often outside a peaceful context, in which case it usually functions to re-establish a (friendly) relationship.

Grooming in an agonistic context: appeasement and tension reduction

Grooming often functions to ease tension, reduce aggression or reconcile opponents (Terry, 1970; Barton, 1983, for primates generally). For example, the grooming rate in the captive Arnhem chimpanzee group was higher when they were locked in their relatively small inside quarters, than when they were outside, an indirect indication of the aggression or tension reducing effects of grooming (Nieuwenhuysen & de Waal, 1982; Clarke et al., 1982 in Hannah, 1989).

Relatively short bouts of "token grooming" form part of the normal submission-reassurance sequence of behaviour after a conflict situation (Nishida, 1970; Goodall, 1986a; Tierney, 1990), but grooming, although common, is not characteristic of post-conflict interactions (de Waal, 1986). However, at Kibale, appeasement grooming in socially stressful situations was observed only sporadically (Ghiglieri, 1984), and at Arnhem it was not part of the first inter-opponent contacts after a conflict at all (de Waal & van Roosmalen, 1979).

Thus, although grooming almost certainly indicates an on-going relationship, and functions to reduce tension in both partners, it cannot be stated with certainty if it serves to mend a relationship after a conflict, or whether it is just the confirmation of the relationship after some other reconciliatory gestures have been made.

Grooming in the feeding context: affinity or tension reduction?

Grooming in wild chimpanzees and bonobos occurs primarily after intensive feeding, during periods of prolonged rest (Reynolds & Reynolds, 1965; Goodall, 1968b; Nishida, 1970; Ghiglieri, 1984. Kano, 1980; Badrian & Badrian, 1984 for bonobos). During feeding grooming was suppressed in captive chimpanzees and bonobos (de Waal, 1989b, c).

Grooming before feeding has been interpreted as an expression of frustration (Goodall, 1968a), arousal (Simpson, 1973), a way to spend time while waiting for food at an artificial feeding site (Wrangham, 1974), or as anticipatory tension reduction (in bonobos, de Waal, 1987). Furthermore, in the context of reunions at Gombe, it was more likely for male display to be followed by grooming at the provisioning site, than in the forest (Bauer, 1976, 1979).

Thus, it is possible that grooming before feeding represents anticipatory tension reduction, or an attempt to create an obligation in the groomee to share food later on. Grooming during feeding perhaps represents attempts at directly obtaining access to food owned by the groomee, and grooming after feeding represents truly peaceful relationships.

Grooming and play

During the development of the young chimpanzee, the frequency (Goodall, 1967) and rate (Merrick, 1977) of grooming are inversely related to the same measures of play. A young captive chimpanzee was more likely to groom a person after playing with that person than after the person groomed the chimpanzee or presented for grooming to the chimpanzee. The only significant sequential relationship between the play system and the affinity system, as defined by van Hooff (1974) was between grooming and hand wrestling.

Although there are indications that with the development of the young chimpanzee grooming increases, while play decreases, it is not known whether these are related processes, or whether they are independently related to the age of the chimpanzee. Studies on the relationship between play and grooming are lacking.

Reciprocity of grooming

Grooming "occurs in the most divers settings and often under conditions which seemingly preclude the expectation of other reward than the satisfaction in the activity itself or in the anticipation of being groomed in return" (Yerkes, 1933). Chimpanzees groom more, the more they are groomed (Simpson, 1973; Merrick, 1977; Pusey, 1978; Nishida, 1988; Hemelrijk & Ek, 1991), even though the amounts given and received might not be equal. Grooming sessions go on for longer if grooming is reciprocated (Pusey, 1978; Ghiglieri, 1984; Goodall, 1986a), and after a period of unilateral grooming, a groomer will often pause and request to be groomed (Goodall, 1986a).

Bonobo males groom females longer than females groom males in 'mutual' grooming (Kuroda, 1980). (Kuroda probably meant reciprocal sessions by 'mutual' sessions).

Grooming exchanged for other favours

Grooming can be used by chimpanzees to gain access to infants (Nishida, 1983b), or to females in oestrus (de Waal, 1986, 1989a), obtain food from others (de Waal, 1989b; Kuroda, 1984 for bonobos), to form alliances (Nishida, 1983a), or mating bonds (Goodall, 1986a, but see Hemelrijk et al., 1992), or to receive support in agonistic interactions (Hemelrijk, 1990a, but see Hemelrijk, 1990b).

However, only the findings by de Waal (1989b), Nishida (1983b), Hemelrijk (1990a, b), and Hemelrijk et al. (1992) were based on quantified data, and there are not enough data to make any firm statements about the use of grooming in exchange for other favours.

The exchange between grooming and access to oestrous females has been termed 'sexual bargaining', and originally it was applied to grooming of dominant males by subordinate males, in order to be allowed to mate with a female (de Waal, 1982). Later, it was also applied to the grooming of oestrous females by males, implying that its function was to establish a mating bond with the female, or to be allowed to mate with her in return for the grooming (Goodall, 1986a) However, there is no direct evidence that grooming is exchanged for matings, and it could just as well function to reduce the likelihood of aggression in the male, and of fear in the female (Hemelrijk et al., 1992), with the result that mating becomes more likely.

Additionally, Hemelrijk (1990b) found that a correlation between grooming and support was the result of correlations of these two variables with a third one, dominance rank, thereby again suggesting that grooming was not exchanged for support, but rather that both grooming and support in agonistic interactions were related to dominance rank. Moreover, 'support' in agonistic interactions could also be interpreted as an opportunistic manoeuvre of the supporter against a common rival (Hemelrijk & Ek, 1991).

The most convincing evidence for exchange comes from de Waal (1989b), who did a food-sharing experiment on a captive group of chimpanzees and found, after having controlled for the effects of proximity and dominance relationships, that an individual was more likely to share food with another if she had been groomed by the other one just before the food was supplied, but less likely to share with those she had been grooming before feeding. However, de Waal's study concerned captive chimpanzees, and his food-sharing occurred under fairly artificial provisioning conditions. Thus, even though he showed that chimpanzees can exchange food for grooming, it is not known whether they actually do so in the wild, or under more natural foraging conditions.

CONCLUSION

Social grooming is no doubt an important aspect of chimpanzee life. It is, therefore, surprising that the literature concerning this behaviour is generally unfocused and anecdotal. Moreover, it is very difficult to compare the available data on grooming from both field and captive studies due to differences in definitions and methodologies. An overview of the existing literature has revealed many aspects of chimpanzee grooming that still need to be elucidated, or revaluated. These are too numerous to be spelled out here, but include the very basic, definitional aspects of grooming, the ontogeny of grooming, the subtle changes in grooming with age or changing social situations, the reciprocation or exchange of grooming by grooming or other favours, the genetic determinants of grooming, and cultural differences in grooming. This dissertation will deal with the definition of grooming units, and with some aspects of grooming reciprocation in the presence and absence of oestrous females.

Table 1.I. Hierarchical representation of different units of grooming, based on the definitions by Nishida (1988). Nishida used the following criteria:
-session: complete interruption of grooming for at least 10 minutes.
-sequence: complete interruption of grooming for at least 10 seconds.
-bout: One-sided interruption of grooming for at least 10 seconds, or a change in the groomer-groomee roles.

LEVEL 1: GROOMING BOUT**

-bout duration
-bout frequency
-no. of bouts per sequence
-no. of bouts per session

LEVEL 2: GROOMING SEQUENCE**

-sequence duration
-sequence frequency
-no. of sequences per session

LEVEL 3: GROOMING SESSION*

-true session duration
-true session frequency

LEVEL 4: GROOMING TIME:

-% of observation time spent in grooming

note: at this level there is no true frequency measure, because a grooming unit is not operative.

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* Can be derived from time samples if Nishida's criterion is used.
**If Nishida's criterion is used, then time sampling is not feasable as the sample interval must then be <<10 sec.

Table 1.II. Sessions and bouts per observation hour, for three studies of mother-offspring grooming: Goodall (1968b, Fig.33), Clark (1977, Table 6) and Nishida (1988,Tables IV, V). A: mother-offspring grooming. B: offspring-mother grooming.

A		Age classes (years)					
		0-0.5	0.5-1	1-4.5	4.5-7	7-9	9-13
Goodall	sessions/h	0.29	0.23	0.079	0.071	0.18	0.42
Clark	bouts/h (totals only)	-	-	1.19	1.12	-	-
Nishida	sessions/h (totals only)	0.45	0.68	0.68	0.64	0.41	0.23

B		Age classes (years)					
		0-0.5	0.5-1	1-4.5	4.5-7	7-9	9-13
Goodall	sessions/h	0.00	0.014	0.043	0.093	0.17	0.26
	totals	0.29	0.24	0.12	0.16	0.35	0.68

Table 1.III. Total time spent in grooming for mother and offspring for Clark (1977) and Nishida (1988). A: mother-offspring grooming. B: offspring-mother grooming.

A				Age classes (years)			
		0-0.5	0.5-1	1-4.5	4.5-7	7-9	9-13
Clark	min/h	-	-	1.80	1.74	-	-
Nishida							
males	min/h	0.95	2.90	2.30	2.00	3.50	1.80
females	min/h	4.90	3.80	2.30	2.00	2.80	1.70
means	min/h	2.90	3.40	2.30	2.00	3.20	1.80

B				Age classes (years)			
		0-0.5	0.5-1	1-4.5	4.5-7	7-9	9-13
Clark	min/h	-	-	1.38	2.30	-	-
Nishida							
males	min/h	0.00	0.00	0.20	0.90	2.10	1.30
females	min/h	0.00	0.00	0.49	0.90	2.00	0.90
means	min/h	0.00	0.00	0.35	0.90	2.10	1.10

Table 1.IV. Additional measures of offspring-mother grooming, derived from Nishida (1988). A: males. B: females. C: means, i.e. (m+f)/2

A	Age classes (years)					
	0-0.5	0.5-1	1-4.5	4.5-7	7-9	9-13
average bouts/h	0.00	0.03	0.30	0.60	0.80	0.50
average sessions/h	0.40	0.80	0.73	0.60	0.50	0.25
bouts/session	0.00	0.038	0.41	1.0	1.60	2.00
mean bout length	0.00	0.05	0.30	1.50	1.80	2.60
N	2	1	7	4	3	8

B	Age classes (years)					
	0-0.5	0.5-1	1-4.5	4.5-7	7-9	9-13
average bouts/h	0.00	0.00	0.36	0.90	0.63	0.30
average sessions/h	0.50	0.55	0.63	0.68	0.33	0.20
bouts/session	0.00	0.00	0.57	1.30	1.90	1.50
mean bout length	0.00	0.00	1.10	1.40	3.00	3.10
N	1	2	6	4	1	1

C	Age classes (years)					
	0-0.5	0.5-1	1-4.5	4.5-7	7-9	9-13
average bouts/h	0.00	0.02	0.33	0.75	0.72	0.40
mean bout length	0.00	0.03	0.70	1.50	2.40	2.90
N	3	3	13	8	4	9

CHAPTER II

GENERAL METHODS

Subjects

This study is concerned with the behaviour of a captive group of common chimpanzees, living at the Scottish National Zoological Park of the Royal Zoological Society of Scotland, also called the Edinburgh Zoo. This group was unusual because it held five mature males who generally lived together in harmony, and it thus provided a unique opportunity to study the interactions between the males. Because of the relatively high number of males did this group provide a good model of the multi-male, multi-female communities found in the wild (e.g. Ghiglieri, 1984; Goodall, 1986; Nishida, 1979). In comparison, the captive group in Arnhem, the Netherlands, which has been studied extensively by de Waal (1982), Adang (1986), and Hemelrijk (1991), generally held no more than three adult males. However, the Arnhem group was larger, containing around 25 individuals, and had many more females and immatures of widely differing ages. The Edinburgh group had five mature males, but only three to five mature females, and there were wide age gaps in the group between the ages of approximately 1-13 and 16-26 (these ages apply to the beginning of the study).

Table 2.I lists individuals present in the group during part or all of the study. In the winter of 1990/1991 two infants, Sembe and Lope, were born. In the summer of 1991 two adult females, Cressida and Emma, were introduced into the group. In the winter of 1991 Sembe died, probably of pneumonia. In the spring of 1992 the older of the two immigrant females, Cressida died, presumably of kidney and lung problems. Thus, at the start of the study in October 1990 there were five males (four adult and one late adolescent), and three females (two adult and one late adolescent). When the observations finished in July 1992, there were five adult males, four adult females, and two infants.

Observations continued through most of these changes, but only the results of relatively stable periods are presented. For example, the period of introduction of the new females into the group has been omitted as the group was usually split into two sub-groups in order to allow a gradual acquaintance between the residents and the newcomers.

Although there were important demographic changes in the group, the five males were a constant factor throughout the study. Tom, who began as a late adolescent male, but matured by the end, was classed as a mature male throughout the study. Ricky, who spent his first five years as a sailor's pet, abnormally directed most of his dominance displays at people, especially one staff member of the Zoo's Education Department. Ricky's grooming technique also seemed different from that of the others: he almost always combed through the hair of his partners with only one hand, and didn't make picking movements. He rarely used his mouth, but often groomed with intense concentration and focused for long periods on one body-part only. Despite these abnormalities, his grooming was treated normally in the analyses. (Ricky groomed and was groomed despite his limited technique). Leo (and Cindy) took part in 'tea parties' that were held in the Zoo until 1973. However, they seemed very well integrated into the group as a whole and were therefore treated as normal.

The males were most likely not related to each other. Leo, Ricky, and Louis all came from different locations outside the Zoo, while Tom and David were born there. Ricky has never been observed to mate, and David's parents had died before the study began.

Tom and Lyndsey were both Cindy's offspring. Lyndsey was normally mother-reared but, due to maternal insufficiency, Tom was taken out of the group for hand-rearing when he was 14 months old (on 19/4/1979) and returned to group when he was almost 30 months old (on 1/8/1980). He did not have a typical mother-son grooming relationship with Cindy (Goodall 1986a; Kawanaka 1989), which suggests that they did not recognize each other as such. However, it must be noted here that Leo and Tom did have a special relationship, in which Tom would often actively seek the companionship of Leo, following him around the enclosures for considerable periods of time. Leo could theoretically have been Tom's father, but it is unlikely that they would have recognized each other as father and son after Tom's absence from the group. Moreover, there is no evidence of paternal recognition in chimpanzees.

Housing

The Chimpanzee House at the Edinburgh Zoo had two sections, an outdoor enclosure, and 14 indoor cages (Fig. 2.1). The indoor quarters were quite small (total of approx. 3 x 40 m., with the four largest cages measuring approx. 3 x 5 m.). They were fairly bare, apart from some ropes, tires, and straw. Light came through windows in the roof, but all cages had artificial lighting as well. The chimpanzees were behind metal bars and a wall with large windows, so that the public could be as close as 1.5 m. without any physical contact, and without being able to feed the chimpanzees. The glass windows also reduced the noise level for the chimpanzees, but at the same time made it impossible for an observer to hear soft vocalisations, such as laughing, or tooth-clapping.

The outdoor enclosure consisted of a single space of approx. 38 x 17 m. and contained an extensive metal climbing frame, several dead tree stumps, ropes, tires, rocky and grassy surfaces, and a dry moat (Fig. 2.1). The public could view the chimpanzees through windows from the same passageway from where the chimpanzees could been seen in their indoor cages. There was also an outside viewing area at the north end of the enclosure, where the chimpanzees could be seen from a minimum distance of approx. 15 m., with a green zone between this viewing area and the north wall of the enclosure. This distance was created to discourage the public from feeding the chimpanzees. The Zoo was situated on a hill, so that from the outdoor vantage point the spectators looked down into the outside enclosure. There was restricted access to the area directly behind the northern wall, which was used by the keepers to feed the chimpanzees in their outside enclosure, and by students for behavioural observations.

The chimpanzees could move between the indoor and outdoor enclosures through tunnels, which ran over the public passageway. Normally, they had access to both enclosures, 24 hours a day. However, when there were management procedures in operation, for example when the cages were cleaned every morning, or one of the chimpanzees had to be isolated for medical treatment, access would be limited to only the outdoor enclosure or one or two of the indoor cages.

Environmental enrichment

During the present study a few short term studies were carried out by other students. These were generally purely observational, but some were concerned with environmental enrichment, so that now and then apparatus was added to the enclosures to make life more interesting for the chimpanzees.

At the outset of this study, there was already an artificial termite mound in the outdoor enclosure. This consisted of a concrete mound, with several holes for dipping. The holes were usually filled with a mixture of milk powder and water, and sometimes with lemonade, mustard, or honey. Later on another food-getting task was introduced, consisting of a metal tube, about 10 cm in diameter, open at one end, and with small side-holes running along its length. One of these tubes was affixed to the climbing frame outside, and one in the indoor cages. The tube would usually be filled with candy bars (wrapper and all) which had to be taken out by inserting a small stick in the side-holes, thereby slowly pushing the bar towards the open end of the tube, until it would be possible to take it out by hand. Indoors, two other devices were used to encourage the chimpanzees to use sticks in order to obtain nuts.

Finally, a lemonade-dipping device was introduced indoors, in which the chimpanzees had to use sticks to dip the lemonade. When these devices were in use, they were usually filled up in the morning, and fully emptied by the early afternoon. When there were no students working on these varying projects, the devices were only filled rarely and irregularly for reasons unknown to the author.

Food and feeding

Apart from the food-stuffs mentioned above, the chimpanzees were fed in the early morning, at noon, at the end of the day and at irregular intervals in between. Food consisted of several kinds of vegetable, fruit, and nut, and monkey chow. Sometimes they were given yoghurt or fresh leafy branches, and twice live grasshoppers. On some occasions they were given one kind of food, for example apples or carrots. At other times different foods were given in one feeding session. Dependent on the weather they would be fed indoors, or outdoors. Frequently, feeding time was associated with loud vocalisations, general excitement, kissing and embracing. At other times there was only a mild response from the chimpanzees. Sometimes aggression would break out in the anticipation of food, and the chimpanzees would only settle down a while after the food had been thrown into their enclosure. Rarely were there serious conflicts over particular food items.

The chimpanzees were fed at irregular times in an attempt to reduce the predictability of feeds. Food was always scattered throughout (large portions of) the enclosure in order to minimize competition. In the mornings, after the outdoor enclosure would be cleaned, food would often be hidden in different places, so that the chimpanzees had to search for it.

All these management routines of feeding, including the environmental enrichment devices were ignored in the analyses of the data. It was assumed that their timing would not have an overall effect on the results of this study. In practice, when a chimpanzees was working on a food device, it was recorded as 'feeding', and when the keeper would come to feed the group, this was recorded as 'provisioning'.

Observation points

Observations were carried out either from the public passageway, from where both indoor and outdoor enclosures could be monitored, or from the restricted access area at the northern wall of the outside enclosure, from where the chimpanzees could be observed only when they were outside. Outside, use was made of binoculars (8 x 40), to allow details of interactions to be scored accurately at long distances.

There were several places in the enclosures where a chimpanzee could not be seen at all. For example, when the chimpanzees would commute between the indoor and outdoor enclosures, they had to pass through the tunnels over the public passage way, in which they were totally concealed. Furthermore, outside there were several large objects, such as the termite mound and several tree trunks, behind which a chimpanzee could not been seen from at least one of the two observation points. A chimpanzee moving in the dry moat was impossible to see from inside and very difficult to observe from behind the outside wall. In the indoor cages the chimpanzees were almost completely out of sight when they climbed high up, above the viewing windows.

As this study was not concerned with individual chimpanzee's time budgets, it was not necessary to compensate for invisibility by increasing the observation time. Moreover, it was rare for two chimpanzees to disappear from view in the same place and at the same time, so that data on grooming was not affected.

Observation methods

There were six observation phases (Table 2.II) The data presented here concern only phases 2 and 6. The pilot phase (1) was when the observer became familiar with the chimpanzees and their behaviour, learned to identify all individuals, and experimented with different sampling methods. On the basis of these observations it was decided that grooming would be suitable for a study of reciprocity in this group, because it occurred frequently and consumed a considerable amount of the chimpanzees' time. The 'no competition' (2) phase was a period in which no females were in oestrus, resulting in the absence of sexual competition between the males. Data on the introduction of the two new females (3) are not used here for reasons outlined above (see section 'Subjects'). Focal animal phases (4 & 5) included periods of oestrus and were designed to obtain data on the intensity of grooming (see below). The last observation phase (6) was designed to obtain data on consecutive grooming sessions.

In general, in all but the last phase of this study observations were done opportunistically. All occurrences of behaviour sampling was used in phases two and six, focal animal sampling in phases four and five (Altmann, 1974; Martin & Bateson, 1986). Observation periods were focussed around times when the chimpanzees were grooming or active in other ways. This was possible because there was usually much synchronization of the activities of the chimpanzees, probably resulting from the relatively small living quarters, in which it was quite difficult for an individual to do anything without the others getting involved, or at least taking notice. This applied especially to very active behaviours, such as play and aggression, and also to grooming. Non-aggressive excitement, such as the loud vocalisations on the arrival of food were often given in concert as well. When there was general inactivity, observations were usually suspended and resumed later. Also, when the chimpanzees were being fed, or when observations were seriously disrupted by the public (this could only happen at the indoor observation point) observation were interrupted.

The second observation phase: no male-male competition

This study was at first intended as a broad analysis of reciprocity in chimpanzees against a theoretical background of the evolution of cooperation, and of evolutionary stable strategies such as TIT-FOR-TAT. In this context, all behaviours that could possibly be involved in reciprocation in chimpanzees, such as play, sex, sharing of food, antagonism, support in fights, and grooming were considered to be of importance and therefore recorded. However, it soon turned out that most of these behaviours did not occur sufficiently frequently (sex, food-sharing, antagonism, support in fights), or were not sufficiently clearly directed (play) to yield a valuable data set. In contrast, however, grooming was easily defined, observed relatively frequently, had a measurable duration, and a clear direction. Thus it was decided to make grooming the primary object of this study.

An all occurrence sampling method (Martin & Bateson 1986) was used to obtain as large a record of grooming as possible. All occurrences of grooming were recorded with pen and paper, using a digital stopwatch, noting down exact starting and stopping times, besides the identity of the individuals involved. The original records were later transcribed to checksheets, which were subsequently put into the computer (StatView on Macintosh) for analysis.

During observation sessions I would constantly walk around, keeping all individuals monitored, and recording whenever I observed grooming. As many details as possible of the grooming interactions were recorded, and it even proved feasible to record more than one grooming interaction at the same time. However, the more chimpanzees were involved in grooming, or the more dynamic a grooming session between two individuals was, the more difficult it became to record anything in addition to who groomed whom, and when. Thus, even though I recorded which body parts were groomed, which hands were used, what position the groomers were in, I found that these additional records were unsystematic, and their accuracy depended on the nature and number of grooming sessions that were going on at the same time. They were, therefore, not used in the analysis of the all occurrences samples.

When there was no grooming, I recorded mainly aggression, sex, and feeding times, also on an all occurrences of behaviour basis. The accuracy of all occurrences samples of behaviour depends on the duration, frequency and conspicuousness of the behaviours recorded. Thus, probably all aggression was recorded, but the details of the interaction were sometimes unclear, either because of very short bursts of aggression, or because too many individuals were involved. As the records of copulations were probably biased against individuals that copulated secretively, they were not used. Aggression was defined narrowly (see Chapter VI) so as to minimize errors of identification that would have resulted from complicated polyadic agonistic interactions. More details of hours and duration of observation sessions in phase two will be given in Chapter IV.

The fourth and fifth observation phase: focal animal samples

The fourth and fifth observation phases were combined to give one data set of focal animal samples. These samples were taken with the following purposes in mind:

- to obtain a straight-forward measure of the time each individual spent in grooming, in order to be able to evaluate the efficiency of the all-occurrences samples used in the second observation phase.
- to investigate the reciprocity of grooming by recording consecutive grooming sessions between the same two individuals.
- to provide details of the intensity of grooming, by recording the grooming techniques as described below.

The initial plan was to observe each chimpanzee for four consecutive hours, on three consecutive days, making for a total of 12 hours of observations per chimpanzee. Dependent on the amount of data needed, this could be repeated several times. The rationale behind observing one individual over three days in periods of four hours, instead of observing all chimpanzees every day for a shorter period of time was that it would be the only sampling method most likely to yield data on consecutive grooming sessions between the same two individuals, while at the same time allowing the details of an individual's grooming to be recorded.

In practice, these focal animal samples were seriously confounded in several different ways. First, during this observation phase there were sometimes one or more females in oestrus present. Thus, the results of this phase cannot easily be used as a standard against which to measure the efficiency of the all-occurrences samples of the second observation phase. Moreover, the cycles of those females were quite irregular. Thus, as the onset of oestrus could not be predicted, one three-day focal period sometimes consisted of one day without an oestrous female and two with an oestrous female or vice versa, with the result that not all individuals were observed for comparable amounts of time in periods with and without oestrous females.

Second, there were major problems with the recording techniques employed in the focal animal samples. As one of its purposes was to record details of an individual's grooming technique (as a measure of grooming intensity) it was imperative to be able to record very quickly. Thus, as written notes proved to be insufficient, a tape recorder was used to record the grooming technique of the focal animal, without having to look away from the grooming. Unfortunately, these audio recordings often became obscured by the sounds of noisy visitors.

Therefore, a pocket PC was programmed with 'Keybehaviour' (Deag, 1990), and used to record observations directly onto a memory card. Unfortunately, the analysis of these records turned out to be extremely complicated (mainly because the PC was programmed to record grooming involving all the other chimpanzees as well, for periods in which the focal animal was inactive). Moreover, the DIP 512 Pocket PC often failed to operate properly, resulting in a loss of approximately 20 hours of focal samples, in addition to many other samples being terminated prematurely.

Finally, it seemed that not all chimpanzees were equally well habituated to observers, and the presence of one observer who would follow them for three consecutive days often seemed too much of a disturbance, so that they would frequently glance at the observer and then disappear from view for prolonged periods of time.

In summary, even though a total of approximately 118 hours of focal samples were collected, the quality of these records was seriously affected by the unpredictable nature of the females' sexual cycles, by the unsuitability and faultiness of the recording techniques and equipment, and by the different degrees of habituation of the chimpanzees. It was therefore decided not to use these data here.

The sixth observation phase: joint project

The aim of this project was to gain insight into the dynamics of grooming reciprocation in the course of consecutive sessions between the same two individuals, and to investigate the influence of the social context (aggression, provisioning, and oestrous females) on the dynamics of grooming reciprocation.

To this end observations were carried out full-time in periods of three to five consecutive days. There were two observers, Miss D. Wardill (who was supported by an A.S.A.B. summer grant), and the author, who alternated observations between them. Usually, one of us would observe the first two hours of the day, then we would alternate every hour until the other would observe the chimpanzees for the last two hours of the day.

After a pilot study of one week, in which again focal animal samples were tried out, we agreed that these would not provide sufficient amounts of grooming data to make an analysis of consecutive sessions possible. Thus, during the main study, we employed an all occurrences of behaviour sampling method, using the ethogram of the second observation phase (see below). However, as data from the second observation phase indicated that there was almost no reciprocation of grooming between the females, we focussed on the males only. Thus, using an all occurrences of behaviour sampling we obtained data on male-male grooming, as well as on the general activities in the group.

Dominance

The Edinburgh chimpanzee group was demographically unusual. The sex ratio was approximately 1:1 and the age distribution showed two gaps of approximately 10 years each: between the ages of 1-13 and between the ages of 16-26. At Gombe, the male:female ratio has fluctuated between 1:1 and 1:3 (Goodall, 1986a). Thus, the ratio of males to females at the Edinburgh Zoo was not outside the naturally occurring range at Gombe. It was, however, high compared to the sex-ratio in the captive Arnhem group (de Waal, 1982). During the second observation phase there was little serious aggression among the males, however, and most aggression was directed from males to females. There may be at least two explanations for the virtual absence of aggression during this period. Firstly, there was almost no competition for food, not only because there was enough food for all, but also because the food was usually scattered throughout the enclosure(s), making it impossible to monopolise. Secondly, there was no sexual competition during the second phase, as both mature females had newborns and were, therefore, not sexually active. The remaining female was not yet sexually mature.

During the remaining observation phases some of the females were sexually cycling, but aggression, although more pronounced, was never as serious as in the Arnhem group (de Waal, 1986a). The low levels of aggression made it difficult to arrive at a clear dominance hierarchy among the males. During conflicts it was typically Leo and David who displayed most vigorously. Usually Leo, accompanied by Tom, would charge over the ground from one end of the outside enclosure to the other end, dragging branches and swinging tires. At the same time, David, Louis and Ricky would be on top of the climbing frame, David displaying, Louis looking on, and Ricky frequently escaping to the top of the telegraph pole. From these and similar observations it became clear that Leo and David were both dominant over Louis, Ricky and Tom, and Louis seemed dominant over Ricky and Tom. However, the exact relationships between Leo and David on the one hand, and Ricky and Tom on the other could not be accurately determined.

Other indications of dominance relationships, such as bowing and pant-grunts (van Hooff 1974; de Waal 1989a; Goodall 1986) were virtually absent throughout the study. However, as dominance plays such a vital role in the social lives of chimpanzees it is important to rank the males. Social status probably affect the benefits of grooming and being groomed and therefore the dynamics of reciprocation. As dominance is correlated with age (Bygott, 1974), I decided to consider the oldest of the two undetermined pairs as dominant. Thus, Leo was considered dominant over David, Ricky over Tom, resulting in the hierarchy presented in Table 2.I. However, as the dominance relationships between the males in this captive group were relatively ambiguous, some of the results will be presented without taking dominance into account.

Ethogram

Categorisation of behaviours was based on van Hooff (1974) and Goodall (1986a). However, instead of always recording every single unit of behaviour, often only the broad motivational system to which the observed behaviour belonged was noted down. For example, when two chimpanzees were playing with one or both of them showing a playface (or 'relaxed open-mouth face' (van Hooff, 1974)), this would be recorded as 'play', and not as 'individual A shows playface'.

When there was a conflict involving all five males, it was often impossible to work out what exactly had happened. In that case, as much detail as possible would be recorded, but in the analyses only those details have been used that were likely to have been recorded accurately. For example, attacks were usually clear events, whereas mounting and embracing often happened in quick bouts, involving more than two individuals, thereby decreasing the accuracy of the record. Thus, the ethogram presented in Table 2.III lists the behaviours that were distinguished in the observations, and how they were recorded. (During the fourth and fifth phases, additional details of the grooming techniques of the chimpanzees were recorded (Table 2.IV), but data of these phases will not be presented here).

Inter-observer reliability

During the sixth observation phase, there were two observers, Ms.Wardill and the author. As Ms.Wardill already had some experience with observing this group of chimpanzees she had no difficulties identifying each individual. Therefore, inter-observer reliability for individual recognition was not determined.

In order to make maximum use of the available time for observations, we never observed the chimpanzees at the same time and it is thus not possible to compare records directly. However, as an indication of inter-observer reliability I calculated the total time spent in unilateral and mutual grooming for each male-male dyad, and correlated Ms Wardill's scores with my own. The results indicate a high level of concordance between the two observers (Spearman rank-order correlation coëfficient: unilateral grooming by the first of the dyads ($N=10$): $r_S=0.794$, $0.01>p>0.005$; by the second of the dyads: $r_S=0.900$, $p<0.001$; mutual grooming: $r_S=0.830$, $0.005>p>0.002$).

Statistics

The data were analysed at the levels of the group and the dyad. For the group, analyses were always done over the entire observation phase. At the dyadic and individual levels, however, data were also analysed over shorter periods, such as a week, day, or grooming session.

On the group level, matrix correlation tests were used, as described by Hemelrijk (1990a). A significance level of $p \leq 0.10$ was used for these tests.

A new method was developed in order to allow statistical analyses at the dyadic level (Chapter III), and only non-parametric statistics were used, as the number of subjects was small and no assumptions could be made about the normality of distribution of behaviour in the group, or over the dyads. I have used the Kruskal-Wallis one-way analysis of variance by ranks, the Friedman two-way analysis of variance by ranks, the permutation test for paired replicates, and Spearman's rho (Siegel & Castellan, 1986). A significance level of $p \leq 0.05$ was used here.

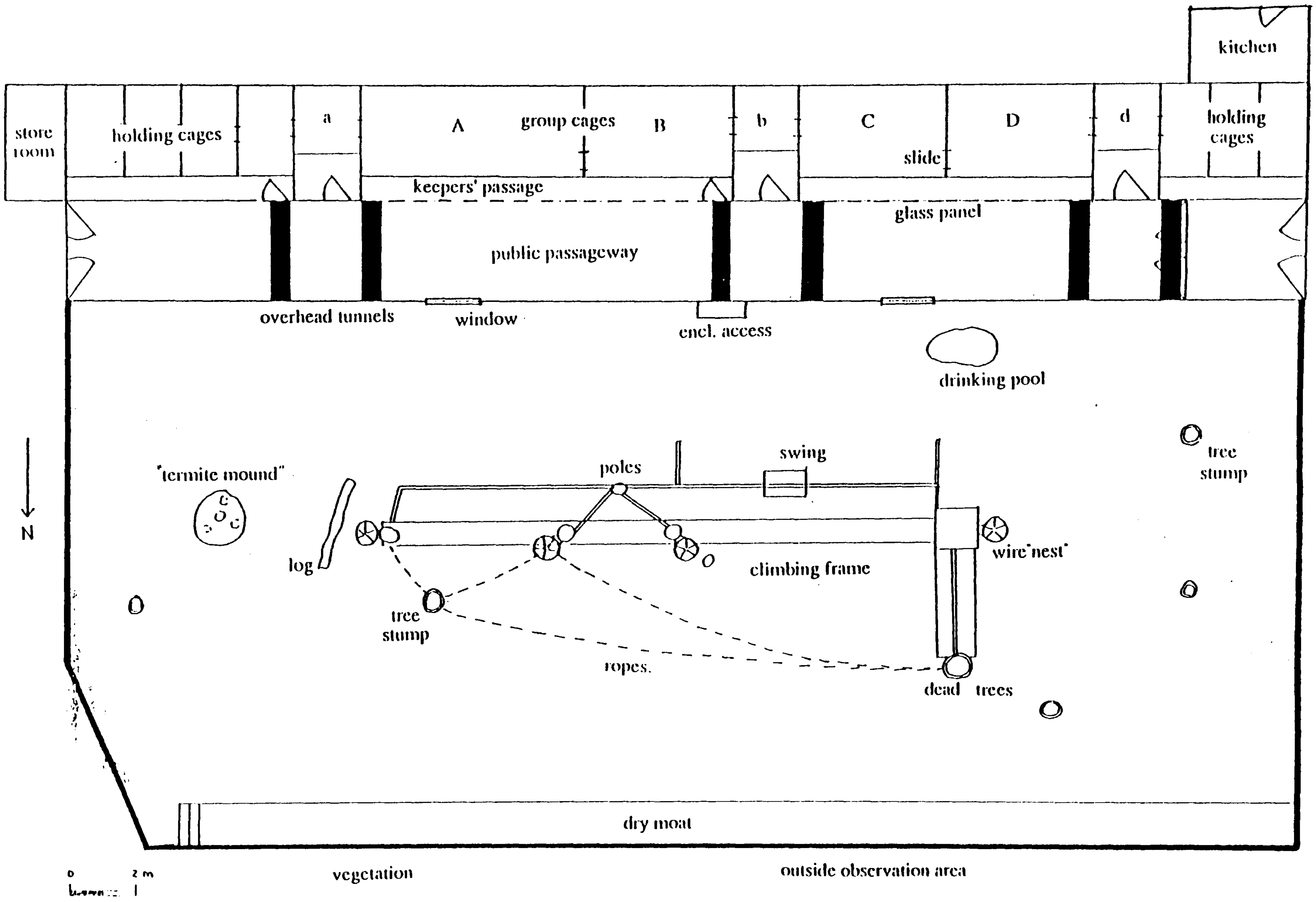


Fig. 2.1. The chimpanzee house of Edinburgh Zoo. Indoor and outdoor enclosures (taken from Tierney, 1990).

Table 2.I. The chimpanzees of the Edinburgh Zoo, October 1,1990 to July 10, 1992. Dominance ranks indicate most likely hierarchy, see text for details.

NAME	SEX	BIRTHDATE (D-M-Y)	COMMENTS	PRESUMED DOM.RANK
Leo	Male	1965?	Wild born	1
David	Male	02-03-1975	Edinburgh born, hand-reared, reintroduced at 3 years.	2
Louis	Male	1976?	Wild born, Sierra Leone	3
Ricky	Male	1961?	Wild born	4
Tom	Male	10-02-1978	From Cindy. Hand-reared from 19-04-1979 to 31-07-1980	5
Cindy	Female	1964?	Wild born	6
Cressida	Female	1967?	Wild born, Introduced April 1991, died 7 May 1992	7
Lucy	Female	11-11-1976	Edinburgh born	8
Emma	Female	1981?	Captive born, Introduced April 1991.	9
Lyndsey	Female	24-12-1983	From Cindy	10
Sembe	Female	22-12-1990	From Cindy, died 8 March 1992	-
Lope	Female	14-01-1991	From Lucy	-
Quafzeh	Male	31-03-1992	From Emma	-

Table 2.II. The six phases of observations, with dates and total number of observation hours.

Observation periods	Dates	Observation hours
1. Pilot study	19/11/1990 - 18/12/1990	45
2. No competition	28/12/1990 - 16/4/1991	111
3. New females	18/4/1991 - 24/6/1991	47
4. Focal animals, notes	4/11/1991 - 27/2/1992	50
5. Focal animals, computer	25/2/1992 - 8/4/1992	68
6. Whole days, joint project.	1/6/1992 - 10/7/1992	187
	Total	508

Table 2.III. Ethogram used in the observations on the chimpanzee group of Edinburgh Zoo. Behaviour was often recorded as broad motivational systems, rather than as single units. Adapted from van Hooff (1974). For more extensive descriptions of some of these behaviours, please see van Hooff (1974) and Goodall (1968b). If nothing between brackets, behaviour was recorded as observed.

BEHAVIOUR OBSERVED (RECORDED AS)	DEFINITION
RELAXED OPEN-MOUTH FACE (PL)	Have mouth open, teeth covered by lips.
GNAW-WRESTLE (PL)	Two or more individuals grasp or gnaw at each other in a boisterous, but free-and-easy way.
PULL LIMB (PL)	Get hold of, and pull or shake other's limb
GNAW (PL)	Make repeated gnawing movements onto another's limb or body.
HAND-WRESTLE (PL)	Two individuals grasp each other's hand or foot, while trying to wrest away from the other's grip
GALLOP (PL)	Fast, but restrained trot, not at full speed. No pilo-erection
BITE (AG)	Brusque biting or snapping movements, directed at another.
HIT (AG)	Arm is usually brought down with force on another individual. Includes hitting with objects.
TRAMPLE (AG)	Jump on top of another and stamping on the other's back.
STAMP (BF)	Stamp with feet or slam with hand on ground or resounding object.
SWAY-WALK or BIPEDAL SWAGGER (BF)	Bipedal walk with arms extended to the sides, and pilo-erection.
MOUTH-MOUTH (BG)	Put mouth close to the mouth of another, who is eating or chewing, and staring at the other's lips.
EMBRACE	Clasp another's body by putting arms around it while standing or squatting.
KISS	Open mouth silent bared-teeth face accompanied by mouth-mouth, or mouth-body contact.
HOLD OUT HAND	Extend arm toward another in a more or less horizontal position, without touching.
GROOM	Pick at the skin or combing through the hair of another chimpanzee, using hands and/or mouth.
GROOM-PRESENTING	Present some part of the body after approaching another individual.
AUTOGROOM	Pick at the own skin or combing through the own hair, using hands and/or mouth.
MALE MATING	Intromission, followed by pelvic thrusts.
COURT	Sway, stamp, hand-shake, while staring intently at a female, by a male with penile erection.
RAPID 'OH OH' SERIES (EX)	Breathy and slightly rough grunts delivered in rapid succession.
SQUAT-BOBBING (EX)	Squat near another, while making bobbing movements with the upper body.
RISING HOOT (EX)	Gradual build-up of 'hoo'-like sounds, gradually increasing in speed and volume, and rising in pitch.
VERTICAL HEAD SHAKE (EX)	Move the head up and down
BARED TEETH SCREAM	Mouth open, lips retracted, with high-pitched, intense screams.
FEEDING	Put food in mouth, or trying to obtain food from an environmental enrichment device.

PL=PLAY; AG=AGGRESSION; BG=BEGGING; EX=EXCITEMENT; BF=BLUFF

Table 2.IV. Techniques of grooming as recorded in the fourth and fifth observation phases.

BEHAVIOUR RECORDED	DEFINITION
MOUTH 1	Application of the lips, tongue, or teeth to the skin of the partner.
MOUTH 2	Put particles, which have been picked from the other's skin or hair, in own mouth.
BOTH HANDS	Use both hands in grooming, rather than just one hand, or just the mouth.
LOOK-UP	Look away from the grooming, thereby moving the whole head, not just the eyes.

CHAPTER III

METHODS: ANALYSIS OF GROOMING RECIPROCATION IN DYADS

Matrix correlation tests

Mantel's Z statistic (Mantel, 1967, in Hemelrijk, 1990a), the R statistic (Hemelrijk, 1990a), and the K statistic (Hubert, 1978, Dietz, 1983, in Hemelrijk, 1990a) were used to test for reciprocity on the level of the group (Hemelrijk, 1990a). These tests indicate whether or not there was reciprocity of a certain behaviour within the group or not, by correlating a matrix of 'behaviour given' with its transposed form of 'behaviour received'. Calculations were done with Hemelrijk's (1990a) 'Matsquar' program. It thus becomes possible to find out whether there was 'relative reciprocity', that is whether individuals tended to give more to those from whom they also received more, or 'absolute reciprocity', that is whether the actual amounts given and received were similar. In the first case, individual A gives B more than C and receives more from B than from C. However, A may have given B ten times as much as he received from B, and given C only three times as much as he received from C. For example, A received 10 units from B, 2 from C, and gives 100 to B, 6 to C. In the second case of absolute reciprocity A gives as much to B and C as he received from them respectively.

Comparative and interactive reciprocity

The actor-receiver model forms the basis of the matrix correlations mentioned above. A significant outcome of the K_r statistic (Hemelrijk, 1990a) indicates that there is 'relative' reciprocity. That is, individuals give more to those from whom more was received, irrespective of the exact amount that was received. The Mantel Z statistic tests for 'absolute' reciprocity. However, as the outcome of the Z statistic can be biased by the existence of only a few extreme values, it is best to use it in combination with the R statistic. A significant outcome of both Z and R statistics indicates that the amounts given and received were similar. (For a more detailed explanation of why the Mantel Z and R statistics can best be used together, see Hemelrijk, 1990a)

The matrix correlations do not imply anything about reciprocity at the dyadic level. It is, therefore, somewhat confusing that Hemelrijk presents models (see Introduction) that state how *individuals* reciprocate. She seems to imply that the matrix correlations, when significant, show that there is reciprocity in the group according to the actor-receiver model, that is, each individual compares what he received from the other, and subsequently gives back most to the one that gave him most, and least to the one that gave him least.

However, this may not be true for behaviours that can be reciprocated almost immediately, such as grooming. If an animal tends to return grooming as soon as he receives it, he does not need to compare the grooming he just received with the grooming he received from the others before. If data of this nature are analysed at the group level, matrix correlations will all be significant, indicating both relative and absolute reciprocity, but the actor-receiver model would not apply.

Here reciprocity at the dyadic level means that an individual gives more to another individual when he received more from that *same* individual. To distinguish between the two different meanings of the term 'reciprocity', the first, as used by Hemelrijk for the group level, will be termed 'comparative reciprocity', because it seems as if each individual compares what he received from all others and then gives back more to those from whom most was received.

The second form of reciprocity will be termed 'interactive reciprocity' because an individual gives more to another individual, the more he receives from that other. It follows that interactive reciprocity can lead to comparative reciprocity: if an individual operates on the basis of interactive reciprocity with all his partners, that is if he tends to groom each of them more, the more grooming he receives, then this will result in comparative reciprocity, in which those from whom more was received were also given more. However, a chimpanzee does not need to compare the grooming he received from the other members in the group to know to whom to give more grooming. If he operates on the basis of interactive reciprocity, he only needs to groom an individual more the more he is groomed by that individual.

Another problem with the matrix correlations is the absence of a criterion for the strength of the effect. When the result of the tests is significant, there is certainly an effect. However, it is not clear whether the effect is strong or weak (see Martin & Bateson, 1986).

Analysing at the dyadic level

As Hemelrijk's statistical method applies to the level of the group only, it says little about how individual chimpanzees reciprocate. An analysis at the dyadic level, i.e. the level of the pair is necessary to obtain insight into an individual's ways of reciprocation. Hemelrijk (1990b) gives, however, three major reasons for not analysing at the dyadic level:

1. Even though reciprocity at the dyadic level, that is, the existence of alternating bouts of giving and receiving, could be tested for by means of a runs test, the underlying assumption that opportunities exist to alternate the behaviour may not always hold (for example, for a behaviour such as support in agonistic interactions it may not, whereas for grooming it usually will).

2. Reciprocity at the dyadic level could also be investigated by looking at the balance of given and received acts over a certain time span, and using a binomial test to determine whether reciprocity (i.e. a balance) does indeed exist. However, this results in a faulty statistical procedure, because reciprocity is thus confirmed by accepting, instead of rejecting, the null-hypothesis.

3. Dyads will only be statistically independent if they are exclusive. That is, for statistical correctness, no individual should occur in more than one dyad. This raises practical problems if the study group is small.

Although all these objections are valid, they are not necessarily final. I will comment on them in the reverse order from that above.

First, there is unfortunately no objective criterion to test for the degree of statistical independence, and it could be argued that even individuals living in the same group are not statistically independent (Martin and Bateson, 1988): they live in a similar habitat, with the same individuals, in the same 'culture'. Furthermore, the question of statistical independence also depends on how social interactions are to be understood: they can be interpreted as a sum of two individual's behaviour, or as a higher level of complexity, with new characteristics, that cannot be predicted from individual behaviour only. It may be possible to explain relationships in terms of individual behaviour, yet the relationships may not have been predictable from individual behaviour (Hinde, 1976). If social behaviour has a dimension that is based on more than just the sum of two individuals' behaviour, then it may be justified to consider relationships, i.e. dyads, as independent of each other.

Second, using a binomial test over a certain time-span, in an attempt to affirm the null-hypothesis that the amount given was equal to the amount received indeed results in faulty statistics. A way to circumvent this problem is by defining an (arbitrary) criterion of reciprocity. For example, Nishida (1988) used a reciprocity index by time (RIT), defined as the difference in grooming given and received, divided by the total duration of grooming. He defined 'virtual reciprocity' (arbitrarily) as $RIT \leq |0.2|$. This index can then be used to compare the grooming of a particular dyad between different periods and over different time-spans, or to compare the grooming of different dyads with each other, without having to use a binomial test.

Third, the objection that there might not be an opportunity for alternation between the individuals of a dyad does not necessarily apply to grooming. Chimpanzees especially often have bidirectional grooming relationships in which two individuals groom each other alternatively. This is one of the reasons that grooming is suitable for an investigation of reciprocity at the dyadic level.

Thus, reciprocation of grooming at the dyadic level can be analysed by using a runs test on consecutive grooming bouts, or by using an index of reciprocation. However, these methods do not take into account that grooming in chimpanzees can be reciprocated both sequentially (i.e. in turns) and mutually (i.e. simultaneously) within a session. In order to gain an understanding of the different roles that sequential and mutual grooming may fulfil in the reciprocation of grooming at the dyadic level, a method was developed which takes the different ways in which grooming can be reciprocated into account. In the following sections I will outline this method.

Definitions of grooming and grooming session

I define allo-grooming as the movement of the fingers, finger nails, lips, tongue, or teeth through the hair, or on the skin of another individual, but excluding scratching, which is the repeated movement of the whole arm while the fingernails scrape over the skin, or the repeated bending/flexing of one or more fingers over the skin. In practice the distinction between social grooming and scratching was unproblematic (in contrast to the distinction between self-grooming and scratching; Kraemer, 1979a), as scratching was always directed to the self. The intensity of social grooming varies, from a mere lazily combing of the hair, to detailed manipulation of the skin combined with close visual inspection (Goodall, 1968b, 1986a; van Hooff, 1974; McGrew & Tutin, 1978; Ghiglieri, 1984).

One of the aims of this study was to determine if the two partners in a grooming episode adjust their grooming to each other. The most direct way to analyse this is to test for correlation between the grooming by both partners over a number of grooming episodes. This is only possible if the total grooming observed between two individuals in a particular study is somehow split into smaller units or 'sessions'. The size of these units can vary. Thus, at one extreme of the spectrum it would be possible to interpret the total grooming between two individuals in a particular observation phase as one data point, and to carry out the correlation over several such observation phases. Alternatively, the analysis could be carried out over days, or, at the other extreme of the spectrum, over grooming bouts, in which a bout is defined as the period in which there is no change in the configuration of grooming (i.e. unilateral, mutual).

Obviously, the choice of the unit of grooming determines the number of data points available for analysis, and has an influence on the outcome of the correlations as well. For example, choosing a large unit of grooming (an observation phase) will reduce the number of available data points, each of which is a good sample, based on a relatively large amount of grooming. With the choice of a small unit of grooming (bout) a larger data set is obtained, but each data point represents one single occurrence of the behaviour.

The interpretation of the outcome of the correlations will also vary according to the size of the chosen unit. A large unit will say little about the immediate interaction between the chimpanzees and may well obscure more subtle processes that can only be revealed by a more detailed analysis. A small unit, such as a bout, (by definition) never contains more than one configuration of grooming and can, therefore, not be analysed by ways of simple correlational techniques, but needs some sort of sequential analysis. Finally, the smaller a unit of grooming is chosen, the more tedious the analysis will be.

In past studies, several criteria have been used to distinguish between different grooming sessions. For example, Goodall (1986a) used an (arbitrary) two minute period of no grooming as an indication of the end of a session, and Nishida (1988) used a 10-minute criterion for the same purpose (see Chapter I).

The best method for determining the bout criterion interval (BCI) for any behaviour is to carry out a log-survivorship analysis. (Note that the term 'bout criterion interval' is used here to denote a criterion for distinguishing between grooming *sessions*, rather than grooming *bouts*. However, 'bout criterion interval' is retained because of its general use in the literature, and a grooming *bout* will be defined separately, below). In the case of grooming, one would plot the logarithm of the number of interruptions larger than t, against the duration t of those interruptions. The BCI can then be determined by visual estimation of the point at which the slope of the graph changes most rapidly (Martin & Bateson, 1988). A better method to determine the BCI is to minimise the number of within-bout interruptions assigned as between-bout interruptions and the number of between-bout interruptions assigned as within-bout interruptions (Slater & Lester, 1982).

Figure 3.1a&b shows the log-survivorship plots for the second and sixth observation phases. Both plots have a steep part in the region of short interruptions in grooming, and a gradual part in the region of longer interruptions. The equations for these parts were found by extrapolation in Macintosh Cricket Graph, and were derived for the ranges of 10s. - 1.5 min., and 10 - 30 min. for phase two, 10s. - 1.5 min. and 12 - 440 min. for phase six. The general forms of the equations are:

Within bouts: $y_w = N_w \cdot 10^{(-ß_w)x}$ $R^2=p$

Between bouts: $y_b = N_b \cdot 10^{(-ß_b)x}$, $R^2=p$

in which N_w and N_b are the number of within bout and between bout interruptions respectively, $ß_w$ and $ß_b$ the rates of the processes generating them, with R^2 indicating goodness of fit, and $0 \leq p \leq 1$. The bout criterion t' can now be determined by:

$$t' = 1/(ß_w - ß_b) \cdot \log(N_w ß_w / N_b ß_b)$$ (Slater & Lester, 1982).

The number of misassignments by:

$N'_w = N_w \cdot 10^{(-\beta t')}$ (within wrongly classified as between)

$N'_b = N_b \cdot (1-10^{(-\beta t')})$ (between wrongly classified as within)

For practical purposes, t' was rounded to the nearest five minutes. Thus, the equations for observation phase two were determined as:

Within bouts: $y = 289.08 \cdot 10^{(-0.2711)x}$ $R^2=0.971$

Between bouts: $y= 94.049 \cdot 10^{(-2.7579e-2)x}$ $R^2=0.972$

BCI: $t' = 6.08$ min. (rounded to 5 min.)

$N'_w = 7$

$N'_b = 30$

and for observation phase six as:

Within bouts: $y = 696.20 \cdot 10^{(-0.11435)x}$ $R^2=0.937$

Between bouts: $y= 355 \cdot 10^{(-5.9304e-5)x}$ $R^2=0.994$

BCI: $t' = 31.9$ min. (rounded to 30 min.)

$N'_w = 0$

$N'_b = 1$

This latter criterion is almost six times that of observation phase two. This difference is probably partly due to the different durations of observation sessions, which were probably too short in the second phase to detect the higher criterion. However, the difference is too large to be thus explained away.

A major difference between the two observation phases was the presence of oestrous females in the sixth phase. This may have resulted in an increase in the frequency of grooming between males and females, as well as between the males as a result of sexual competition.

Thus, the chance of grooming to resume after 6 min. interruption was much higher in the sixth observation phase than in the second. In other words, grooming bouts in phase six were interrupted for longer than in phase two, without that interruption indicating the end of the bout.

Some problems with the log-survivorship method for determining the bout criterion interval remain. First, as indicated above, the accuracy of the method depends on the duration of the observation sessions. Short observation sessions are unlikely to pick up on a large BCI. Furthermore, there is a 'border effect', where interruptions in the behaviour approach the duration of the observation periods. This is probably the reason for the tailing off of the curve for phase two at higher interval durations, and it was corrected for by applying the curve-fit for the gradual part of this curve only to the range of 10-30 min.

Second, the method does not take into account the duration of the behaviour, only the frequency. Thus, in the case of grooming, a pause after 20 min. of grooming is not distinguished from a pause after 20 s. of grooming. During phase six, however, there was no correlation between the duration of grooming, and the subsequent interval until the next grooming episode between the same two individuals (r_S=0.021; N=747), or the previous interval (r_S=0.018).

Third, the method lumps data for different dyads, each of which contributes a different number of intervals to the curve, a procedure which is statistically incorrect. Also, the shape of the log-survivorship curve may well be different for each dyad, so that the overall BCI is not necessarily the right criterion for any dyad.These problems seriously reduce the value of this method for splitting behaviour into bouts, but they are not generally discussed in the literature (Martin & Bateson, 1986; Slater & Lester, 1982, and refs. therein).

A grooming 'bout', 'sequence' , and 'session' have been defined in many different ways (Chapter I). Only Nishida (1988) defined all three. Similarly, I define grooming bout as grooming without interruptions of longer than 10 s. or changes in groomer-groomee roles. A grooming session is grooming not interrupted by a pause of more than 5 min. in observation phase two, 30 min. in observation phase six (but see below).

Sessions applied to dyads of chimpanzees and were defined on the basis of these time criteria only. However, the total time and duration measures presented in the results apply only to the grooming in bouts and sessions, not to the interruptions in grooming. For example, a session between A and B that consisted of 10 min. of grooming, 4 min. interruption in which A groomed C and B played with D, and then again 5 min. of grooming was scored as a session of (10+5=)15 min. duration, even though the session was spread out over a total of 19 min. of observations, and irrespective of the behaviour that the members of a dyad had shown in the interruption.

One of the objects of this study was to compare the distribution of grooming over different session types (see next section) between periods with and without oestrous females, and to determine over what time-span grooming is reciprocated. As the above analysis has indicated, however, the BCI in phase two (without oestrous females) was much shorter than in phase six. To compare the two periods, using the two different criteria, means we are dealing with actual grooming sessions, but differences would be partly the result of differences between the BCIs. Another possibility would be to use the same (arbitrary) criterion, which would give a clearer idea of differences in the grooming in the two phases.

As the author had already used such a criterion for the analysis of grooming in observation phase two (Oberski, 1993), I decided to use the same criterion for phase six. It was based on the accumulative distribution of interruptions in grooming during phase two. Fig. 3.2 indicates that to be 90% certain that grooming did not resume after it stopped, 20 min. had to pass without grooming. The number of interruptions in grooming misassigned by this criterion were:

observation phase two: $N'_w = 0$
$N'_b = 68$
observation phase six: $N'_w = 4$
$N'_b = 1$

Thus, only the number of inter-session intervals misclassified as intra-session intervals in phase two were much higher than with the formal criterion.

Grooming will be analysed over the whole observation periods, days, sessions (20 min. criterion) and bouts.

Categorisation of grooming sessions

In this section I will outline a method, which was specially designed to allow an analysis of grooming sessions at the dyadic level.

As dominance status affects grooming (Crawford, 1942a&b, in Mason, 1970; Goodall, 1986a; Hemelrijk, 1990b; Kawanaka, 1990a; Okano et al., 1973; Simpson, 1973; Takahata, 1990b), it will be taken into account in a general presentation of the method, even though some of the Edinburgh chimpanzees' dominant-subordinate relationships were vague. Additionally, it is best to analyse age-sex classes separately, as grooming dynamics often differ between these (Bygott, 1974, 1979; Goodall, 1968b; Ghiglieri, 1984; Kraemer et al., 1982; Merrick, 1977; Nishida, 1970; Pusey, 1978, 1990; de Waal, 1986; Yerkes, 1933). Furthermore, dominance status, age, and sex could have an effect on the costs and benefits of grooming and being groomed (Seyfarth and Cheney, 1988).

First, each dyad is made to conform to the structure A-B in which A is the dominant and B the subordinate of a pair in a specific age-sex class. Thus, it becomes possible to combine the average (or median) values for all dyads in order to obtain average (or median) values of dyadic grooming for an age-sex class, group, or population as a whole. Also note that an individual, who is dominant in one dyad, may simultaneously be subordinate in another dyad, so that this individual will be classified as A in one dyad, and as B in another dyad. Of course, dyads could also be structured according to other variables, such as age, or sex, in order to investigate the dynamics of grooming reciprocation between the sexes or between individuals of different ages respectively.

At any moment during a grooming episode of a dyad A-B, only one of three basic configurations of grooming occurs:

-D: grooming by the dominant (i.e. by A), or

-S: grooming by the subordinate (i.e. by B), or

-M: mutual, or simultaneous grooming by both.

Seven different types of grooming session can be logically distinguished, depending on the presence or absence of these three, mutually exclusive, configurations:

'D' sessions with only unilateral grooming by the dominant
'S' sessions with only unilateral grooming by the subordinate
'M' sessions with only mutual grooming
'DS' sessions with unilateral grooming by both the dominant and the subordinate
'DM' sessions with unilateral grooming by the dominant and mutual grooming
'SM' sessions with unilateral grooming by the subordinate and mutual grooming
'DSM' sessions with unilateral grooming by the dominant and by the subordinate, and with mutual grooming.

Each observed grooming session can now be assigned to one of these seven categories, and a distribution of sessions and of the total grooming time over these types can be obtained. These distributions will give insight into how individual chimpanzees reciprocate grooming within grooming sessions. The different session types can be compared statistically by using, for example, the permutation test for paired replicates, or Friedman two-way analysis of variance by ranks (Siegel & Castellan, 1988).

Also, the distribution of grooming over the different sessions can be determined for each dyad separately, so that dyads can be compared. This would be especially interesting in larger groups, for example during a period of stable dominance hierarchy, and could be used to investigate how grooming reflects the particular dominance relationship between two chimpanzees. Furthermore, the influence of one individual's grooming on the grooming of the other, in terms of duration, can be investigated by correlating the different configurations that occurred in the same session (e.g. D, S, and M in 'DSM' sessions) with each other, for each dyad separately, using Spearman's rho.

Unfortunately, there was no clear dominance hierarchy between the males in the Edinburgh chimpanzee group, even though dominant-subordinate relationships were fairly unambiguous for eight out of ten male-male dyads. Thus, when the results were analyzed for each dyad separately the above method was used. However, when all dyads were combined in order to obtain more general results, dominance was not taken into account, and no distinction was made between grooming by the dominant and grooming by the subordinate. Thus, in that case only two, instead of three configurations of grooming were recognized. Again, these were based on within-session grooming between two chimpanzees:

U: One-sided, or unilateral grooming by one individual only.
M: Simultaneous, or mutual grooming by both.

These configurations will be referred to as U, and M, respectively. Five, instead of seven, different types of grooming session can now logically be distinguished, dependent on the presence or absence of the two configurations outlined above:

'U' sessions, in which only one individual grooms.
'M' sessions, in which both individuals groom, but only mutually.
'UU' sessions, in which both individuals groom, but never mutually.
'UM' sessions, in which there is unilateral grooming by only one, and mutual grooming.
'UUM' sessions, in which there is unilateral grooming by both individuals, as well as mutual grooming.

In reality, grooming sessions do not always fall neatly in one of the categories, but sometimes fall in between. For example, If chimpanzee A grooms chimpanzee B for ten minutes, after which B grooms A for 5 seconds, this would be classified as a session with both kinds of unilateral grooming (DS, or UU session). However, this session would be more like a session with unilateral grooming only (D, S, or U session), because the grooming by B was very short compared to the grooming by A. Therefore, it should be kept in mind that the categorisation of grooming sessions only distinguishes between reciprocal and non-reciprocal sessions, and between unilateral and mutual grooming, irrespective of the actual grooming balance in the session.

Another method attempted to take into account the actual grooming balance of each session, by comparing each individual's relative contribution to the grooming session as a whole, as outlined in the next section. Thus, whereas a more general picture of grooming reciprocation could be obtained with the first method, details about the balance of grooming in the sessions themselves were provided by the second method, as presented below.

An index of reciprocity for individual grooming sessions

The categorisation of grooming sessions presented above distinguishes between reciprocal (in which both groom) and non-reciprocal (in which only one grooms) sessions, and between unilateral and mutual grooming. It allows one to say something about relative (interactive) reciprocity at the dyadic level, that is, whether one individual in a dyad grooms the other more the more that other grooms him back, and about the use of mutual grooming in reciprocal sessions. It does not imply anything about the actual balance of grooming, that is about absolute (interactive) reciprocity in each session at the dyadic level. Another measure is therefore needed to express each chimpanzee's actual contributions to the grooming session.

For example, Nishida (1988) used an Index of Reciprocity by Time (RIT), defined as:

$$RIT = (A-B)/(A+B+2C),$$

in which A is grooming by one individual, B the grooming by the other, and C the duration of mutual grooming. In other words, this index relates the difference in the grooming by both individuals of a dyad to the total minutes of grooming between them. Its value falls between $RIT=-1$ (total asymmetry, $A=0$), and $RIT=1$ (total asymmetry, $B=0$), with a value of $RIT=0$ ($A=B$) indicating perfect reciprocity.

However, Nishida's index does not take into account that grooming sessions of different durations may have different significance. For example, if a grooming session lasted for 30 minutes, in which one individual groomed unilaterally for a total of 16 minutes, the other for a total of 10 minutes, and in which there were 4 minutes of mutual grooming, the index would give $RIT=(16-10)/(16+10+8)=0.18$. If a session lasted for only 30 seconds, with the same ratios of unilateral and mutual grooming, the index would again be $RIT=0.18$. However, when a session is of only short duration, it is much more likely that the value of RIT arose by chance, or is confounded by limitations in the accuracy of observations. The more grooming there was in a session, the more meaningful it becomes to use the RIT.

Another example may make this point even stronger: suppose a session consisted only of unilateral grooming by one individual. Then, whatever the duration of this session would be, the RIT would always be 1 or -1, even though it is much more significant if the session lasted for 10 min., than if it only lasted for 10 s. In 10 s. there is not much chance for alternating grooming, so that the likelihood of obtaining RIT values of 1 or -1 is high. This is not withstanding the possibility that short, unilateral grooming sessions occur in different contexts than long ones, for example as 'token grooming' (Goodall, 1986a).

Thus, Nishida's RIT should only be used for comparing the grooming balance of different dyads over a longer time-span, such as whole days, or weeks, as he himself indeed did (Nishida, 1988), so that the duration of individual sessions is no longer of importance. A different index of reciprocity for sessions needs to be found, which does not only express the balance of grooming in a session, but which also expresses the significance of this imbalance by taking the duration of the session into account.

Another problem associated with Nishida's RIT is that its value depends both on the difference in grooming by the two individuals, as well as on the duration of mutual grooming. Furthermore, the mutual grooming is multiplied by two, presumably in an attempt to represent the grooming by both individuals separately. In other words, the denominator (A+B+2C) represents the sum of grooming by the two individuals, rather than the actual duration of the grooming, which would be A+B+C. The consequence of thus doubling the time spent in mutual grooming in an index of reciprocity is that two or more sessions with quite different distributions of unilateral and mutual grooming may have the same value of RIT.

For example, consider a session of 10 min. total duration (i.e. A+B+C = 10), 2 min. of mutual grooming (C), and a difference of 4 min between the grooming by the two individuals involved (i.e. A-B = 4). The value of RIT = (A-B)/(A+B+2C) = 4/12 = 0.33. Now compare this with a session of the same duration of 10 min., but with A-B = 5 min., and C = 5 min., which has a RIT = 5/15 = 0.33 as well. Thus, two sessions of the same duration, but with a different grooming imbalance may have the same value of RIT. It would seem that the second session, in which there was a larger imbalance (5 min. vs. 4 min.) should have a higher value of the RIT.

As another example, compare a session of 10 min. duration, with A-B = 2 min. and C = 4 min., with one of 20 min. duration, A-B = 3 min. and C = 1 min. Both sessions have a RIT = 0.14, even though the relative imbalance in grooming in the first session is 2/10 = 0.20 (i.e. 20%), compared to 3/20 = 0.15 (i.e. 15%) on the second session. The second session is thus clearly more reciprocal than the first one, but this is not expressed by Nishida's RIT. Unfortunately, this problem remains even when the RIT is only used to calculate the balance in grooming over a longer period, instead of over individual sessions, and where Nishida compared RIT values of different dyads, these comparisons may have been confounded in the manner just described.

In order to investigate the balance between grooming given and received within sessions, or over a longer observation period, an index of reciprocity was used, very similar to Nishida's (1988) RIT:

$$\mathrm{RIT} = (A-B)/(A+B+C),$$

in which A, B, and C apply to the grooming within a session.

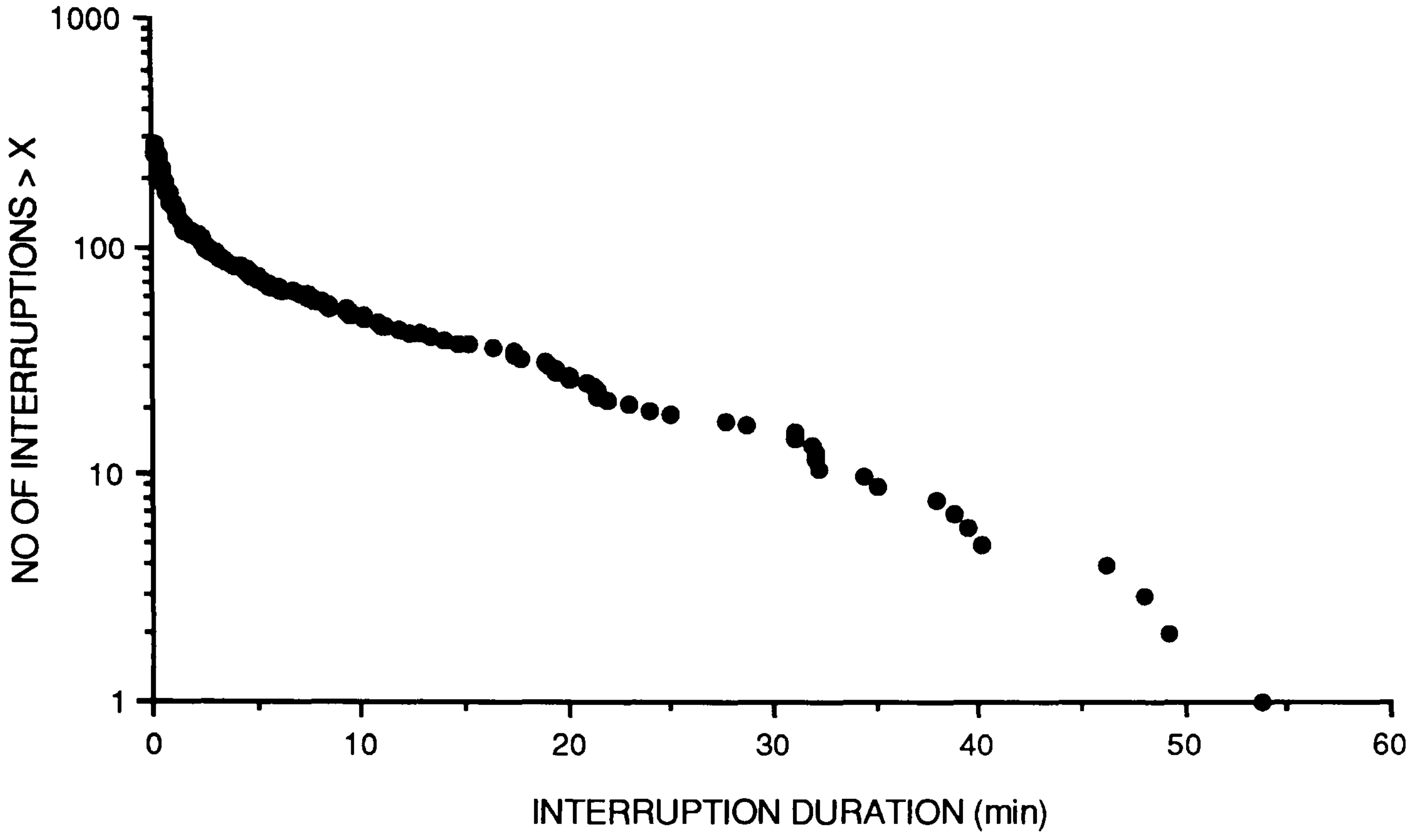
For the investigation of the balance in grooming given and received over consecutive grooming sessions between the same two individuals, the imbalance in grooming was related to the total amount of grooming that was recorded for that particular dyad up to that session. Thus, this cumulative index of reciprocity becomes:

$$\mathrm{RIT}_C=(A_C-B_C)/\sum_{s=1}^{s=q}(A+B+C),$$

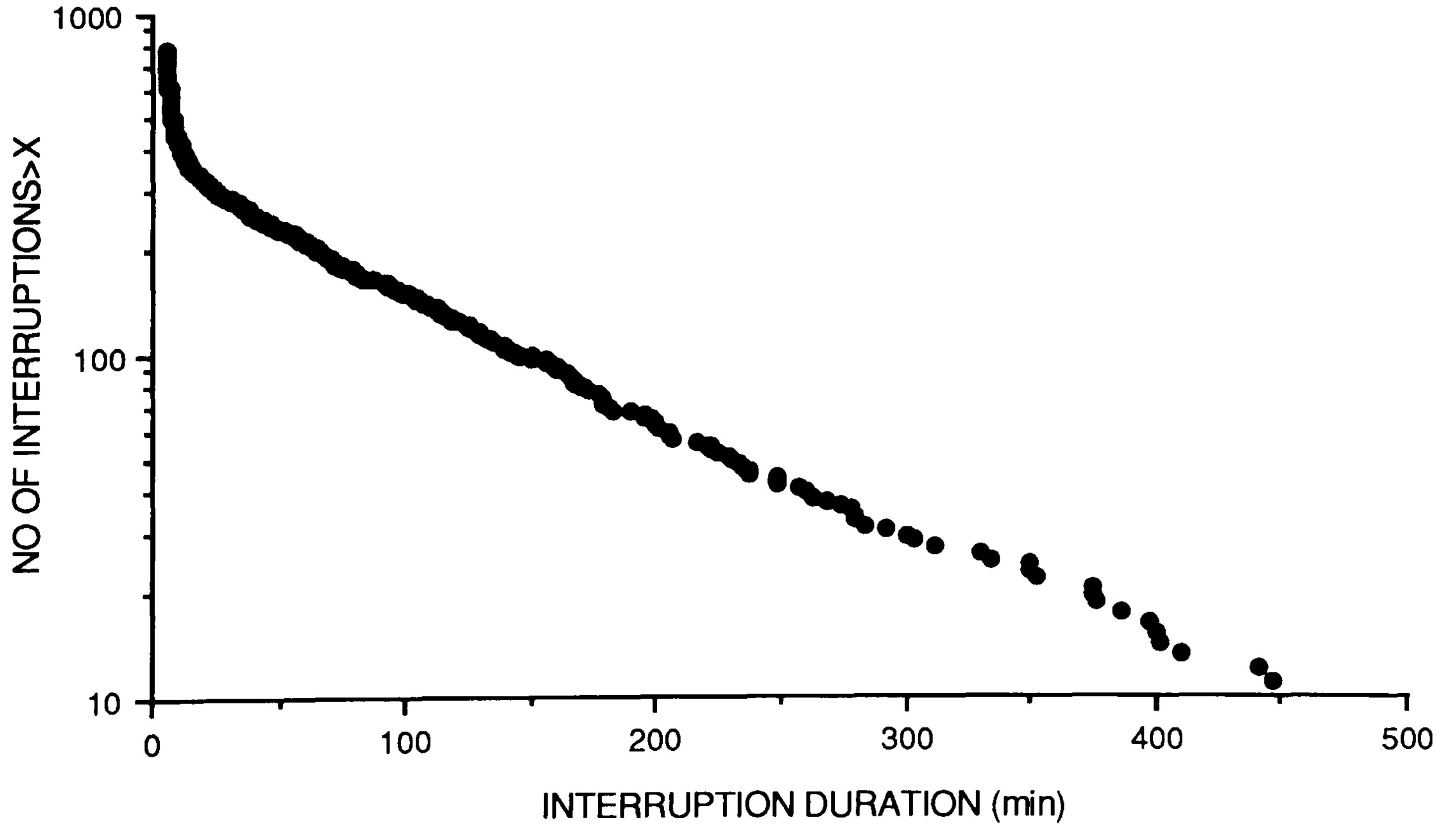
in which A_C is the accumulative grooming by the dominant individual up to and including session q, B_C the accumulative grooming by the subordinate up to and including session q, and $\sum_{s=1}^{s=q}(A+B+C)$ the accumulative grooming between A and B up to and including session q. Session s=1 is the first session of a sequence of consecutive sessions between A and B. Thus, the difference in the grooming by A and B up to and including the q^{th}

session is divided by the accumulative grooming of A and B up to and including session q.

Note that in both indices mutual grooming is only counted once, and the total time (A+B+C) therefore reflects the real time spent in grooming, rather than the sum of grooming by the two individuals, as in Nishida's RIT. In order to give an indication of the significance of the RIT values, they will always be presented together with the total grooming time for which they were calculated.



A: Phase two



B: Phase six

Fig. 3.1. Log-survivorship curves of the number of grooming interruptions longer than x, against the duration x of those interruptions.

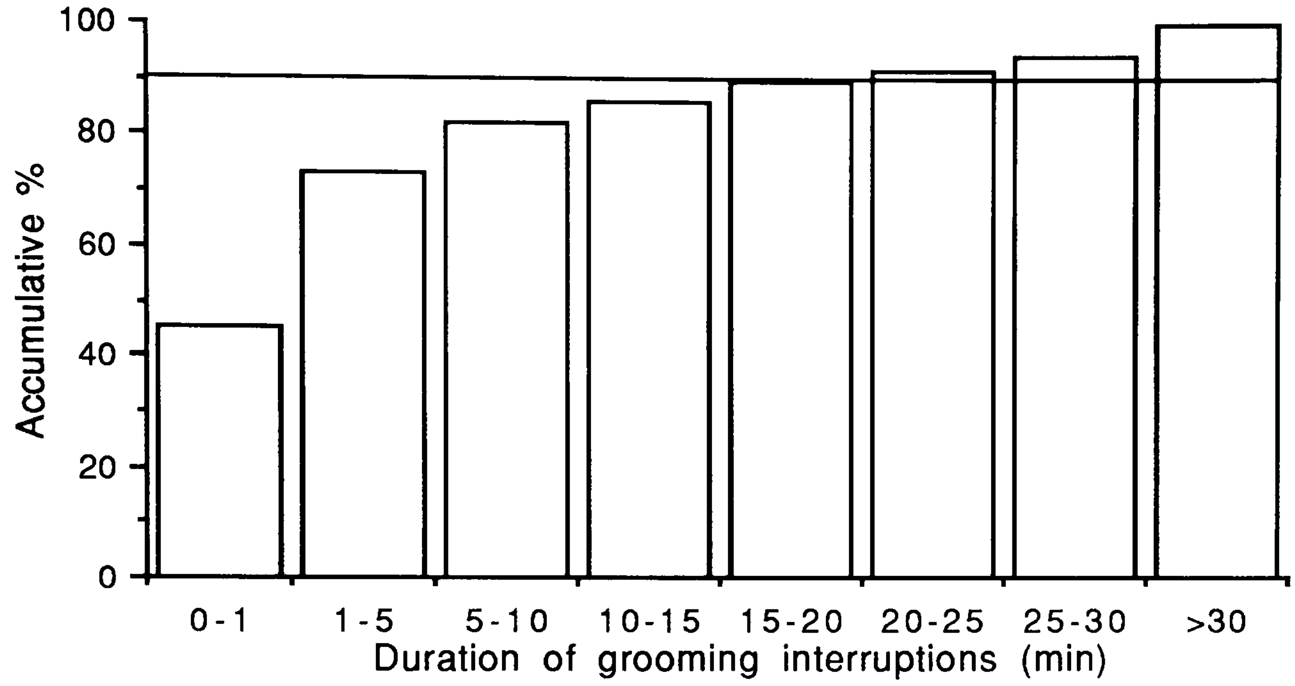


Fig. 3.2. Accumulative percentage of all grooming interruptions in phase two, plotted against length of interruption. The figure shows that in 90 % of all interruptions (N=377) grooming between the same two individuals resumed within 20 minutes. Thus, grooming session is defined as grooming without interruption of more than 20 minutes.

CHAPTER IV

THE SECOND OBSERVATION PHASE: RECIPROCATION OF GROOMING IN THE ABSENCE OF OESTROUS FEMALES

INTRODUCTION

It is not so clear what exactly the benefits are of grooming and being groomed, but it is often thought that to be groomed is more advantageous than to groom (e.g. Falk, 1958; Mason et al., 1962), and consequently that grooming is altruistic. However, more recently, Dunbar and Sharman's (1984) study of wild baboons (Papio sp.) did not provide evidence for this assumption. They found a significant negative correlation between time spent in feeding and time spent resting, but no significant correlation between feeding time and grooming time.

In other words, when extra time was needed for feeding, it was created by spending less time in resting, without affecting the time spent grooming. This could mean that grooming is not altruistic. At the same time, however, it clearly indicated the importance of grooming to the baboons: they continued to groom in spite of having to spend more time in looking for food. In fact, it can be concluded from Dunbar and Sharman's study that it was more important to the animals to maintain the level of grooming, than to maintain the current level of resting (see also Struhsaker, 1980, in Walters & Seyfarth, 1987).

Thus, the ultimate benefits of grooming are not well understood, but the behaviour is clearly an activity of importance to primates, and the immediate benefits include at least all the functions mentioned in Chapter I: hygiene, affiliation, tension reduction, and appeasement, and these may apply to the groomer as well as to the groomee. Furthermore, the extent of these benefits depends on age, sex, and social status of the individuals involved (e.g. Seyfarth & Cheney, 1988), and it is, therefore, difficult to see how grooming would be suitable to an analysis in terms of the Prisoner's Dilemma Game.

We know that chimpanzees often groom each other on a reciprocal basis. It is, however, not clear what the temporal and structural patterns of reciprocation are, that is whether grooming is reciprocated in the same session, on the same day, or at some later stage, and whether grooming is reciprocated in turns, or simultaneously.

Chimpanzees may be the only primates that make considerable use of mutual grooming, a form of grooming in which both partners groom each other at the same time (lemurs are an exception, see Barton, 1987; Appendix A), and the fact that they groom both mutually and unilaterally means that they have two different ways to reciprocate. There are at present no studies of the role of unilateral and mutual grooming in the reciprocation of grooming in adult chimpanzees. The aim of this chapter is to investigate the dynamics of grooming within sessions, and to evaluate the contribution of mutual and unilateral grooming to the reciprocation of grooming.

METHODS

Subjects

The composition of the group during this part of the study was as follows: two mature females, both with infants; one early adolescent female; one late adolescent male; two early adult males; two prime males (Table 2.I).

Observations

Observations for 111 hours were done over 48 days between 28/12/1990 and 16/4/1991. Given the irregular feeding of the chimpanzees, it was inconvenient to observe at fixed times of the day. Instead, observations were carried out on an opportunistic basis between 9:30 and 15:00 h. Observation sessions were generally not longer than two hours (N=86, x±SEM = 85±5.3 min.).

Statistics

For the analysis of grooming reciprocity at the group level I have used the Kr test, Mantel Z test, and Mantel test on within-matrix-ranks (Hemelrijk, 1990a, using 2000 permutations). The first indicates whether individuals tend to groom those others more from whom they receive more (relative reciprocity), whereas the last two indicate whether the amounts given and received are also similar (absolute reciprocity).

It would be statistically incorrect to treat each grooming session as a separate data point and then to lump all sessions, because several sessions will involve the same dyad, and are thus not independent. Therefore, totals (of number and time), and medians (for duration of sessions) were first calculated for each dyad separately. Then, the median of these values was taken to represent the group as a whole.

RESULTS

Please note that 'total number' refers to the total number of grooming sessions for a dyad, 'total time' refers to the total time of grooming (in a particular kind of session) for a dyad, and 'median duration' refers to the median duration of a particular session for a dyad.

A total of 38.7 hours of grooming was recorded. The overall pattern of grooming followed a similar pattern to that of wild chimpanzees (Table 4.I): males tended to groom each other longer and more often than females, who groomed each other least (e.g. Goodall, 1986). This lends support to the generalisation of the results of this study to other chimpanzee groups.

Is there reciprocity of grooming at group level?

Tables 4.IIa&b give the total grooming matrix and the matrix of unilateral grooming for the Edinburgh chimpanzees during the study period. In order to establish whether this chimpanzee group showed reciprocation of grooming at the group level, Hemelrijk's (1990a) tests were applied to the first matrix (Table 4.IIa). The correlation of this matrix with its transposed form gives both relative ($N=8$, $K_r=61$, $p=0.025$) and absolute ($N=8$, $Z=531790$, $p=0.010$; $R=51271$, $p=0.0040$) reciprocity. However, analysing males and females separately reveals that there is no reciprocity between females or between males and females, but only between males (Total grooming: $N=5$, $K_r=17$, $p=0.028$; $Z=109409$, $p=0.030$; $R=2623$; $p=0.021$) For the males there was also relative and absolute reciprocity for unilateral grooming

(N=5, Kr=16, p=0.04; Z=105926, p=0.017; R=2661; p=0.016).

Inspection of the matrices reveals that the majority of male-female grooming was almost completely one-sided, with the male doing almost all the grooming. Similarly, the only female-female dyad that did show reciprocity of grooming concerned a mother-daughter pair (Cindy-Lyndsey).

As grooming at the group level was only reciprocal for the males, and because grooming between the sexes and within females follows different patterns from that between males (Goodall, 1965; Sugiyama, 1969; Nishida, 1979; Ghiglieri, 1984; de Waal, 1986; Takahata, 1990), only the males will be considered here.

Do dyads groom more in reciprocal than in non-reciprocal sessions?

Non-reciprocal (NR) sessions are sessions in which only one individual groomed (U sessions), reciprocal sessions (R) are sessions in which both individuals groomed ('M', 'UU', 'UM', and 'UUM' sessions). The 10 male-male dyads were observed to groom in a total of 155 sessions, or 1347 min. Table 4.III illustrates how these were distributed over reciprocal and non-reciprocal sessions.

Dyads groomed as often in non-reciprocal session as in reciprocal ones (Permutation Test: p=0.50, 2-tailed). However, dyads spent more time in reciprocal sessions than in non-reciprocal sessions (Permutation Test: p=0.03, 2-tailed), and groomed significantly longer in reciprocal sessions than in non-reciprocal sessions (Permutation Test: p=0.0039).

Do dyads with strong grooming relationships groom more reciprocally?

The ratio of reciprocal over non-reciprocal sessions (i.e. R/NR) was calculated (both for total number and total time), in order to obtain a measure of the importance of reciprocal grooming sessions to the dyadic relationships. These values were then correlated with the total values of grooming (R+NR) (Fig. 4.1a&b). The result was significant (total number: r_S=0.685, 0.05>p>0.02, 2-tailed; total time: r_S=0.709, 0.05>p>0.02; N=10 dyads, 2-tailed). Thus, reciprocal grooming sessions were progressively more important the more a dyad groomed.

Do males groom in turns on consecutive sessions?

There was a total of 72 non-reciprocal sessions (46% of all sessions), equal to 250.94 min. of grooming (19% of the total grooming time), with a median duration of 1.99 min. (Table 4.III). It could be that if A grooms B in one session, B grooms A in the next session and so on.

However, correlating the grooming by one with grooming by the other for total number, total time, and median duration gives no significant results (total number: r_S=-0.359; time: r_S=-0.354; duration: r_S=-0.429; N=10; all n.s.) On the contrary, the negative values of the coefficients imply that the more one male groomed, the less the other groomed him back.

Indeed, 6 out of ten dyads had non-reciprocal sessions in one direction only (i.e. it was always the same male who groomed); 3 dyads had most sessions in one direction, but some sessions in the opposite direction; only 1 dyad had some degree of balance between the two directions of grooming (Table 4.IV).

Do males groom in turns within sessions?

There was a total of 83 reciprocal sessions (54% of all sessions), totalling 1095.73 min. of grooming (81% of the total grooming time), with a median duration of 7.1 min. (Table 4.III). However, of all the reciprocal sessions, only 8% consisted of sessions in which both individuals groomed without grooming simultaneously ('UU' sessions). These sessions took up 3% of the total time spent in reciprocal grooming and had a median duration of 2.35 min. (N=5 dyads: those dyads that did not have any of these sessions were omitted from the analysis; Figs. 4.2a&b).

Sessions with only mutual grooming ('M' sessions) were relatively rare as well, comprising 11% of all reciprocal sessions, 2% of total time, with a median duration of 1.89 min. (N=4 dyads). Thus, grooming was not reciprocated by grooming in turns within sessions, and the duration of sessions with only mutual grooming ('M') or with only unilateral grooming ('UU') by both males was comparable to the duration of non-reciprocal sessions (see previous section).

Is there a difference in the duration of the four types of reciprocal grooming sessions?

Sessions with mutual grooming and unilateral grooming by at least one of the two males accounted for 94% of the total time spent in reciprocal sessions. Of these, sessions with mutual grooming and unilateral grooming by just one individual ('UM' sessions) comprised 41% of all reciprocal sessions, 31% of the total time, and had a median duration of 7.22 min. (N=8 dyads; Figs. 4.2a&b).

Sessions with mutual grooming and unilateral grooming by both males ('UUM') amounted to 40% of sessions, 64% of total time, and had a median duration of 11.08 min. (N=5 dyads; Figs. 4.2a&b). There was a significant difference in the duration of the four different types of reciprocal grooming session (Friedman Two-way Analysis of Variance by Ranks: N=3 dyads with all four types, $0.05>p>0.01$).

However, even though the median duration of sessions increased in the order 'M', 'UU', 'UM', 'UUM', only the difference between the 'M' and the 'UUM' sessions was marginally significant ($p<0.10$). This was probably due to the small number of dyads with all four types of reciprocal grooming session.

Why are 'UUM' sessions long: mutual or unilateral grooming?

Of the 10 possible male-male dyads, only 5 had sessions with mutual grooming and unilateral grooming by both males (Table 4.Va). Both mutual grooming and unilateral grooming were much longer in 'UUM' sessions than in other sessions (Table 4.Vb), whereas there was no such difference in the median duration of mutual and unilateral grooming between 'M', 'U', 'UU', and 'UM' sessions.

Is there a relationship between mutual and unilateral grooming in 'UUM' sessions?

Within the 'UUM' sessions there was a strong correlation between the median duration of unilateral grooming (UU) and mutual grooming ($N=5$, $r_s=1.0$, $p=0.05$). However, there was no significant correlation between the median duration of unilateral grooming by one male and unilateral grooming by the other (N=5, r_S=0.8, p=0.20).

Do dyads with a strong reciprocal grooming relationship have more mutual grooming?

Correlation of the ratio of mutual grooming time over unilateral grooming time (M/U) for reciprocal sessions, with the total grooming time of reciprocal sessions (M+U), is significant and negative (N=6 dyads with more than 5 min. of mutual grooming, r_S=-0.829, p=0.05, 1-tailed).

DISCUSSION

The results of this chapter indicate that reciprocation of grooming primarily occurred between males. This corresponds to findings from Gombe, and the low level of grooming between the females could be the result of a reluctance by the females to reciprocate (Goodall, 1986a). However, it is surprising that the males groomed the females almost totally unilaterally, during a period of sexual inactivity. Possibly this grooming represents an attempt by the males to maintain long-term bonds with the females, which might pay off at a later stage. There are several examples of long-term relationships between individuals of opposite sex at Gombe (Goodall, 1986a).

Most of male-male grooming was reciprocated within sessions, rather than between sessions. Reciprocal sessions (i.e. sessions in which both males groom) were longer than non-reciprocal sessions (sessions in which only one male grooms). This is in accordance with reports that grooming in chimpanzees tends to go on for longer if there is either mutual grooming or sequential grooming (i.e. grooming in turns; Pusey, 1978; Ghiglieri, 1984; Goodall, 1986a). However, in the light of the results presented here, this statement needs some qualification: if grooming in reciprocal sessions was the sum of grooming by the two individuals of a dyad, that is, each chimpanzee groomed independently of how much he was groomed by his partner, then sessions with only unilateral grooming by both males ('UU') should have been the longest sessions, and approximately twice as long as non-reciprocal sessions. In reality, these sessions were short, having a median duration similar to non-reciprocal sessions.

Sessions with only mutual grooming ('M') should have been the shortest sessions, and equal to the duration of grooming by just one individual. These sessions are indeed similar in duration to non-reciprocal sessions.

Sessions with both mutual and unilateral grooming ('UM' and 'UUM') should be somewhere between the 'UU' and the 'M' sessions in duration, because there is some, but not a total overlap between the grooming of both individuals. However, the results indicate that 'UM' and 'UUM' sessions were longer than the other sessions. Clearly, the duration of a male's grooming depended on the kind of session he was involved in, and reciprocation did not necessarily result in longer sessions. A male only continued to groom unilaterally when there was both mutual grooming and unilateral grooming by the other, and not when there was just mutual or sequential grooming

Within the sessions with mutual and unilateral grooming by both males ('UUM'), each male adjusted his unilateral grooming to the duration of mutual grooming, but not to the duration of unilateral grooming by the other male. Thus, grooming was not reciprocated on the basis of TIT-FOR-TAT. The correlation between mutual and unilateral grooming suggests that mutual grooming may serve as an indication of the motivation to groom unilaterally. If one male starts to groom before the other has stopped grooming, resulting in mutual grooming, he thereby indicates a high motivation to groom.

When a male starts to groom after the other has stopped, as in sessions with only unilateral grooming by both males ('UU'), he is not very motivated to groom, as judged from the very short median durations of these sessions. Thus, mutual grooming in 'UUM' sessions indicates a motivation to reciprocate in the *same* session, and creates confidence in the other that his grooming efforts will be paid back.

However, why are sessions with only mutual grooming ('M') so short, if mutual grooming implies a strong motivation to groom? During mutual grooming access to the others' body is very limited, because the chimpanzees are usually constricted to a face-to-face position. For example, they can only use one hand if the other hand is being groomed, and visual inspection is very difficult if, as regularly happens, they are grooming each other's faces. Thus, for grooming to be fully effective, unilateral grooming is needed. Perhaps in sessions with only mutual grooming, both chimpanzees are primarily motivated to be groomed. Thus, each male grooms the other only in order to be groomed in return, and neither is willing to continue grooming after the other has stopped.

Finally, dyads with a strong grooming relationship tended to groom more in reciprocal sessions, but they used proportionally less mutual grooming. This confirms the notion that unilateral grooming is more efficient than, and therefore preferred to mutual grooming. In this context it is interesting to note that chimpanzees are probably the only primates that use mutual grooming to a significant degree (a quantitative comparison has not been published, but see Appendix A).

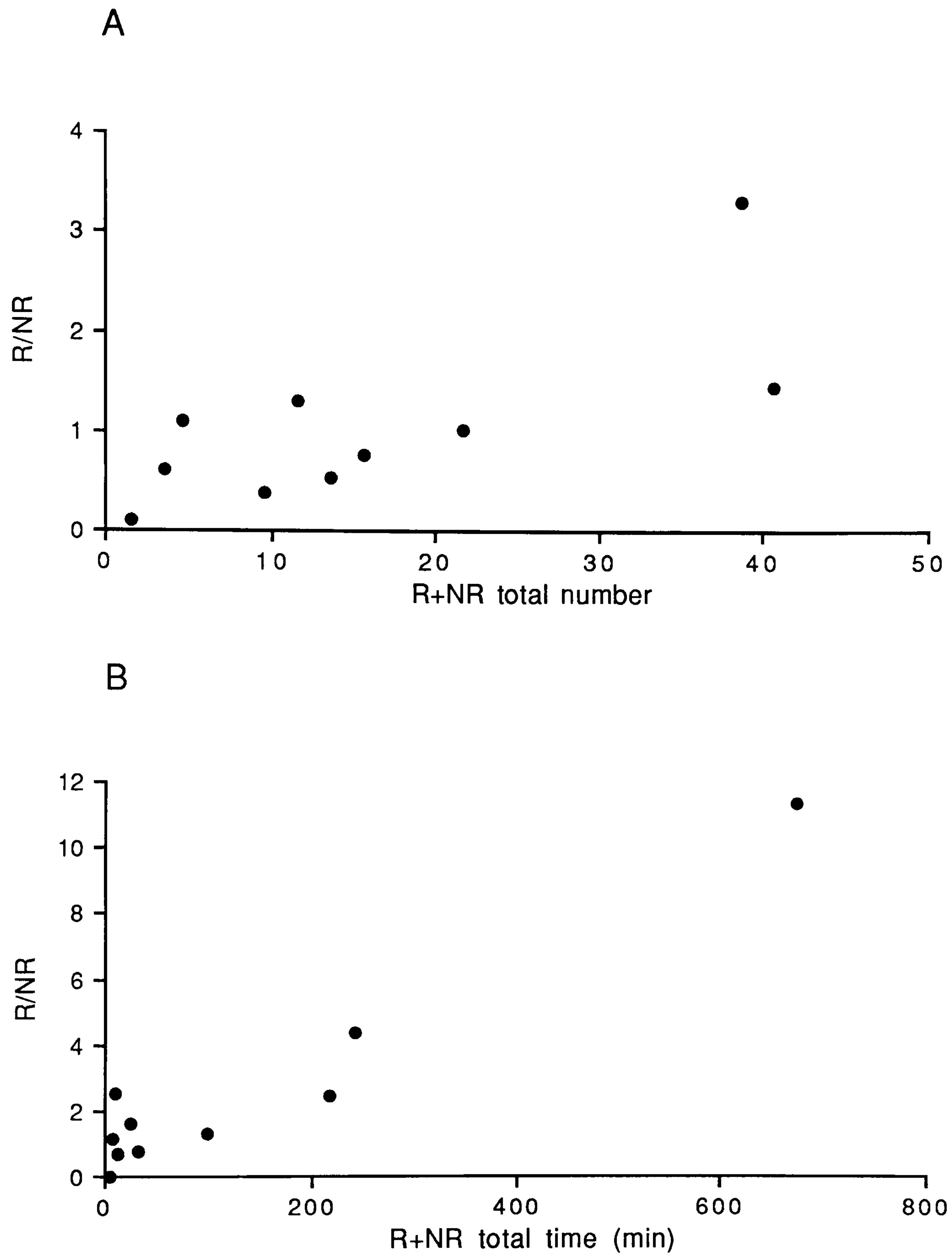


Fig. 4.1. A: Proportion of the total number of reciprocal to non-reciprocal sessions (R/NR) plotted against the total number of sessions (R+NR).

B: Proportion of the total time of reciprocal to non-reciprocal grooming (R/NR), plotted against the total time of grooming (R+NR).

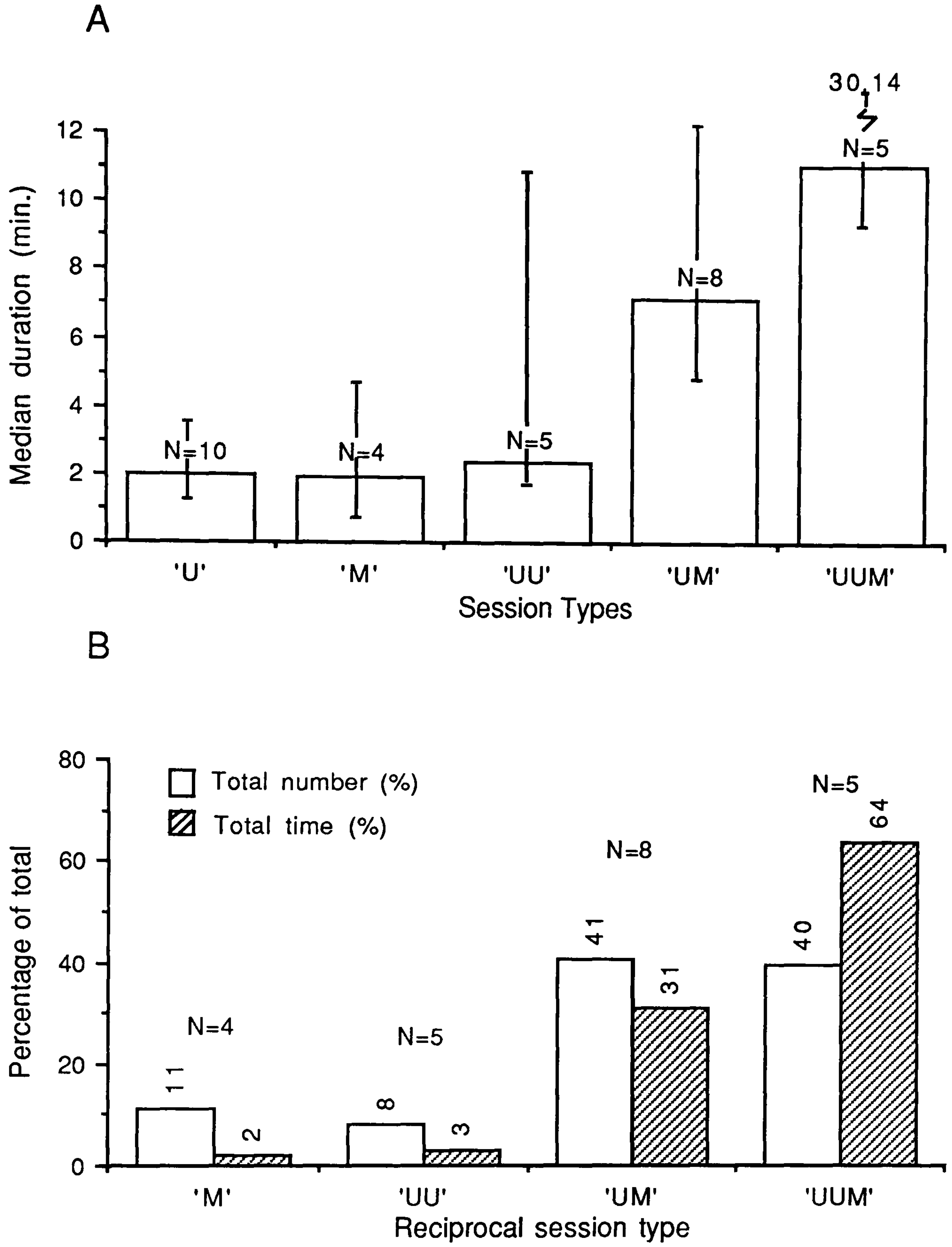


Fig. 4.2. A: Median duration of the different types of reciprocal grooming session. N-values indicate number of dyads that were observed to groom in the particular kind of session.

U: sessions in which only one individual grooms.

M: sessions in which there is only mutual grooming.

UU: sessions in which both individuals groom, but never mutually.

UM: sessions in which all grooming involves one individual, with the other's grooming resulting in mutual grooming.

UUM: sessions in which there is unilateral grooming by both individuals, and mutual grooming.

B: Distribution of total time and total number of reciprocal grooming sessions. N-values indicate number of dyads that were observed to groom in the particular kind of session.

Table 4.I. Distribution of grooming time (38.7 hours) over different kinds of dyad (rounded to the nearest minute). All possible dyads were observed.

Dyad	No. of dyads.	Total min./dyad	Total number/dyad
Male/Male	10	134	16
Male/Female	15	60	13
Female/Female	3	23	6
All dyads	28	82	13

Table 4.IIA. Grooming matrix for the Edinburgh chimpanzees in phase two. The values express total minutes of grooming (rounded to the nearest minute).

		GROOMEE							
		MALES					FEMALES		
		Le	Da	Lo	Ri	To	Ci	Lu	Ld
	Le	-	491	36	33	152	133	148	170
	Da	416	-	9	6	4	12	103	1
	Lo	91	6	-	85	13	82	163	2
GROOMER	Ri	24	3	197	-	23	1	17	0
	To	190	0	22	15	-	8	20	3
	Ci	10	0	8	0	0	-	0	14
	Lu	0	23	35	0	8	18	-	0
	Ld	0	0	0	6	0	41	1	-

Table 4.IIB. Matrix with only unilateral grooming for the Edinburgh chimpanzees in phase two. Values express total minutes of unilateral grooming (rounded to the nearest minute).

		GROOMEE							
		MALES					FEMALES		
		Le	Da	Lo	Ri	To	Ci	Lu	Ld
	Le	-	257	9	9	51	124	148	170
	Da	183	-	6	5	4	12	84	1
	Lo	64	3	-	22	10	82	146	2
GROOMER	Ri	0	1	133	-	10	1	17	0
	To	90	0	18	2	-	8	19	3
	Ci	1	0	8	0	0	-	0	8
	Lu	0	4	17	0	7	18	-	0
	Ld	0	0	0	6	0	35	1	-

Table 4.III. Total numbers of, total times (min.), and median durations (min.) of reciprocal and non-reciprocal grooming sessions for all male-male dyads in phase two.

Dyad	Total no. (reciprocal)	Total no. (non-reciprocal)	Total time (reciprocal)	Total time (non-reciprocal)	Median dur. (reciprocal)	Median dur. (non-reciprocal)
Le-Da	29	9	619.49	54.33	19.28	4.00
Le-Lo	6	9	55.92	43.98	11.15	3.00
Le-Ri	2	2	30.35	2.50	15.18	1.25
Le-To	23	17	196.54	45.17	7.12	2.27
Da-Lo	2	7	4.71	6.64	2.40	1.12
Da-Ri	1	2	3.88	3.40	3.88	1.70
Da-To	0	1	0.00	4.00	-	4.00
Lo-Ri	10	11	155.35	63.52	16.06	3.45
Lo-To	4	9	13.93	17.86	3.54	1.42
Ri-To	6	5	15.56	9.54	2.21	0.90
Total	83	72	1095.73	250.94	-	-
Median	5	8	22.96	13.70	7.12	1.99

Table 4.IV. Distribution of the frequency and total time of non-reciprocal grooming sessions ('U' sessions) over the ten male-male dyads in phase two.

Dyad A-B	Total time A	Frequency A	Total time B	Frequency B
Le-Da	39.85	4	14.48	5
Le-Lo	0.00	0	43.98	9
Le-Ri	2.50	2	0.00	0
Le-To	4.85	2	40.32	15
Da-Lo	5.34	6	1.30	1
Da-Ri	3.40	2	0.00	0
Da-To	4.00	1	0.00	0
Lo-Ri	0.00	0	63.52	11
Lo-To	0.00	0	17.86	9
Ri-To	9.14	4	0.40	1
Totals	69.08	21	181.86	51

Table 4.Va. Distribution of all reciprocal grooming sessions over the ten different dyads in phase two. For explanation of session types see Chapter III. First values are total numbers, second values are total times (min.).

Dyad X-Y	'UU' sessions	'M' sessions	'UM' sessions	'UUM' sessions	Totals
Le-Da	1; 5.65	1; 0.78	10; 145.89	17; 467.17	29; 619.49
Le-Lo	0; 0.00	0; 0.00	3; 27.61	3; 28.31	6; 55.92
Le-Ri	0; 0.00	0; 0.00	2; 30.35	0; 0.00	2; 30.35
Le-To	2; 2.51	3; 7.77	8; 62.06	10; 124.20	23; 196.54
Da-Lo	1;0.62	0; 0.00	1; 4.09	0; 0.00	2; 4.71
Da-Ri	0; 0.00	0; 0.00	0; 0.00	1; 3.88	1; 3.88
Da-To	0; 0.00	0; 0.00	0; 0.00	0; 0.00	0; 0.00
Lo-Ri	2; 25.60	2; 11.98	4; 44.64	2; 73.13	10; 155.35
Lo-To	1; 2.35	0; 0.00	3; 11.58	0; 0.00	4; 13.93
Ri-To	0; 0.00	3; 6.60	3; 8.96	0; 0.00	6; 15.56
Totals	7; 36.73	9; 27.13	34; 335.18	33; 696.69	83; 1095.73

Table 4.Vb. Median duration of mutual and unilateral grooming as it occurred in different types of grooming session in phase two. M=mutual grooming, U=unilateral grooming by one male, UU=unilateral grooming by both males. For session types see fig. 4.2a.

Configuration (session type)	Median duration (min.)
M (M)	1.89
U (U)	1.99
UU (UU)	2.51
M (UM)	2.97
U (UM)	2.25
M (UUM)	5.29
UU (UUM)	6.19

CHAPTER V

TESTING TWO HYPOTHESES OF MUTUAL GROOMING

INTRODUCTION

In the previous chapter it was suggested that mutual grooming serves as an indication of the motivation to groom unilaterally. There are, however, two more basic hypotheses of mutual grooming. These are often implicit in the literature on primate grooming, as most studies do not distinguish between mutual and unilateral grooming. One hypothesis states that mutual grooming is the result of a chance overlap in the grooming by two partners. The other states that mutual grooming functions as a way to minimize the time spent in grooming, leaving more of it free for other activities. In this chapter an attempt will be made to test these two hypotheses.

METHODS

If mutual grooming is the result of a chance overlap in the grooming of the two individuals involved, then the amount of mutual grooming for each session or observation period can be predicted from the total amounts of grooming in that session or period by each member of the dyad. The chance that mutual grooming occurs is then the product of the chances that each member of the dyad is grooming the other.

For example, if A groomed B for a total (i.e. including mutual grooming) of 10 min., and B groomed A for a total of 5 min. during a particular grooming session (or observation period) then the following chances applied:

$P(A\text{-->}B) = 10/15 = 0.67$

$P(B\text{-->}A) = 5/15 = 0.33,$

in which A-->B indicates A groomed B, and B-->A indicates B groomed A. Thus, the chance that A and B groomed each other at the same time is given by:

P(A<-->B) = P(A-->B) • P(B-->A) = 0.67 • 0.33 = 0.22,

in which A<-->B indicates mutual grooming between A and B. The expected duration of mutual grooming was then:

A<-->B = P(A<-->B) • [(A-->B) + (B-->A)] = 0.22 • 15 = 3.30 min.

The expected durations of unilateral grooming were:

A-->$_{u}$B = [P(A-->B) - P(A<-->B)] • [(A-->B) + (B-->A)] =
(0.67 - 0.22) • (15) = 6.75 min., and

B-->$_{u}$A = [P(B-->A) - P(A<-->B)] • [(A-->B) + (B-->A)] =
(0.33 - 0.22) • 15 = 1.65 min.,

in which A-->$_{u}$B indicates unilateral grooming from A to B, and B-->$_{u}$A from B to A. The total time spent in grooming was then:

A-->$_{u}$B + B-->$_{u}$A + A<-->B = 6.75 + 1.65 + 3.30 = 11.70 min.

Thus, if mutual grooming arises by chance, we can calculate the amount of mutual (and unilateral) grooming on the basis of the total amounts both individuals groomed, and then compare this with the actual amount of mutual grooming in that session to test the hypothesis.

If, as the second hypothesis states, mutual grooming serves to reduce the time each individual spends in grooming, then it would be expected that sessions of long duration have higher proportions of mutual grooming than sessions of short duration. Additionally, dyads that groomed each other more are expected to have higher proportions of mutual grooming as well. Thus, a positive correlation would be expected between the total amount dyads groomed, and the proportion of their grooming that was mutual.

These two hypotheses will be tested using data from observation phase two, because in this phase grooming was not confounded by competition between the males over oestrous females.

RESULTS

The first hypothesis can be tested over different time-spans. For example, each session can be taken separately and the expected duration of mutual grooming calculated and compared with the observed value. Alternatively, the same analysis can be done over a whole observation period, which will be done here for observation phase two. From Table 4.IIa chances of grooming by each male with each other male can be determined. These chances are given for each dyad in Table 5.Ia. The expected and observed durations of mutual and unilateral grooming are presented in Table 5.Ib&c. Permutation test (in which the expected values are taken as imaginary replicates) suggests a marginally significant difference between observed and expected values of mutual grooming for the males in phase two (p=0.0625; N=10 dyads; 2-tailed).

From Table 5.Ib it can be seen that the observed values of mutual grooming are usually higher than the expected values. Only the four dyads with very little or no mutual grooming at all had observed values that were lower than expected. Excluding these dyads from the analysis gives an even more significant result (p=0.03; N=6; 2-tailed). Thus, between the males there was more mutual grooming than would be expected by chance, indicating that the first basic hypothesis is not the right one.

The second hypothesis says that mutual grooming is used as a time-saving device. This implies that the more time two individuals spend grooming, the more of that grooming will be mutual in an attempt to reduce the total time in grooming. This would result in a positive correlation between total grooming time and the proportion of mutual grooming. The previous chapter found a negative correlation between total grooming time and the ratio of mutual to unilateral grooming for reciprocal grooming sessions, indicating that for this kind of grooming session mutual grooming is not used to save time. Fig. 5.1 shows the relationship between the total amounts each dyad groomed (here the sum of the unilateral grooming by both individuals of each dyad), and the proportion of that total that was spent in mutual grooming for all sessions. There was no significant correlation between these two measures (r_S=0.52; N=10; p>0.10).

From Fig. 5.1 it seems that, in fact, two distinct processes may be at play. Therefore, the ten dyads were split into two groups of five dyads on the basis of their total grooming score, resulting in a 'low grooming' and a 'high grooming' group. Correlations were then carried out for these two groups separately. The results were not significant, with for 'low grooming' dyads rs=0.700 (dyads 5, 6, 7, 9, 10 in fig. 5.1), and for 'high grooming' dyads rs=-0.625 (dyads 1, 2, 3, 4, 8 in fig. 5.1).

The opposite signs of the correlation coefficients do, however, indicate that mutual grooming may play a different role for dyads which only groom little and for dyads that groom a lot. Thus, the hypothesis that mutual grooming serves to reduce the time spent in grooming seems to be true for some dyads, but not for others. Generally speaking, this relationship may hold for those dyads that groomed only little. In contrast, dyads that groomed more decreased the proportion of their mutual grooming with increasing time spent in grooming.

DISCUSSION

The previous chapter analysed grooming sessions according to type and presented a model of mutual grooming. This chapter showed that for the same observation phase, in which there were no oestrous females, two basic hypotheses of mutual grooming could not fully explain the results. Mutual grooming is not the result of a chance overlap of the grooming of two individuals, nor is it just a way by which chimpanzees try to minimize the time they spend in grooming.

Dyads with only little grooming had less mutual grooming than predicted, but the ratio of mutual to total grooming for these dyads increased with increasing total grooming. On the other hand, dyads involved in more grooming had mutual grooming values higher than predicted, with a decreasing mutual:total ratio.

It is interesting that dyads that groomed only little seemed to use mutual grooming as a way to reduce their grooming time. It is as if the chimpanzees in these dyads did not want to spend time grooming each other at all, but when they did, they tried to minimize this time by grooming more mutually. The fact that these dyads nevertheless groomed less mutually than expected by chance lends support to the idea that mutual grooming can serve as an indication of the motivation to groom unilaterally. In other words, when both partners in a dyad are hardly motivated to groom, the chance that they will do so at the same time is much lower than when one or both are very motivated to groom.

Thus, individuals in dyads with a lot of grooming were clearly more motivated to groom each other: their mutual grooming was higher than expected by chance. They did not seem to use mutual grooming as a time-saving method, but rather mutual grooming became less important in stronger grooming relationship (see previous chapter).

The results of this chapter point again to the importance of analysing at the dyadic level and clearly indicate that mutual grooming can be used for different purposes, either to save time, or as an indication of the motivation to groom unilaterally. Which function mutual grooming fulfils depends on the strength of the grooming relationship of the dyads involved.

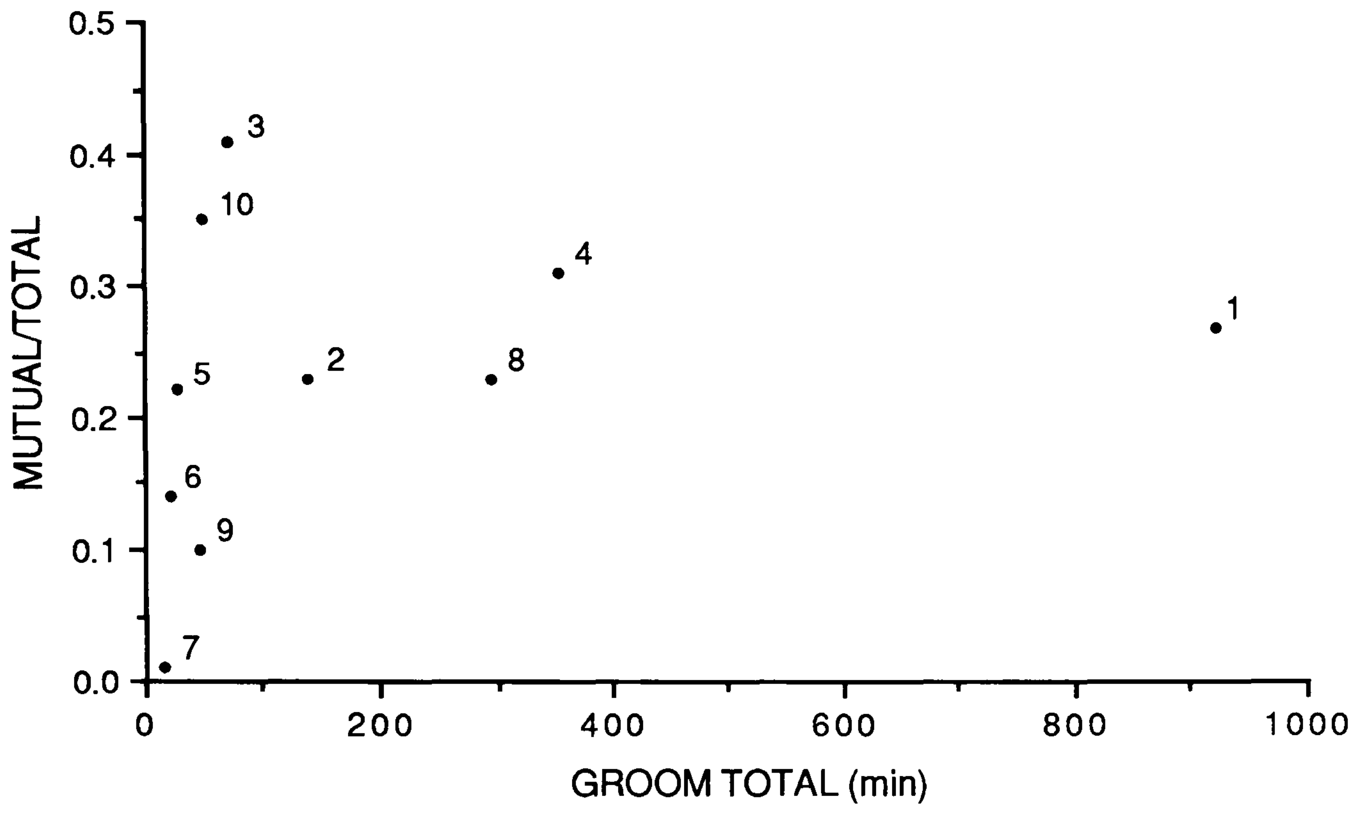


Fig. 5.1. Scatterplot of the ratio of mutual to total grooming against total grooming in phase two for the ten male-male dyads. Numbers in graph refer to dyads as follows:1: Le-Da, 2: Le-Lo, 3: Le-Ri, 4: Le-To, 5: Da-Lo, 6: Da-Ri, 7: Da-To, 8: Lo-Ri, 9: Lo-To, 10: Ri-To.

Table 5.IA. Phase two: Proportions of their total grooming time each individual of a dyad spent grooming the other.

A

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM
LEO	-	0.54	0.28	0.58	0.44
DAVID	0.46	-	0.61	0.70	1.00
LOUIS	0.72	0.39	-	0.30	0.38
RICKY	0.42	0.30	0.70	-	0.60
TOM	0.56	0.00	0.62	0.40	-

Table 5.IB. Phase two: Expected and observed values (min.) of mutual grooming for each dyad. Figures above the diagonal are observed values, below the diagonal expected values. For calculation of expected values, see text.

B

OBSERVED EXPECTED	LEO	DAVID	LOUIS	RICKY	TOM
LEO	-	233.93	27.75	24.05	100.53
DAVID	225.39	-	3.01	1.1	0
LOUIS	26.00	3.41	-	63.18	3.10
RICKY	13.88	1.77	59.57	-	12.9
TOM	84.50	0	8.23	9.15	-

Table 5.IC. Phase two: Expected (top of cells) and observed (bottom of cells) values (min.) of unilateral grooming for each dyad. For calculation of expected values, see text.

C

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM
LEO	-	265.92 257.38	16.35 36.35	18.97 8.80	67.40 51.37
DAVID	191.05 182.51	-	5.40 5.79	4.06 4.73	4.00 4.00
LOUIS	65.30 63.56	0.78 1.45	-	25.91 22.30	5.07 10.20
RICKY	10.17 0.00	1.77	136.96 133.35	-	13.45 9.70
TOM	0.00 0.00	0	13.35 18.48	6.23 2.48	-

CHAPTER VI

OBSERVATION PHASE SIX:

THE INFLUENCE OF OESTROUS FEMALES, AGGRESSION AND PROVISIONING ON THE RECIPROCATION OF GROOMING.

INTRODUCTION

Grooming has been observed in many different contexts. It has been suggested that in some of these, grooming may be actively used by the chimpanzees as an object of exchange or interchange. For example, it may be used in sexual bargaining, interchanged for food, or support in fights (for references, see Chapter I).

It can then be expected that in periods with oestrous females, more grooming will be unilateral rather than mutual, than in periods without oestrous females. Furthermore, there will be a greater imbalance in the grooming of dyads in the direction of the dominants, because it will usually be the subordinates that groom the dominants in order to gain access to the females in oestrus. The same argument applies to grooming in the feeding context: if grooming is interchanged with food, it will be primarily unilateral in the context of feeding, and subordinates will groom more than dominants, although this effect is probably less marked than with oestrous females, as food is not a limited resource, at least in captive circumstances.

METHODS

The data in this chapter were collected during the sixth observation phase, in which there were five adult males, four adult females, and two infants. There were periods with and without females in oestrus. During this phase, observations were done by two observers (see Chapter II), recording all occurrences of behaviours, focussing on grooming between the males only. Table 6.I gives the details of this observation period.

Female oestrus was defined as the presence of a female with a fully swollen perineum. Thus, phase six could be broken down into four periods, starting with four consecutive days in which the oldest female, Cindy, had a full swelling. The next two sequences of four days were taken together as one period without oestrous females. This was followed by a period of three days in which the youngest female, Lyndsey, was in oestrus, and a period of five consecutive days in which both Cindy and Lyndsey were in oestrus. This whole phase, in which oestrous females were present at least part of the time, will be compared with phase two, in which there were never females in oestrus.

Grooming in the feeding context was defined as grooming sessions that started within 60 min. after provisioning by the keepers, and it was compared with grooming 60 min. before provisioning. As the group was provisioned four to five times each day, I compared only the grooming after the last provisioning of each day with grooming before the first provisioning, thereby avoiding the problem that grooming sessions in between provisionings would sometimes have to be classified as both before and after feeding.

Aggression was defined as the physical attack of one male on another male. An initial analysis was done on the first inter-opponent grooming session after an attack. Next, I compared the grooming of all male dyads on days with attacks with the grooming on days without attacks, to avoid having to use an arbitrary criterion for 'before attack' and 'after attack' periods, and because the total number of male-male attacks was small. Grooming in the context of aggression was then analysed by investigating the distribution on those days of unilateral and mutual grooming, and of the balance of grooming sessions.

RESULTS

Grooming and female oestrus

Mutual and unilateral grooming. In phase six there were 283 grooming sessions between the males, totalling 1866.51 min. Fig. 6.1 gives the total duration of grooming recorded between the males in phases two and six, as percentages of the total observation time, and the total time spent in each grooming configuration as percentage of the total grooming time. It can be seen from the figure that males groomed each other less in phase six than in phase two. Dominants groomed subordinates less unilaterally in phase six, subordinates groomed dominants more unilaterally in phase six, and there was less mutual grooming in phase six. The RIT values illustrate these points further, with a much larger imbalance towards grooming by the subordinates in phase six than in phase two.

These results indicate that, in the presence of oestrous females (phase six), subordinates groomed dominants more, and dominants groomed subordinates less unilaterally than when no oestrous females were present, as predicted by the 'sexual bargaining' theory: if dominants have easy access to oestrous females, while subordinates do not, then subordinates have to groom dominants in 'exchange' for access to the females in oestrus. At the same time, if it is assumed that dominants groom subordinates partly because they want to be groomed back, then in the presence of oestrous females, dominants do not need to groom subordinates as much, because they already receive grooming for access to oestrous females. However, these results are only indirect support for a sexual bargaining theory.

In order to verify these results a comparison was made between the chance expectations of the total time spent in mutual grooming in the two observation phases. Using the same method as in Chapter V to determine expected values for mutual grooming for each observation phase it was found that in phase two there was more mutual grooming than expected (C_{exp}=335.54 min. vs. C_{obs}=471.45 min.), whereas in phase six there was almost as much mutual grooming as expected (C_{exp}=439.75 min. vs. C_{obs}=445.60 min.). In both phases there was less unilateral grooming by the dominants than expected (phase two: A_{exp}=465.32 min. vs. A_{obs}=377.16 min; phase six: A_{exp}=489.4 min. vs. A_{obs}=424.09 min.), but subordinates groomed less unilaterally than expected in phase two (B_{exp}=546.14 min. vs. B_{obs}=498.37 min.), and more than expected in phase six (B_{exp}=937.36 min. vs. B_{obs}=996.82 min.).

Thus, in the absence of oestrous females both dominants and subordinates groomed less than expected, and there was more mutual grooming than expected by chance. When oestrous females were present, subordinates groomed more than expected, dominants less, and there was about as much mutual grooming as was expected by chance. In other words, there was a shift from mutual grooming towards unilateral grooming by the subordinates, a pattern that could also be deduced from Fig. 6.1.

It cannot be determined from this analysis whether the changes in the patterns of unilateral and mutual grooming are the direct result of sexual bargaining between the males, or whether the presence of oestrous females had a more general effect on the relationships between the males. For example, dominance relationships between the males could have become more polarised by an increase in the levels of aggression due to sexual competition, with the result that subordinates started to groom dominants more. In order to investigate the direct relationship between grooming and sex, it is necessary to compare grooming sessions in a mating context with sessions outside that context. Unfortunately, the current data were insufficient to do this.

Reciprocity at group level. Phase six had periods with zero, one and two oestrous females. A comparison between these periods may reveal how different numbers of oestrous females influence the reciprocation of grooming. This comparison will be made here at group level only. Tables 6.II-6.V give the matrices for total and unilateral grooming between the males over the whole phase six, and in the periods with zero, one and two oestrous females, together with results of matrix correlation tests (for the meaning of K_r, Z, and R, see Chapter III). In general there was significant ($p \leq 0.10$) relative and absolute reciprocity for total grooming in all periods. For unilateral grooming there was only relative reciprocity in the periods without and with two oestrous females. There was never absolute reciprocity for unilateral grooming in phase six, in contrast to phase two, in which there was both relative and absolute reciprocity for total and unilateral grooming (Chapter IV).

Reciprocal and non-reciprocal sessions. Here, the influence of oestrous females on the distribution of grooming over the different session types will be investigated, by comparing phase six with phase two (see Chapter IV, Tables IV.III-IV.Vb). Table 6.VI gives the total time, total number and median duration that dyads spent in reciprocal and non-reciprocal sessions in phase six. Dyads spent more time and groomed longer in reciprocal sessions than in non-reciprocal sessions (Perm. test: p=0.047 for total time; p=0.003 for median duration; N=10 dyads; 1-tailed). There was a significant correlation between the total time dyads spent in reciprocal and non-reciprocal grooming (r_S=0.76; N=10; 0.01>p>0.005; 1-tailed). Similar results were found for phase two.

In phase two it was found that the more a dyad was involved in grooming, the higher the proportion of reciprocal to non-reciprocal grooming was. However, in phase six there was no significant correlation between the ratio of reciprocal to non-reciprocal grooming and total grooming for total time, but a marginally significant negative correlation for total number (total time: r_S=0.248; N=10; p=0.25; 1-tailed. Total number: r_S=-0.462; N=10; 0.10>p>0.05; 1-tailed). Thus, in phase six, reciprocal grooming was not more important to dyads that groomed more, but there was a tendency for non-reciprocal sessions to be more important the more often dyads groomed.

Non-reciprocal sessions. There were 176 non-reciprocal sessions (47% of all sessions), totalling 650.95 min. (35% of total grooming time), with a median duration of 1.46 min. Thus, in phase six, non-reciprocal sessions occurred more often, took up more time, but were slightly shorter than in phase two. As in phase two, there was no correlation between grooming by the one and by the other (Table 6.VII. Total number: r_S=-0.364; total time: r_S=-0.394; median duration: r_S=-0.152; N=10; all N.S.).

Reciprocal sessions. There were 107 reciprocal sessions (53% of sessions), totalling 1215.56 min. (65% of total grooming time), with a median duration of 5.59 min. (Table 6.VIIIa, Fig. 6.2a&b). Dominance has been taken into account in the session types presented in these figures, because dominance-subordinate relationships were clearer in phase six than in phase two. Values for session types independent of dominance are also included for comparison with phase two (see Chapter III for definition of session types, Chapter IV for results of phase two).

Thus, reciprocal sessions occurred more often, but took up less time than in phase two, even though they had the same median duration. Of these sessions, 17% were 'DS' sessions in which both dominant and subordinate groomed, but not mutually. 'DS' sessions took up 13% of of reciprocal grooming time, and lasted a median of 3.26 min. (N=5 dyads, Fig 6.2a). Thus, these sessions occurred much more often, took up more time, and were also somewhat longer than 'UU' sessions in phase 2.

'M' sessions comprised 17% of sessions (N=8 dyads), 3% of total reciprocal grooming time. They had a median duration of 0.50 min. which is shorter than in phase two, but they occurred more often, and took up a similar relative amount of time (Fig. 6.2a&b).

'DM' sessions totalled 18% of all sessions (N=7 dyads) and 11% of grooming time, with a median duration of 2.59 min. 'SM' sessions totalled 25% of sessions (N=6 dyads), 28% of time, lasting a median of 7.27 min. 'DM' and 'SM' sessions together (cf. 'UM' sessions in phase two) totalled 43% of sessions (N=10 dyads), 39% of time, with a median duration of 6.38 min. (Fig. 6.2a&b). Thus, these sessions occurred about as often, but were shorter and took up more time than in phase two.

'DSM' sessions ('UUM' in phase two) totalled 23% of sessions (N=8 dyads), 44% of grooming time, and had a median duration of 13.85 min. (Fig. 6.2a&b). Thus, these sessions contributed less than in phase two, but they were slightly longer than in phase two. The difference in duration between the four session types (taking 'DM 'and 'SM' together as 'UM') was only marginally significant (Friedman Two-Way analysis: $F_r=6.3$; df=3; $p<0.10$).

<u>'DSM' sessions</u>. There were 8 dyads with 'DSM' sessions. As in phase two, these sessions were the most important reciprocal sessions. Table 6.VIIIb gives the median duration of each configuration, as it occurred in the different session types. Again, mutual grooming was longest in 'DSM' sessions. Unilateral grooming by the dominant was also longest in 'DSM' sessions. However, unilateral grooming by the subordinate was shortest in 'DSM' sessions, and longest in 'SM' sessions.

Correlation between unilateral grooming by the dominant and unilateral grooming by the subordinate was marginally significant ($r_s=0.548$; N=8; $0.10>p>0.05$; 1-tailed), but correlations between mutual and unilateral grooming were not ($r_{s[D\&M]}=0.381$; N=8; $p>0.10$; $r_{s[S\&M]}=0.333$; N=8; $p>0.10$). These results are opposite to those found in phase two, where unilateral grooming was correlated with mutual grooming but not with unilateral grooming by the other. Note, however, that only three dyads (Le-Da, Le-To, and Lo-Ri) in phase two, and two in phase six (Le-Da, Lo-Ri) had more than two 'DSM' sessions.

Grooming and aggression

There was a total of 22 attacks by males on other males, in which the observers were reasonably certain about who was involved. Table 6.IX shows how these were distributed over the male dyads. Three (14%) of the 22 attacks were in the opposite direction from that expected on the basis of the assumed dominance hierarchy. Most attacks were made by the two highest ranking males, who each had about the same number.

The total number of attacks per male did not contradict the assumed hierarchy, but did not strongly support it either, with the relationship between the alpha and beta males, and the two lowest ranking males unresolved. Lo and To received most attacks, whereas Ri received least. Although Da and Le each directed about as many attacks to Lo and To, Le directed most of his attacks to Da's ally Lo, and Da directed most of his attacks to Le's ally To.

Of the 22 attacks recorded, 10 (45%) were followed by grooming between the opponents. In the remaining 12 cases grooming between the opponents was not observed, but could have occurred after observations had stopped. There was great variation in the time-lag between an attack and subsequent inter-opponent grooming (median=143.47 min., 1st quartile=116.57 min., 3rd quartile=260.21 min.; N=5 dyads).

Fig 6.3 gives the expected and observed values of unilateral and mutual grooming for the total time of inter-opponent post-attack grooming sessions. There were no large differences between observed and expected values. Fig. 6.4 gives the distribution of these grooming sessions over the different session types. Although most types occurred, grooming sessions after an attack were usually short (median=0.62 min., 1st quartile=0.35 min., 3rd quartile=3.33 min.; N=10 sessions). However, dyads did not groom significantly shorter in post-attack sessions than in other sessions (Perm. test: p=0.44; N=5 dyads), but the grooming imbalance over these sessions was more towards the subordinates (RIT=-0.36 for post-attack grooming vs. RIT=-0.30 for other grooming).

As the total number of post-attack, inter-opponent grooming sessions was small, an additional analysis was done over all male-male grooming on days with and without attacks.

The rate of male-male attack (Fig. 6.5) was lowest in the absence of oestrous females, and highest when Ci was in oestrus. Thus, the overall effect of aggression on grooming between the males can only be evaluated by controlling for the presence of oestrous females. Fig. 6.6 shows how grooming between the males was distributed over unilateral and mutual grooming on 'attack days' and 'no attack days', for different oestrous situations, and also gives the values of RIT (the period in which only Ci was in oestrus was omitted because attacks had occurred on each day of this period).

It can be seen from the figure that dominants groomed much less unilaterally (relative to total grooming time) on attack days than on no-attack days in the absence of oestrous females, but much more on attack days than on no-attack days when oestrous females were present. Subordinates groomed about as much unilaterally on attack and no-attack days in the absence of oestrous females, but less on attack days than on no-attack days in the presence of oestrous females. There was about as much mutual grooming on attack and no-attack days when there were one or two oestrous females present, but more mutual grooming on attack days in the absence of oestrous females.

The RIT values illustrate these differences as well, with the imbalance in grooming being less negative on attack days with oestrous females, and more negative on attack days without oestrous females, compared to no-attack days. Note, however, that the imbalance on no-attack days with oestrous females was much larger than without oestrous females. At the same time, the RIT values in the figure show that the presence of oestrous females on no-attack days resulted in a greater grooming imbalance towards the subordinates. The reverse was true for attack days.

An analysis of session types for the different oestrus/aggression periods was not done as the numbers of sessions of each type for each dyad were too small.

Grooming and feeding.

Fig. 6.7 shows the distribution over the three different configurations of grooming before and after feeding. Although there was a difference for some dyads (not shown), the distribution for all dyads together was the same before and after feeding.

The expected and observed values of mutual and unilateral grooming were also similar, both before and after feeding (Fig. 6.8). Thus, there was no overall difference in the distribution of unilateral and mutual grooming before and after feeding.

DISCUSSION

There was less grooming between the males in the presence of oestrous females than when there were no oestrous females. As oestrous females no doubt increase the sexual competition between the males (judging from the increase in the level of aggression, see Shefferley & Fritz (1992), but cf. Bloomsmith et al. (1992)), it would be expected that grooming between them would increase to keep the tension down, just as a group of captive chimpanzees at Arnhem groomed more in their relatively small indoor living quarters compared to outside (Nieuwenhuysen & de Waal, 1982). Clearly the effect of crowding (competition for space) on grooming cannot easily be compared with the effect of competition for females on grooming.

The grooming between the males, in the presence of oestrous females, shifted from unilateral grooming by the dominant and mutual grooming to unilateral grooming by the subordinate, perhaps confirming the 'sexual bargaining' theory (de Waal, 1982): subordinates groom dominants to gain access to oestrous females. However, the changes in grooming might also have been the direct result of heightened competition between the males, and more clearly defined dominance relationships.

At the same time, there was a decline in the level of grooming reciprocation between the males, as expressed by the absence of both absolute reciprocity, and reciprocity for unilateral grooming at the group level, as well as by the lesser occurrence of sessions with mutual and unilateral grooming by both males ('DSM' or 'UUM'), and the absence of any clear relationship between the grooming by the two males in these sessions.

At Arnhem, grooming sessions between males lasted longer when an oestrous female was present (de Waal, 1982; I have not been able to find the quantitative report which gives more details of this result). At Edinburgh, however, only sessions with unilateral grooming by both males ('DS' or 'UU') and with mutual grooming and unilateral grooming by both males

('DSM' or 'UUM') were longer when there were oestrous females present, although 'UUM' sessions occurred less frequently, took up less time, and were more imbalanced than in the absence of oestrous females. This suggests less grooming cooperation between the males in the presence of oestrous females.

Aggression in the absence of oestrous females resulted in a shift from unilateral grooming by the dominant to mutual grooming, indicating that the direct effect of aggression on grooming was an increase in the tendency of subordinates to reciprocate grooming, and to declare their commitment to their grooming partners by grooming mutually (cf. Simpson, 1991).

However, aggression in the presence of oestrous females resulted in a shift from unilateral grooming by the subordinates, to unilateral grooming by the dominants, but had no effect on mutual grooming. This unilateral grooming by dominants may represent attempts to create or maintain alliances, which are probably more important when males compete for females, and which will be particularly vulnerable in the context of aggression.

In this study, no relationship was found between grooming and feeding. In contrast to an earlier study (de Waal, 1989b), in which there was a clear relationship between grooming and food sharing, competition between the males during provisioning bouts was low or even absent. De Waal (1989b) used a concentrated and limited food resource in his experiments, thereby creating a high level of competition for food. Thus, these two studies do not contradict each other, and it would be expected that grooming in the context of food competition will shift toward unilateral grooming by subordinates, similarly to grooming in the presence of oestrous females. It would, however, be difficult to make further predictions about the combined effects of oestrous females, aggression, and competition for food on grooming, in line with the results of this chapter, which indicate that the function and/or meaning of grooming depends on these different contexts.

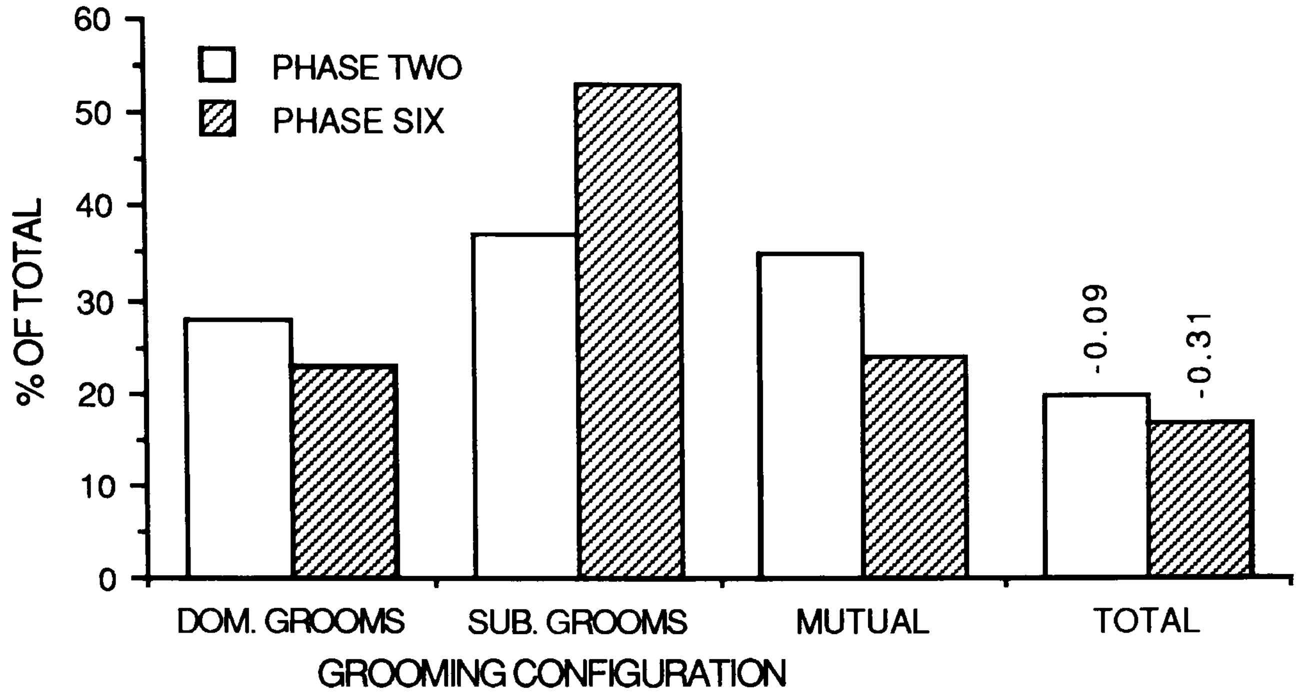


Fig.6.1. The percentage of observation time spent in grooming, and the percentage of grooming time spent in mutual and unilateral grooming by the males in phases two and six. Values of RIT are given above totals columns.

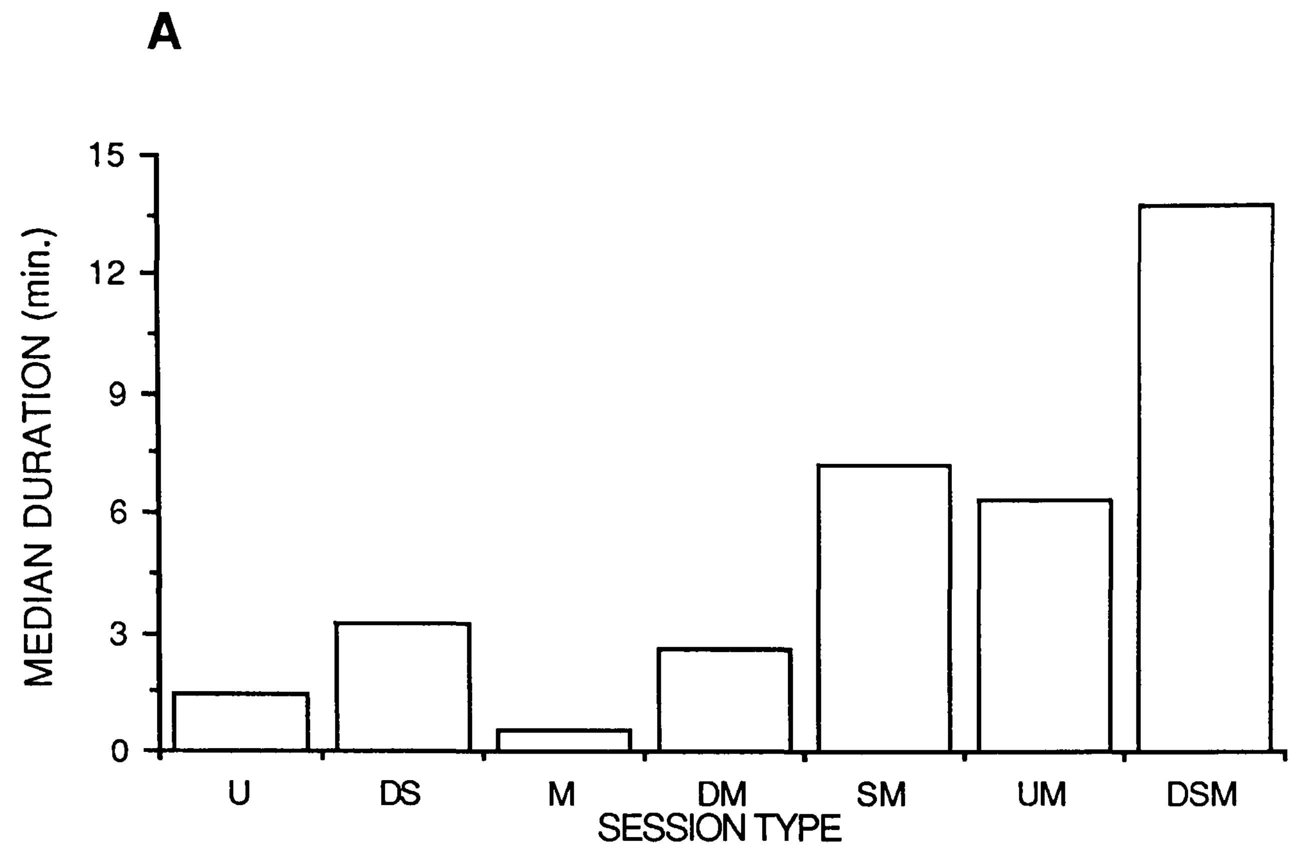


Fig. 6.2a. Median durations of session types during phase six, in the presence of oestrous females.

'U' sessions with unilateral grooming by one male only
'DS' sessions with unilateral grooming by both the dominant and the subordinate
'M' sessions with only mutual grooming
'DM' sessions with unilateral grooming by the dominant and mutual grooming
'SM' sessions with unilateral grooming by the subordinate and mutual grooming
'UM' sessions, in which there is unilateral grooming by only one, and mutual grooming.
'DSM' sessions with unilateral grooming by the dominant and by the subordinate, and with mutual grooming.

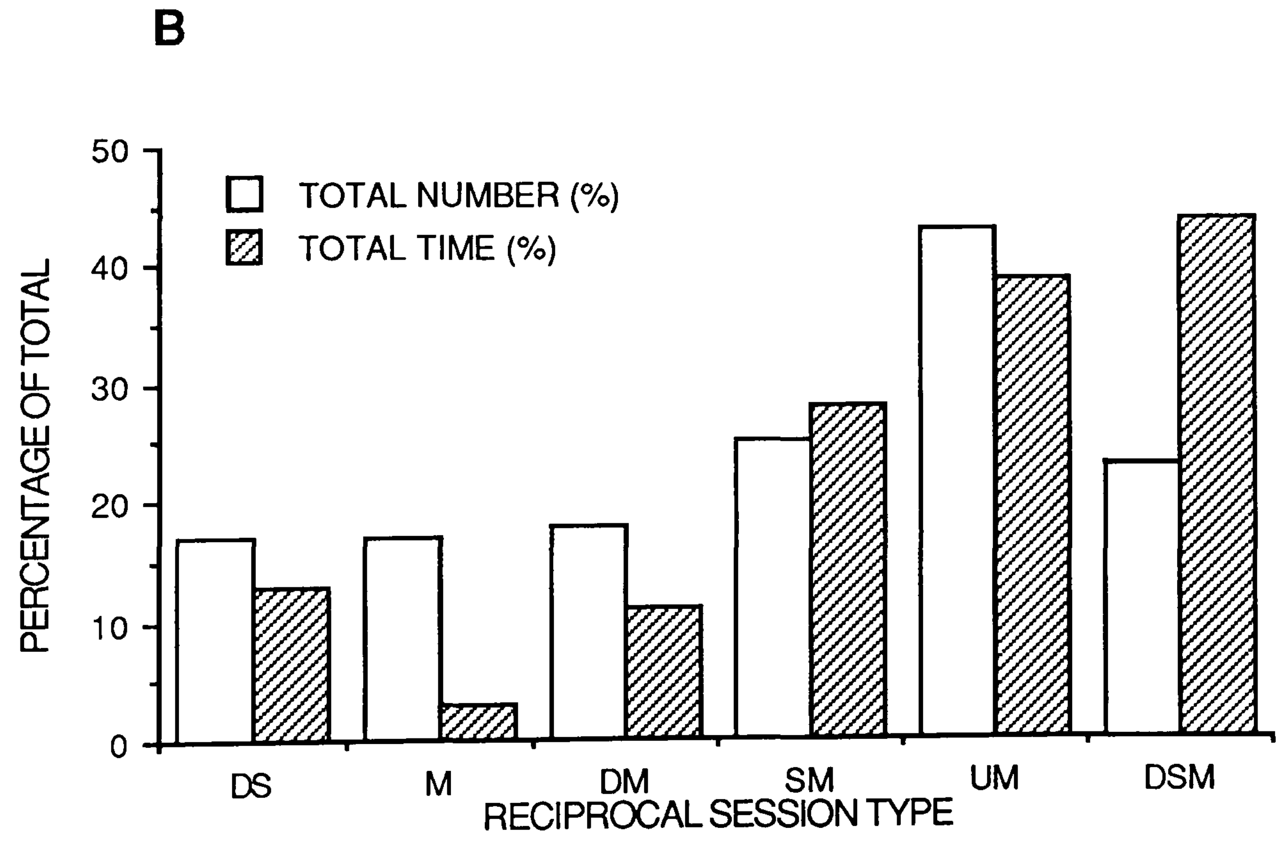


Fig. 6.2b. Percentages of total time and number of reciprocal grooming sessions during phase six, in the presence of oestrous females.

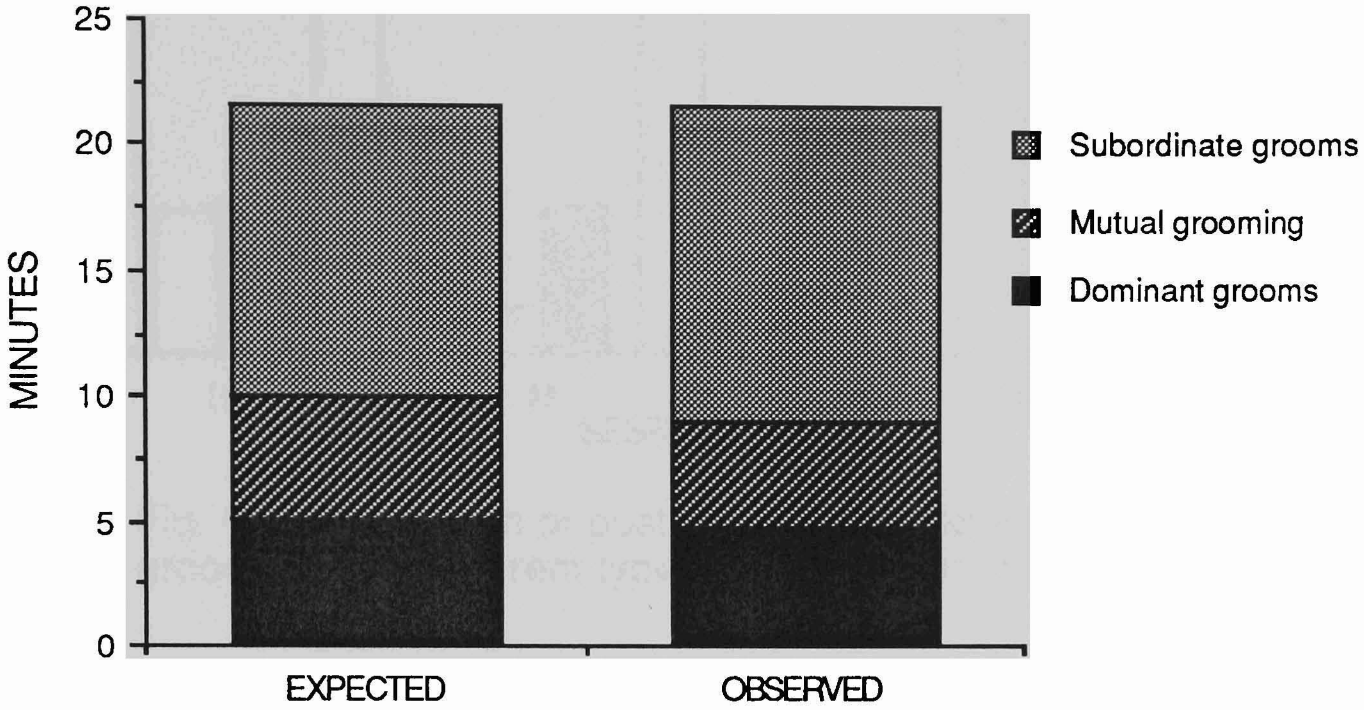


Fig. 6.3. Expected and observed values of unilateral and mutual grooming for inter-opponent post-attack grooming sessions in phase six.

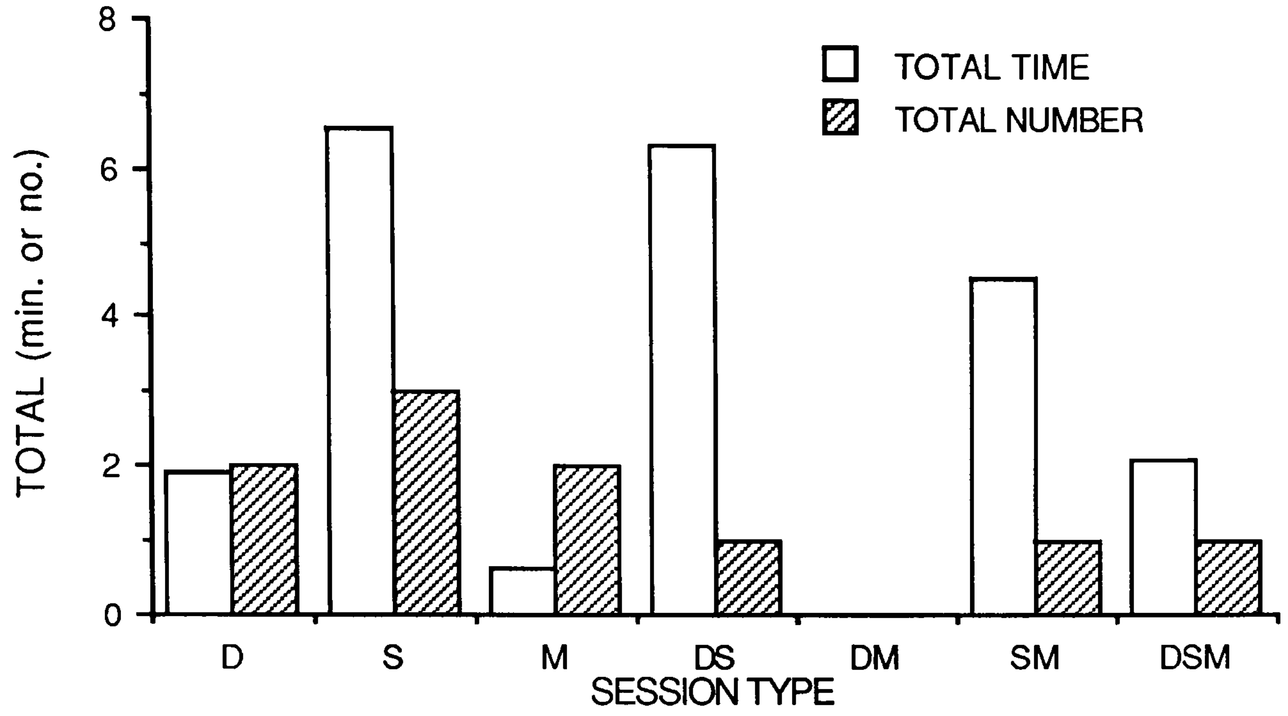


Fig. 6.4. Distribution of post-attack inter-opponent grooming over different types of session, in phase six.

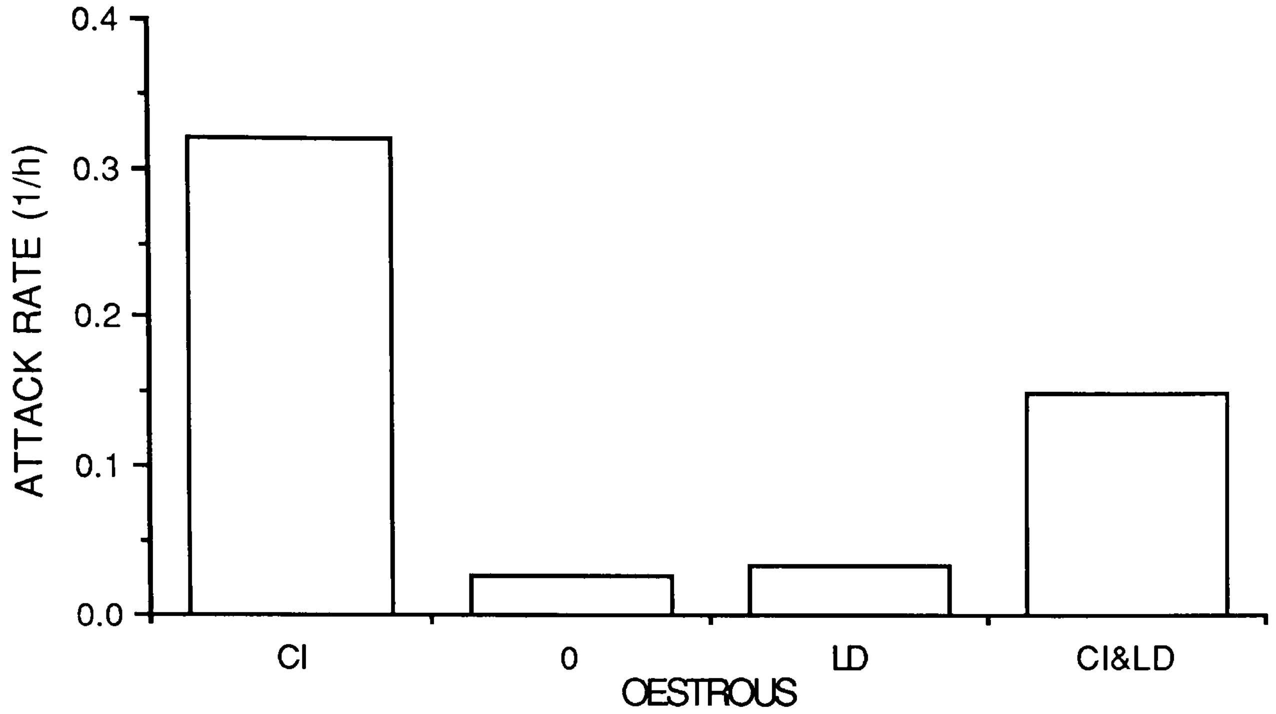


Fig. 6.5. Rate of male-male attacks during periods with and without oestrous females in phase six. CI: Cindy oestrous; LD: Lyndsey oestrous; 0: none oestrous.

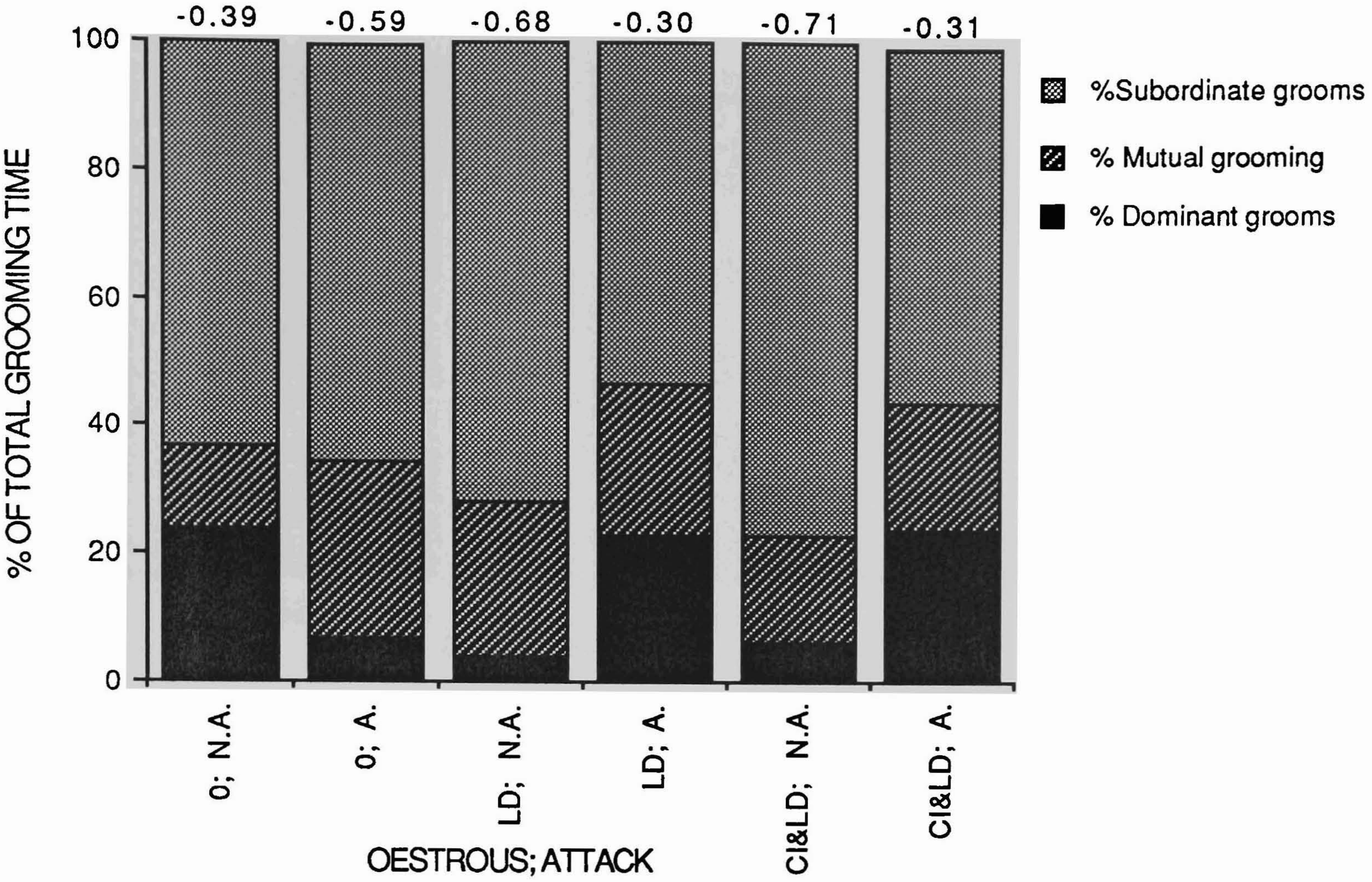


Fig. 6.6. Distribution of grooming time in phase six over 'attack days' (A) and 'no attack days' (N.A.) with and without oestrous females (CI: Cindy oestrous; LD: Lyndsey oestrous; 0: none oestrous).

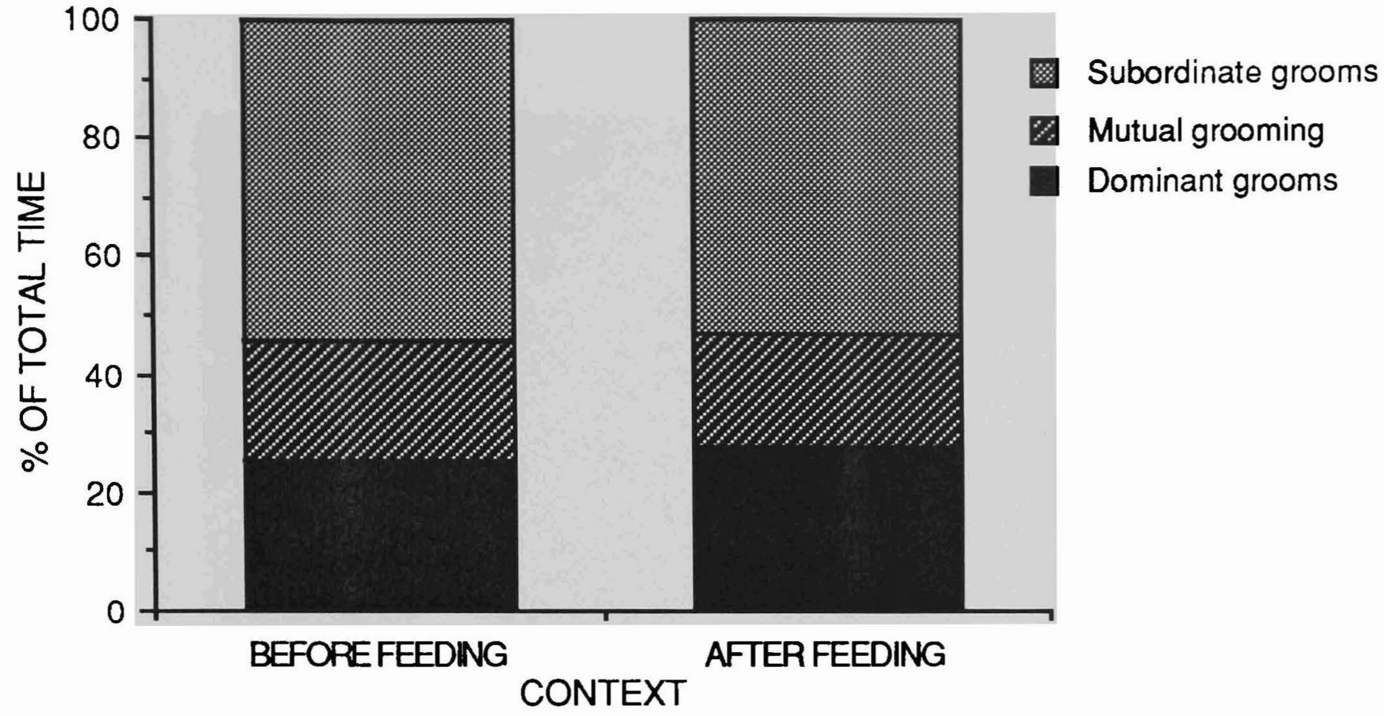


Fig. 6.7. Distribution of time spent in grooming before and after feeding over unilateral and mutual, in phase six.

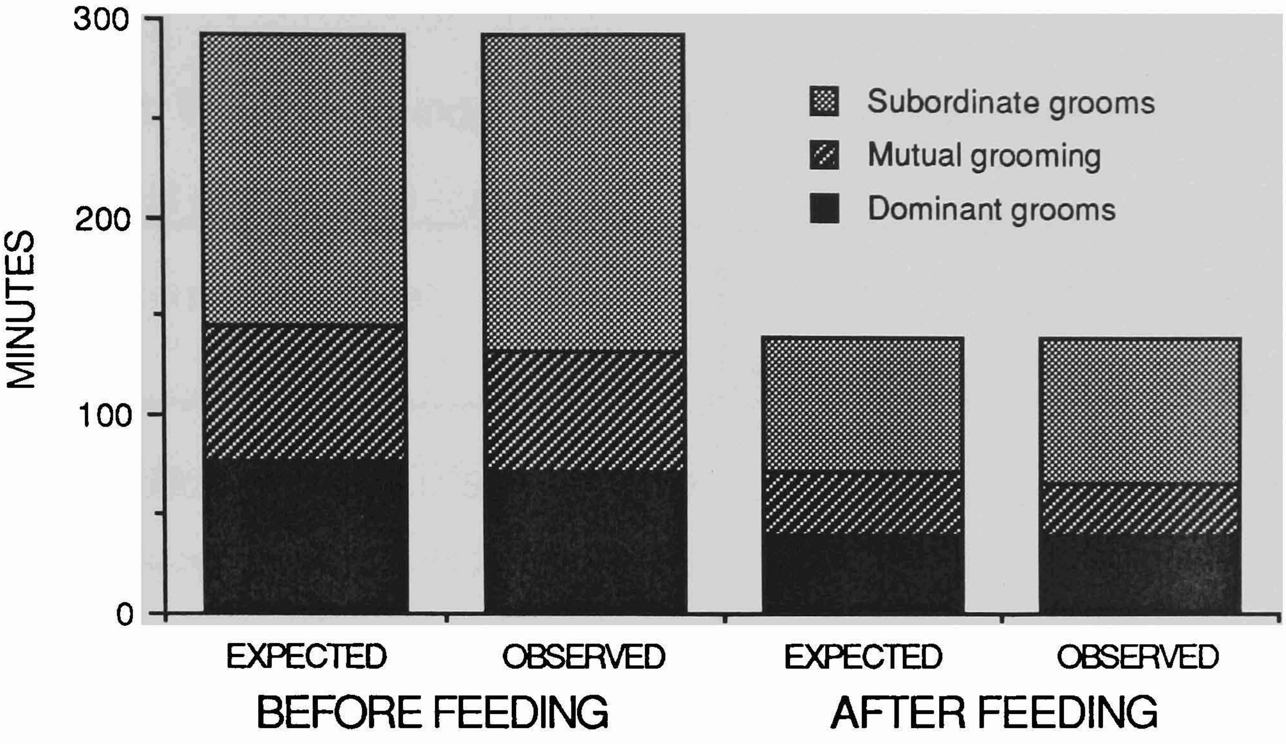


Fig. 6.8. Expected and observed values of unilateral and mutual grooming, before and after feeding in phase six.

Table 6.I. The four periods of observations in phase six, with dates and total number of observation hours.

Observation periods	Dates	Days from October 1, 1991	Observation hours (rounded)
1. Cindy oestrous	9/6/1992 - 12/6/1992	253-256	38
2. no oestrous	16/6/1992 - 19/6/1992 23/6/1992 - 26/6/1992	260-263 267-270	74
3. Lyndsey oestrous	29/6/1993 - 1/7/1992	273-275	29
4. Cindy & Lyndsey oestrous	6/7/1992 - 10/7/1992	280-284	47
	Total	20	188

Table 6.II. Matrices of grooming totals (A), and of unilateral grooming (B, in minutes) given and received in observation phase six. Figures were rounded to the nearest minute for the matrix correlations, which were done for male-male grooming only. Female-female grooming was not recorded systematically and, therefore, omitted from the table. Male-female grooming was recorded less systematically than male-male grooming, but is included here for completeness.

A

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM	CINDY	LUCY	EMMA	LYNDSEY	TOTALS
LEO	-	110.00	8.98	42.46	101.14	45.29	68.79	242.66	92.73	712.05
DAVID	263.72	-	115.95	37.57	27.13	112.67	26.61	7.86	32.19	623.70
LOUIS	112.20	34.56	-	331.55	90.75	340.71	31.41	7.86	18.33	969.48
RICKY	54.27	38.85	645.90	-	4.16	0	10.49	0.27	0	753.94
TOM	246.02	6.84	36.50	3.56	-	11.77	2.12	7.95	0	314.76
CINDY	4.53	0	0	0	0	-	-	-	-	4.53
LUCY	25.53	3.3	9.19	6.94	7.6	-	-	-	-	52.56
EMMA	91.31	2.96	0	.27	9.14	-	-	-	-	103.68
LYNDSEY	1.03	1.95	0	0.40	0	-	-	-	-	3.38
TOTALS	798.61	198.46	816.52	422.75	239.92	510.44	139.42	268.71	143.25	3538.08

Male-male matrix:
K_r=20; p_r=0.0180
R=2584.50; p_r=0.0570
Z=561496; p_r=0.0750

B

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM	CINDY	LUCY	EMMA	LYNDSEY	TOTALS
LEO	-	74.81	0.08	3.02	29.74	45.19	61.36	222.21	92.73	529.14
DAVID	228.53	-	82.93	32.91	22.16	112.67	24.79	6.06	32.19	542.24
LOUIS	103.30	1.54	-	120.32	56.34	340.71	31.41	9.97	18.33	681.92
RICKY	14.83	34.19	434.67	-	1.78	0.00	7.80	0.00	0.00	493.27
TOM	174.62	1.87	2.09	1.18	-	11.77	18.00	4.07	0.00	213.60
CINDY	4.43	0.00	0.00	0.00	0.00	-	-	-	-	4.43
LUCY	18.10	1.45	9.19	4.25	7.60	-	-	-	-	40.59
EMMA	70.86	1.16	0.00	0.00	5.26	-	-	-	-	77.28
LYNDSEY	0.00	1.95	0.00	0.40	0.00	-	-	-	-	2.35
TOTALS	614.67	116.97	528.96	162.08	122.88	510.34	143.36	242.31	143.25	2584.82

Male-male matrix:
K_r=16; p_r=0.0515
R=2331.00; p_r=0.2744
Z=152232; p_r=0.1609

Table 6.III. Matrices of grooming totals (A), and of unilateral grooming (B, in minutes) given and received in part of observation phase six, when no females were in oestrous.

A

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM	CINDY	LUCY	EMMA	LYNDSEY	TOTALS
LEO	-	40.66	2.56	23.7	9.07	25.10	24.36	90.14	8.22	712.05
DAVID	67.78	-	15.26	5.41	4.13	0.40	5.65	0.85	0	623.70
LOUIS	36.60	1.02	-	33.29	2.98	150.85	9.73	0.68	0.92	969.48
RICKY	26.93	3.07	164.04	-	3.56	0	2.02	0	0	753.94
TOM	11.54	1.32	3.33	2.96	-	0	0.29	0.45	0	314.76
CINDY	0	0	0	0	0	-	-	-	-	4.53
LUCY	10.46	2.05	5.49	0.80	2.79	-	-	-	-	52.56
EMMA	37.52	0.53	0	0	0.75	-	-	-	-	103.68
LYNDSEY	0	0	0	0	0	-	-	-	-	3.38
TOTALS	798.61	198.46	816.52	422.75	239.92	510.44	139.42	268.71	143.25	3538.08

Male-male matrix:
K_r=10; p_r=0.0990
R=2477.50; p_r=0.0650
Z=18244; p_r=0.1000

B

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM	CINDY	LUCY	EMMA	LYNDSEY	TOTALS
LEO	-	20.93	0.08	2.94	3.43	25.10	20.63	78.45	8.22	159.78
DAVID	48.05	-	15.26	4.56	4.13	0.40	3.80	0.85	0.00	77.05
LOUIS	34.12	1.02	-	16.10	0.43	150.85	9.56	0.68	0.92	213.68
RICKY	6.17	2.22	146.85	-	1.78	0.00	1.22	0.00	0.00	158.24
TOM	5.90	1.32	0.78	1.18	-	0.00	0.29	0.45	0.00	9.92
CINDY	0.00	0.00	0.00	0.00	0.00	-	-	-	-	0.00
LUCY	5.26	0.20	5.32	0.00	2.79	-	-	-	-	13.57
EMMA	25.83	0.53	0.00	0.00	0.75	-	-	-	-	27.11
LYNDSEY	0.00	0.00	0.00	0.00	0.00	-	-	-	-	0.00
TOTALS	125.33	26.22	168.29	24.78	13.31	176.35	35.50	80.43	9.14	659.35

Male-male matrix:
K_r=8; p_r=0.1079
R=2348; p_r=0.2134
Z=6854; p_r=0.1664

Table 6.IV. Matrices of grooming totals (A), and of unilateral grooming (B, in minutes) given and received in part of observation phase six, when there was one oestrous female present.

A

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM	CINDY	LUCY	EMMA	LYNDSEY	TOTALS
LEO	-	36.38	3.06	18.41	76.32	9.13	25.09	62.01	26.22	256.62
DAVID	124.04	-	56.22	14.96	17.85	55.31	6.88	2.07	0.00	277.33
LOUIS	44.89	20.95	-	192.44	90.32	24.36	16.12	4.65	0.53	394.26
RICKY	26.87	6.17	233.97	-	0.40	0.00	7.94	0.00	0.00	275.35
TOM	163.73	5.07	29.61	0.40	-	11.77	0.49	0.15	0.00	211.22
CINDY	4.53	0.00	0.00	0.00	0.00	-	-	-	-	4.53
LUCY	4.01	0.40	1.63	6.14	3.89	-	-	-	-	16.07
EMMA	25.39	0.45	0.00	0.00	0.94	-	-	-	-	26.78
LYNDSEY	1.03	1.95	0.00	0.40	0.00	-	-	-	-	3.38
TOTALS	394.49	71.37	324.49	232.75	189.72	100.57	56.52	68.88	26.75	1465.54

Male-male matrix:
K_r=20; p_r=0.0340
R=2664.5; p_r=0.0480
Z=133066; p_r=0.0150

B

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM	CINDY	LUCY	EMMA	LYNDSEY	TOTALS
LEO	-	29.56	0.00	0.00	23.86	9.03	22.70	61.28	26.22	172.65
DAVID	117.22	-	35.27	14.83	13.33	55.31	6.88	2.07	0.00	244.91
LOUIS	41.83	0.00	-	67.40	51.71	24.36	16.12	4.65	0.53	206.60
RICKY	8.46	6.04	108.93	-	0.00	0.00	6.05	0.00	0.00	129.48
TOM	111.27	0.55	0.00	0.00	-	11.77	0.49	0.15	0.00	124.23
CINDY	4.43	0.00	0.00	0.00	0.00	-	-	-	-	4.43
LUCY	1.62	0.40	1.63	4.25	3.89	-	-	-	-	11.79
EMMA	24.66	0.45	0.00	0.00	0.94	-	-	-	-	26.05
LYNDSEY	1.03	1.95	0.00	0.40	0.00	-	-	-	-	3.38
TOTALS	310.52	38.95	145.83	86.88	93.73	100.47	52.24	68.15	26.75	923.52

Male-male matrix:
K_r=12; p_r=0.1069
R=2306.5; p_r=0.3093
Z=27160; p_r=0.2139

Table 6.V. Matrices of grooming totals (A), and of unilateral grooming (B, in minutes) given and received in part of observation phase six, when there were two oestrous females present.

A

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM	CINDY	LUCY	EMMA	LYNDSEY	TOTALS
LEO	-	32.96	3.36	0.35	15.75	11.06	19.33	90.51	58.29	231.61
DAVID	71.90	-	44.37	17.20	5.15	56.96	14.08	4.94	32.19	246.79
LOUIS	30.71	12.59	-	105.82	6.45	165.18	5.56	4.64	16.88	347.83
RICKY	0.47	29.61	247.89	-	0.20	0.00	0.53	0.27	0.00	278.97
TOM	70.75	0.45	3.56	0.20	-	0.00	1.34	7.35	0.00	83.65
CINDY	0.00	0.00	0.00	0.00	0.00	-	-	-	-	0.00
LUCY	13.53	0.85	2.07	0.00	0.92	-	-	-	-	17.37
EMMA	28.40	1.98	0.00	0.27	7.45	-	-	-	-	38.10
LYNDSEY	0.00	0.00	0.00	0.00	0.00	-	-	-	-	0.00
TOTALS	215.76	78.44	301.25	123.84	35.92	233.20	40.84	107.71	107.36	1244.32

Male-male matrix:
K_r=22; p_r=0.0045
R=2684; p_r=0.0045
Z=61998; p_r=0.0695

B

GROOMED GROOMS	LEO	DAVID	LOUIS	RICKY	TOM	CINDY	LUCY	EMMA	LYNDSEY	TOTALS
LEO	-	24.32	0.00	0.08	2.45	11.06	18.03	82.48	58.29	196.71
DAVID	63.26	-	32.30	13.52	4.70	56.96	14.08	3.14	32.19	220.15
LOUIS	27.35	0.52	-	36.82	4.20	165.18	5.56	4.64	16.88	261.15
RICKY	0.20	25.93	178.89	-	0.00	0.00	0.53	0.00	0.00	205.55
TOM	57.45	0.00	1.31	0.00	-	0.00	1.34	3.47	0.00	63.57
CINDY	0.00	0.00	0.00	0.00	0.00	-	-	-	-	0.00
LUCY	11.22	0.85	2.07	0.00	0.92	-	-	-	-	15.06
EMMA	20.37	0.18	0.00	0.00	3.57	-	-	-	-	24.12
LYNDSEY	0.00	0.00	0.00	0.00	0.00	-	-	-	-	0.00
TOTALS	179.85	51.80	214.57	50.42	15.84	233.2	39.54	93.73	107.36	986.31

Male-male matrix:
K_r=11; p_r=0.0840
R=2455; p_r=0.1004
Z=17298; p_r=0.1384

Table 6.VI. Total numbers of, total times (min.), and median durations (min.) of reciprocal and non-reciprocal grooming sessions for all male-male dyads in phase six. See Table 4.III for phase two.

Dyad	Total no. (reciprocal)	Total no. (non-reciprocal)	Total time (reciprocal)	Total time (non-reciprocal)	Median dur. (reciprocal)	Median dur. (non-reciprocal)
Le-Da	19	35	217.96	120.57	10.21	1.65
Le-Lo	5	19	37.65	74.63	4.54	1.95
Le-Ri	15	5	54.01	3.28	3.02	0.23
Le-To	16	23	195.35	80.41	10.17	2.09
Da-Lo	6	23	53.08	64.41	6.67	1.85
Da-Ri	3	17	18.20	53.56	1.40	1.27
Da-To	10	11	14.16	14.85	1.24	0.63
Lo-Ri	21	32	558.02	208.20	23.32	5.12
Lo-To	9	8	64.35	28.49	6.63	0.59
Ri- To	3	3	2.78	2.56	0.40	0.60
Total	107	176	1215.56	650.95	-	-
Median	18	9.5	53.55	58.99	5.59	1.46

Table 6.VII. Distribution of the frequency and total time of non-reciprocal grooming sessions (D and S sessions) over the ten male-male dyads in phase six. See Table 4.IV for phase two.

Dyad D-S	Total time D	Frequency D	Total time S	Frequency S
Le-Da	19.67	6	100.90	29
Le-Lo	0.08	1	74.55	18
Le-Ri	2.23	1	1.05	4
Le-To	7.87	4	72.54	19
Da-Lo	63.39	22	1.02	1
Da-Ri	21.24	11	32.32	6
Da-To	14.32	10	0.52	1
Lo-Ri	11.72	3	196.48	29
Lo-To	28.49	8	0	0
Ri-To	1.38	1	1.18	2
Totals	170.39	67	480.56	109

Table 6.VIIIa. Distribution of all reciprocal grooming sessions over the ten different dyads in phase six. For explanation of session types see Methods. First values are total numbers, second values are total times (min.). See Table 4.Va for phase two.

Dyad D-S	DS sessions	M sessions	UM sessions	DSM sessions	Totals
Le-Da	10; 120.37	0; 0	3; 23.81	6; 73.78	19; 217.96
Le-Lo	0; 0	1; 2.03	4; 35.62	0; 0	5; 37.65
Le-Ri	2; 6.52	6; 25.04	6; 10.24	1; 12.21	15; 54.01
Le-To	4; 32.55	1; 4.32	9; 120.20	2; 38.28	16; 195.35
Da-Lo	0; 0	1; 0.55	4; 37.02	1; 15.51	6; 53.08
Da-Ri	1; 1.32	0; 0	1; 1.40	1; 15.48	3; 18.20
Da-To	1; 2.05	4; 1.16	4; 8.84	1; 2.11	10; 14.16
Lo-Ri	0; 0	0; 0	10; 187.55	11; 370.47	21; 558.02
Lo-To	0; 0	3; 8.04	4; 46.26	2; 10.05	9; 64.35
Ri-To	0; 0	2; 0.60	1; 2.18	0; 0	3; 2.78
Totals	18; 162.81	18; 41.74	46; 473.12	25; 537.89	107;1215.56

Table 6.VIIIb. Median duration of mutual and unilateral grooming as it occurred in different types of reciprocal grooming session in phase six. M=mutual grooming, D=unilateral grooming by the dominant male, S=unilateral grooming by the subordinate male. U=unilateral grooming by any male (see Table 4.Vb for phase two).

Configuration (session type)	Median duration (min.)
D (D)	1.16
D (DS)	0.73
D (DM)	1.92
D (DSM)	2.88
M (M)	0.50
M (DM)	1.32
M (SM)	3.38
M (UM)	3.45
U (UM)	3.77
M (DSM)	6.85
S (S)	1.65
S (DS)	3.22
S (SM)	4.73
S (DSM)	1.37

Table 6.IX. Total number of attacks between males in the sixth observation phase.

ATTACKED ATTACKS	LEO	DAVID	LOUIS	RICKY	TOM	TOTAL
LEO	-	1	5	0	4	10
DAVID	2	-	3	1	5	11
LOUIS	0	1	-	0	0	1
RICKY	0	0	0	-	0	0
TOM	0	0	0	0	-	0
TOTAL	2	2	8	1	9	22

CHAPTER VII

INDIVIDUAL DIFFERENCES BETWEEN DYADS AND ANALYSIS OF GROOMING OVER DIFFERENT TIME-SPANS.

(With an emphasis on the relationship between the alpha and beta males)

INTRODUCTION

In the previous chapters data were analysed for all dyads together. In this chapter, differences between dyads in the distribution of their grooming over unilateral and mutual grooming, and over different session types will be investigated. Additionally, the balance of grooming given and received will be traced over consecutive sessions between the same individuals, occurring on the same day, on several consecutive days, and over the whole of phase six, in order to investigate whether grooming is reciprocated over time-spans longer than a session.

RESULTS

Total grooming time and distribution over mutual and unilateral grooming

Fig. 7.1 gives for each dyad the distribution over mutual and unilateral grooming and the percentage of observation time spent in grooming, in the different observation periods. Fig. 7.2 gives the absolute values of grooming for each dyad in the different observation periods. These two figures reveal marked differences between the dyads. There were large differences in the time each dyad spent in grooming, as well as differences between the dyads in the way grooming changed in the presence of oestrous females. For example, the alpha and beta male, Le and Da, groomed more than any other dyad in phase two, but in the period with one oestrous female they groomed less than Le-To and Lo-Ri (Fig. 7.2).

Grooming between Da-Lo, Da-Ri, and Lo-Ri increased from phase two to oestrus=2, whereas grooming between Le-Da, Le-To, and Lo-To first decreased from phase two to oestrus=0, increased in oestrus=1, and decreased in oestrus=2 (Fig. 7.1). This latter pattern seemed to be confirmed in the remaining four dyads, which never had more grooming in the periods without or with two oestrous females than in the period with one oestrous female in phase six.

Le-Lo groomed less in oestrus=0 than in phase two, and their grooming was always lower in phase six than in phase two. Grooming increased again in oestrus=1, but stayed the same in oestrus=2.

Da-To's grooming conformed to the second pattern during phase six, but they generally groomed more, instead of less in phase six than in phase two. Ri-To groomed less in oestrus=0 than in phase two, and less in oestrus=2 than in oestrus=1, but they groomed as much in oestrus=1 as in oestrus=0.

Only the grooming between Le-Ri seemed to follow a unique pattern, in which grooming in oestrus=0 was higher than in phase two and stayed the same in oestrus=1, with almost no grooming at all in oestrus=2. However, Le-Ri , Da-To, and Ri-To never groomed more than 1% of observation time.

Closer inspection of the grooming by Le-Da reveals that, at the same time, there was a gradual increase in unilateral grooming by Da, and a decrease in both unilateral grooming by Le and mutual grooming from phase two to oestrus=1. This trend then reversed in oestrus=2, in which Le's unilateral grooming and mutual grooming increased slightly, while Da's unilateral grooming decreased again.

However, there was never a clear association between the changes in the amount of grooming over the different periods, and the distribution of grooming in those periods over the different configurations. Thus, dyads that showed a gradual increase in the total time spent grooming in the different periods, did not all show similar changes in the relative time spent grooming unilaterally or mutually. The same was true for the dyads that showed the other pattern of changes over the oestrus periods.

From the figures it can be seen that the alpha and beta males had quite different grooming 'tactics'. Le was always groomed more unilaterally than he groomed unilaterally (except in phase two by Da and Ri). Da, however, almost always groomed more unilaterally than he was groomed unilaterally. Perhaps this means that Le's relationships were quite stable, whereas Da had to keep working on the other males in order to make or keep them as his allies. For example, Da's ally Lo (see section 'Dominance' in Chapter II) groomed Le almost totally unilaterally, probably indicating his subordinance, whereas Le's ally To was almost exclusively groomed unilaterally by Da, probably in an attempt to make him his ally.

It is of interest to have a closer look at the grooming relationships of Ri. As Ri never showed any sexual interest in the females and was certainly never observed to mate, no changes would be expected in his grooming relationships over the different oestrus periods. However, there was a gradual increase in Ri's unilateral grooming of Le from phase two to oestrus=1 in phase six (ignoring their grooming at oestrus=2, when they only groomed for a total of 0.55 min.).

As aggression occurred more frequently when there were females in oestrus, Ri's grooming relationship with Le suggests that the influence of oestrous females on the grooming relationships between the males in general is indirect, through an increase in the level of aggression, rather than direct, through sexual bargaining.

Session types and their balance with and without oestrous females

Here dyads will be compared in how their grooming was distributed over the different session types in phase two and phase six, in which phase six as a whole was a period with, and phase two a period without oestrous females. Fig. 7.3 gives for each dyad the total number of grooming sessions, and the percentages of total grooming spent in each session type, for the two observation phases (see also Table 6.VIIIa). Fig. 7.4 gives for each dyad the median duration and the RIT values of grooming sessions in the two observation phases.

For each dyad there were differences between the two observation phases in the distribution of grooming over the session types. However, please note that most dyads had only few sessions of each type, and a comparison of the median duration of those particular session types may therefore not be valid.

Therefore, only sessions with a total number of three or more in both phases two and six will be compared. Thus, Le-Da spent a lower proportion of time in 'D' and 'DSM' sessions in phase six, and a higher proportion in S sessions in phase six (Fig. 7.3). Their 'DSM' sessions were less balanced in phase six than in phase two (Fig. 7.4).

Le-Lo spent a higher proportion of time in 'S' sessions in phase six (Fig. 7.3). Le-To also spent a higher proportion of time in 'S' sessions, and a lower proportion in 'DM' sessions in phase six (Fig. 7.3). These latter sessions were similarly balanced in both phases (Fig. 7.4). Da-Lo spent a higher proportion of time in 'D' sessions in phase six (Fig. 7.3). Lo-Ri a higher proportion of time in 'S' and 'SM' sessions in phase six than in phase two (Fig. 7.3). These latter sessions were similarly balanced in both phases (Fig. 7.4).

Fig. 7.5 gives the median duration of mutual and unilateral grooming for the DSM sessions between Le-Da, and the DM sessions between Le-To. All configuration in the DSM sessions between Le-Da had a shorter median duration in phase six, the difference being largest for mutual grooming, and smallest for unilateral grooming by Le. Mutual grooming by Le-To was also shorter in DM sessions in phase six, but unilateral grooming by Le in these sessions had a higher median duration in phase six than in phase two.

Grooming balance over consecutive grooming sessions on the same day

If grooming would be reciprocated on consecutive sessions, then the cumulative RIT values (RIT_C) for a sequence of sessions should follow a wave-like curve, as the imbalance in one session will be brought into balance by a similar but opposite imbalance in the next session. This wave pattern will gradually die out as the relative imbalance decreases with increasing accumulated grooming time. Finally, it will stabilise at $RIT=0$ for an 1:1 exchange rate, or at $RIT\neq0$ for any other exchange rate (Fig. 7.6). The same argument holds for reciprocation of grooming over days.

Fig. 7.7a-h gives for each dyad the accumulative time and accumulative RIT of grooming for each day that a dyad had three or more sessions. Fig. 7.8 gives for each dyad the accumulative time and RIT of grooming for consecutive days within each observation period of phase six.

With consecutive grooming sessions on the same day the RIT_C usually changed in the general direction of the RIT value of the particular period (Fig 7.7 & 7.9). There were eight days on which Le-Da had more than two consecutive grooming sessions (Fig. 7.7a). At the end of days 253 and 254, during a period with one oestrous female (Table 6.I), their RIT_C

was similar to the total RIT of -0.57 in the presence of one oestrous female (Fig. 7.9). On day 280 and 282, the RIT_C was similar to the total RIT of -0.40 for the period with two oestrous females. The RIT_C at the end of day 267, without oestrous females, is also similar to the total value of RIT (-0.31) in the absence of oestrous females. This was not clearly visible on days 261, 270 and 275. However, on days 261 and 275 Le-Da groomed only very little, making the RIT values less significant. There is no strong indication of grooming reciprocation across sessions.

Grooming between Le-Lo on day 281 (Fig 7.7b) ended at the same level of imbalance as their grooming over the whole of phase six (Fig. 7.9), and grooming between Le-Ri on day 267 stayed almost perfectly reciprocal (Fig. 7.7c), as their grooming for the whole period without oestrous females (Fig. 7.9), but on day 263 their grooming ended in an imbalance. There is no strong indication of grooming reciprocation across sessions.

Grooming between Le-To was almost fully imbalanced on day 254, but on days 255, 256, 280, and 282 the balance at the end of the day was similar to the total balance for the period in which each day occurred (Fig 7.7d & 7.9). On day 284 Le-To had three consecutive sessions, but these were very short, and totally unilateral.

Da-Lo had more than two consecutive sessions on five days (Fig 7.7e). On three of these did the final imbalance in grooming compare to the total imbalance over the particular period (Fig. 7.9, days 256, 281, 282). On day 254 grooming was fully imbalanced throughout, whereas on day 253 grooming at the end of the day was more balanced than over the total period.

Grooming between Da-Ri was more imbalanced at the end of day 282, and less at the end of day 253 than over the whole of the periods with two and one oestrous females respectively (Fig 7.7f & 7.9). Da-To's grooming seemed to reach an imbalance at the end of day 254, similar to the total imbalance over the period with one oestrous female, but their grooming totals were quite low (Fig 7.7g & 7.9 & 7.2). There was some reciprocation of grooming across sessions between Da-Lo on day 253 and 255, and between Da-Ri on day 253 (Fig 7.7e, f & 7.9).

Lo-Ri had 9 days with more than two consecutive sessions (Fig. 7.7h). When there was one oestrous females (days 254-256) grooming at the end of the day had always reached a balance similar to the balance over the whole period with one oestrous female (Fig. 7.9). On day 262 grooming ended less imbalanced than at the end of the whole period without oestrous females. Of the days with two oestrous females, three ended at a greater imbalance, one at the same imbalance and one at a smaller imbalance than the total imbalance for that period. There was no reciprocation of grooming across sessions.

Lo-To had three days with more than two consecutive session, all during a period with one oestrous female (Fig. 7.7i). On two of these (253 and 255) did the imbalance at the end of the day compare with that for the whole period (Fig. 7.9). On day 256 there was a smaller imbalance than over the whole period. There was no reciprocation across session.

Grooming balance of sessions over consecutive days in phase six

Perhaps grooming is reciprocated, not in the next session, but over a series of consecutive sessions over several consecutive days. Fig. 7.8 shows the RIT_C for each dyad in each period of three to five consecutive days in phase six.

Le-Da's grooming followed a pattern of grooming reciprocation across sessions, or even days, in which the imbalance in their grooming at the beginning of each period was first small or in the direction of Le (RIT>0), but then gradually tailed off in the direction of Da (RIT<0). This did not just happen at the beginning of a series of consecutive days (at which point the RIT is based on one grooming session only, and the effect thus amplified), but also within such series. Thus, a session in which the imbalance moved towards Le was often followed by a number of sessions that shifted the imbalance back towards Da. The level at which the imbalance stabilised at the end of each series of consecutive days depended on the presence of oestrous females. Note, for example, how during the two periods without oestrous females (day 260-263 and 267-270) there was a step-wise shift of the imbalance in the direction of Le, which reached its maximum during Ld's oestrus, and then shifted back to Da when both Ld and Ci were in oestrus.

A similar pattern was also recognized in the grooming between Lo-Ri in the first period without oestrous females (day 260-263), in which there was a step-wise shift in the imbalance of their grooming towards Ri. The grooming pattern of Da-Ri showed an approximation of a wave-like pattern in the value of RIT_C during days 253-256 and 280-283, and that of Le-To perhaps on days 253-256. The other dyads either did not show such patterns (Le-Lo, Le-Ri, Da-Lo, Da-To, Lo-To), or their grooming patterns could not be determined because they had not groomed enough on consecutive days (Ri-To).

Grooming balance during phase six

Fig. 7.10 gives the RIT_C (per day) for each dyad over the whole observation phase six. The graphs in this figure illustrate how the balance in grooming changes in the course of a relatively long period of five weeks, and reveals some important aspects of the dyadic relationships.

Excluding Ri-To, three general patterns emerge: a gradual increase in the imbalance in grooming, a stable imbalance in grooming, and a gradual decrease in the imbalance of grooming. It is also clear that at this level of analysis (i.e. days instead of sessions) there were generally only small fluctuations in the level of imbalance, reflecting the little importance short-term imbalances in grooming have to established grooming relationships.

The three patterns just mentioned give some insight into the degree of reciprocity of the grooming relationships. Thus, if there is almost no reciprocation of grooming, a movement towards a greater imbalance results (Lo-Ri, Le-To). This kind of grooming relationship is probably primarily governed by dominance-subordinance dynamics.

If there is some degree of reciprocation, but at an unequal exchange rate (i.e. only a certain proportion of grooming received is given back), then the imbalance in grooming will be stable over time (Le-Lo, Da-Lo, Da-To, and Lo-To). These grooming relationships are governed by both dominance and grooming reciprocation, i.e. they are less polarized than the relationship between Lo-Ri and Le-To.

If, however, there is a high degree of grooming reciprocation, the imbalance in grooming will become smaller with time (Le-Da, Le-Ri, Da-Ri). In these grooming relationships reciprocation rather than dominance is most important. Thus, the pattern of RIT_C over time, rather than the final value of RIT at the end of an observation period, indicates the real nature of reciprocation in a specific grooming relationship.

DISCUSSION

There were two patterns of changes in the amount of time spent in grooming in the presence of varying numbers of oestrous females. In the first pattern, time spent in grooming increased when there were more oestrous females present, and was higher in the period without oestrous females in phase six than in phase two, probably as a result of 'spill-over' from the preceding and following periods with oestrous females. This pattern applied only to the grooming between Da-Lo, Da-Ri, and Lo-Ri, but changes in unilateral and mutual grooming were not consistent between these dyads.

The second pattern of changes showed generally a lower level of grooming in phase six than in phase two, but within phase six grooming was highest when there was only one oestrous female present. This pattern was only clear for Le-Da, Le-To, and Lo-To, but seemed to apply to the remaining four dyads as well, which never had more grooming in the periods without or with two oestrous females than in the period with one oestrous female in phase six.

Clearly the presence of oestrous females affected the dyads in different ways, depending on the nature of their grooming relationship. For example, the low levels of mutual grooming by Le-Da indicate that grooming cooperation within this dyad broke down in the presence of oestrous females. In the presence of one oestrous female, their total grooming was slightly up, probably as a result of increased tension, but their mutual grooming reached its lowest point, indicating the absence of cooperation.

In contrast, the other dyads often groomed more when there were oestrous females, and in some of them grooming increased with an increasing number of oestrous females, indicating that competition in these dyads increased when there were more oestrous females. However, changes in their mutual and unilateral grooming did not follow such a clear pattern.

In the presence of oestrous females, a higher proportion of grooming sessions was totally unilateral from subordinate to dominant, and DSM sessions between Le-Da were considerably more imbalanced in the presence of oestrous females. These results suggest a polarisation of dominance relationships, and confirm the breakdown of co-operation in grooming. Alternatively, the increase in sessions with only unilateral grooming by the subordinate could indicate a higher occurrence of 'sexual bargaining' (de Waal, 1982), or the declaration of a higher commitment to the relationship by the subordinates (Simpson, 1991).

Reciprocation of grooming over consecutive sessions generally resulted in a grooming imbalance at the end of most days similar to the total imbalance in grooming over the specific period in phase six, for a particular dyad. Thus, although grooming was primarily reciprocated within sessions in both phases two and six (see Chapter IV&VI), the nature of the grooming relationship, in terms of the overall (im)balance in grooming, became apparent only at the end of each day.

There was some indication of reciprocation of grooming over consecutive sessions, and even over consecutive days, but there was no evidence for the use of a simple strategy, such as TIT-FOR-TAT, in the reciprocation of grooming across sessions, or days. This is in contrast to the TIT-FOR-TAT like system of allogrooming in impala (Hart & Hart, 1992) which is the only example of the use of this strategy in allogrooming. Instead, some dyads groomed according to an 'investment' strategy, in which an initial imbalance in grooming was gradually reciprocated in the course of several days.

No strategies of grooming reciprocation emerged from an analysis over the whole of phase six, but important differences between dyads emerged, which suggested that dyads differ in the importance dominance and grooming cooperation have to their relationship.

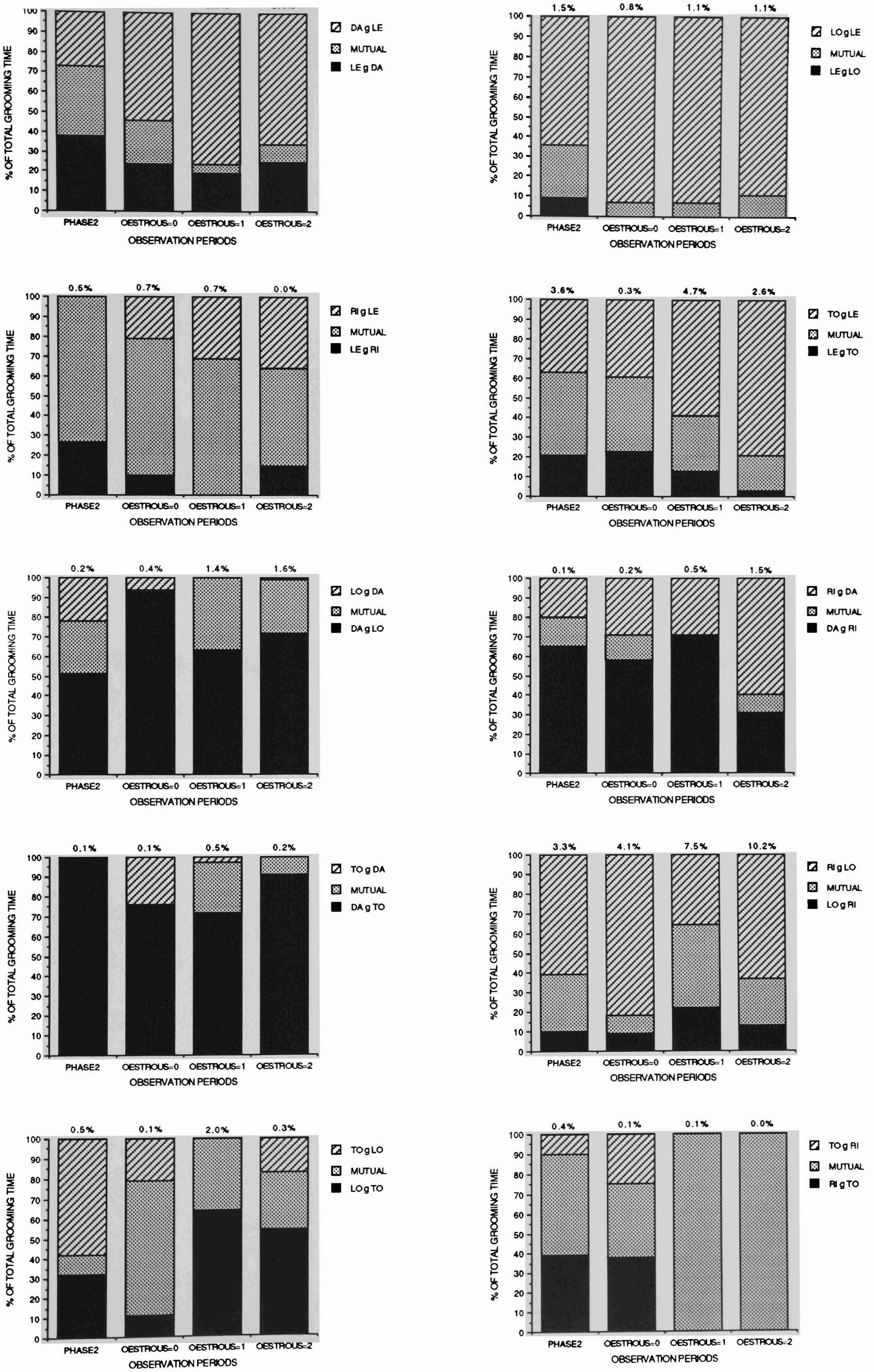


Fig. 7.1. Percentages of total grooming time spent in unilateral and mutual grooming in phase two and six. Figures at top of bars are percentages of observation time spent in grooming in each period.

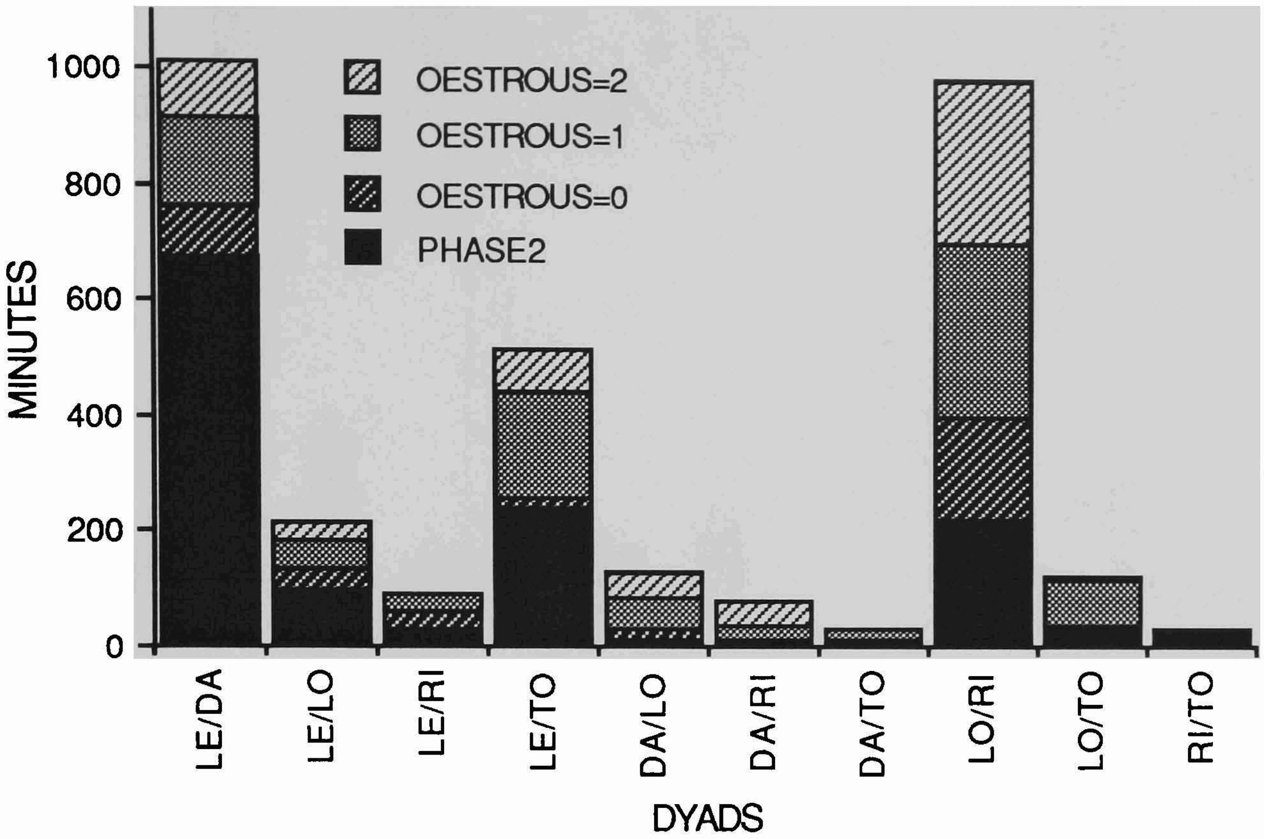


Fig. 7.2. Total grooming times of the male dyads during phases two and six.

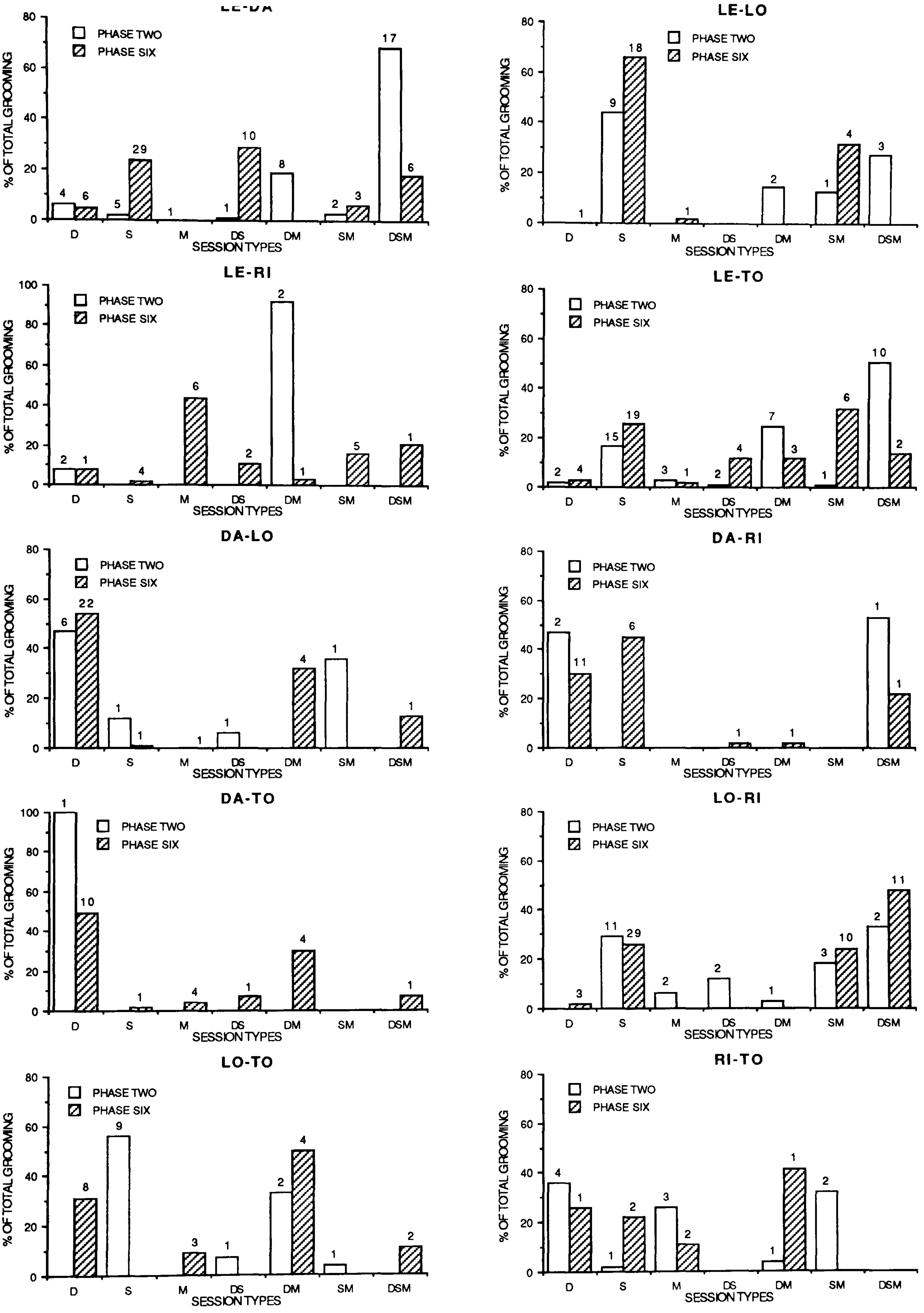


Fig. 7.3. Percentages of total grooming time spent in the different types of grooming sessions. Values on top of bars are absolute numbers of sessions.

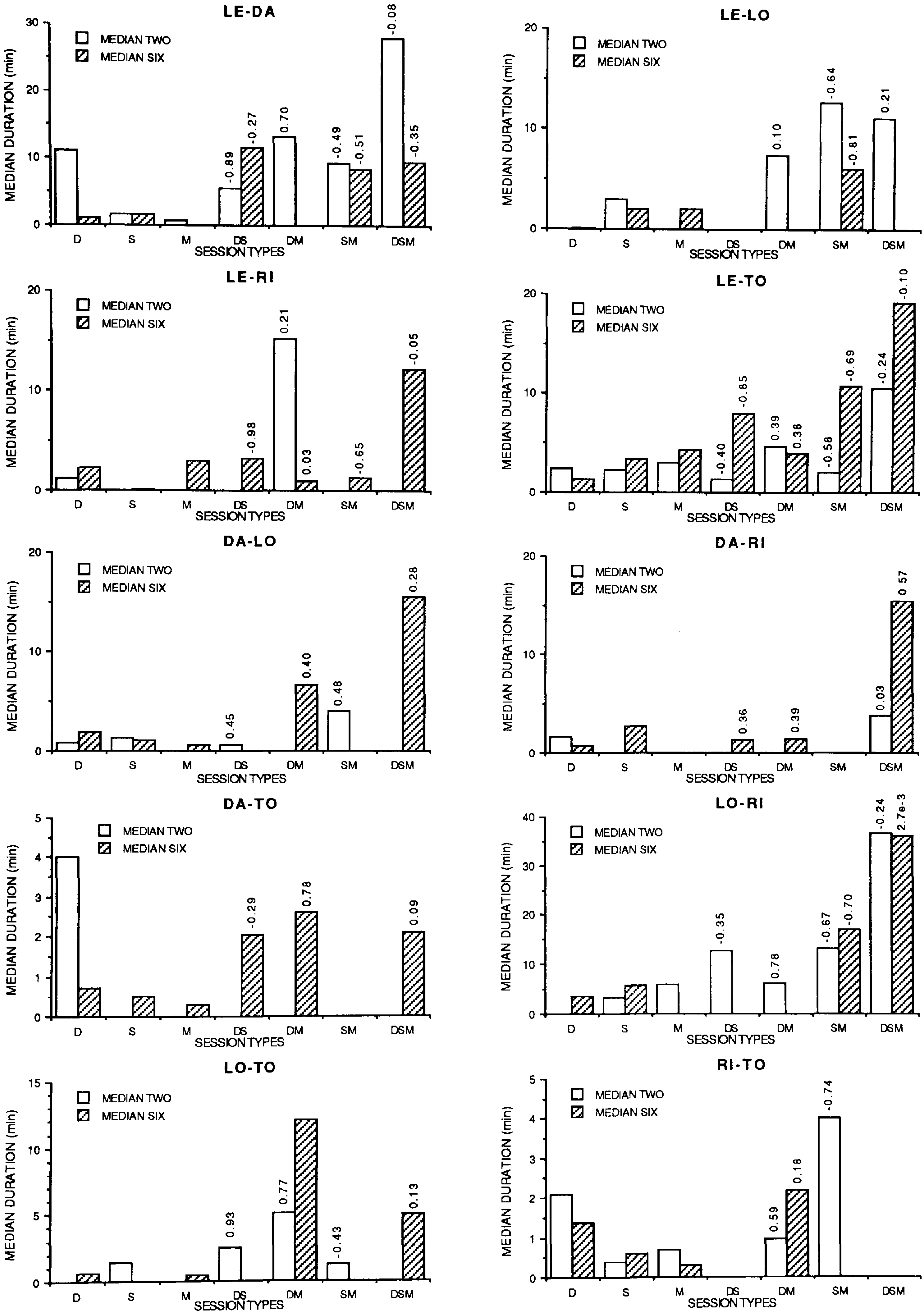
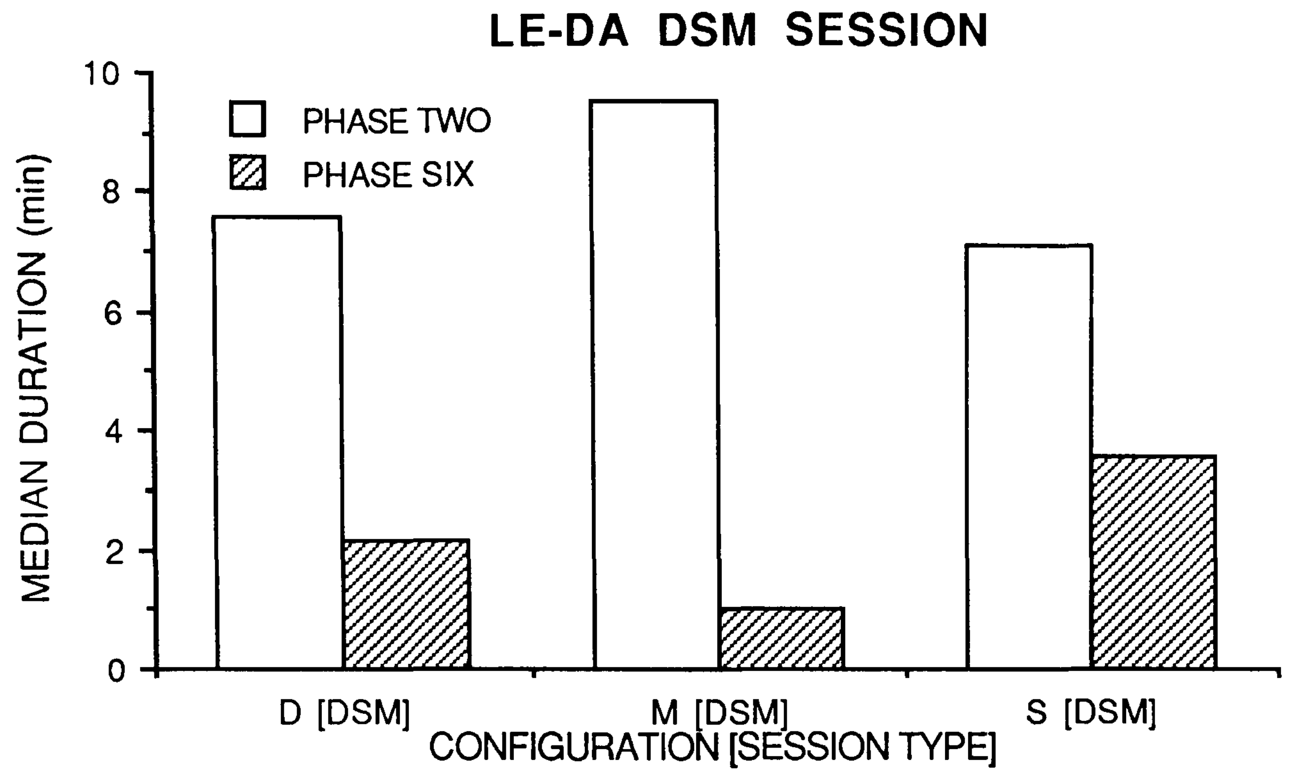


Fig. 7.4. Median duration of the different types of grooming session in phases two and six. RIT values on top of bars.



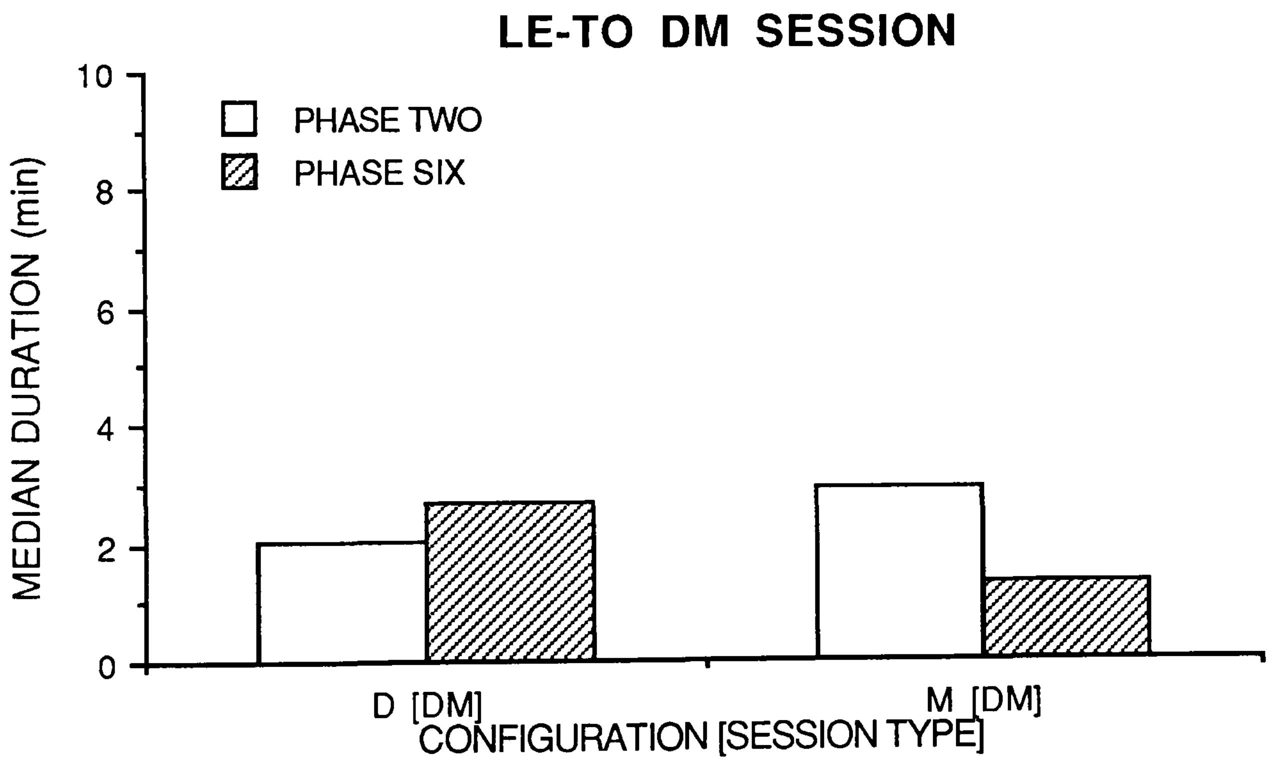


Fig. 7.5. Median duration of unilateral and mutual grooming as it occurred in Le-Da's DSM sessions and Le-To's DM sessions.

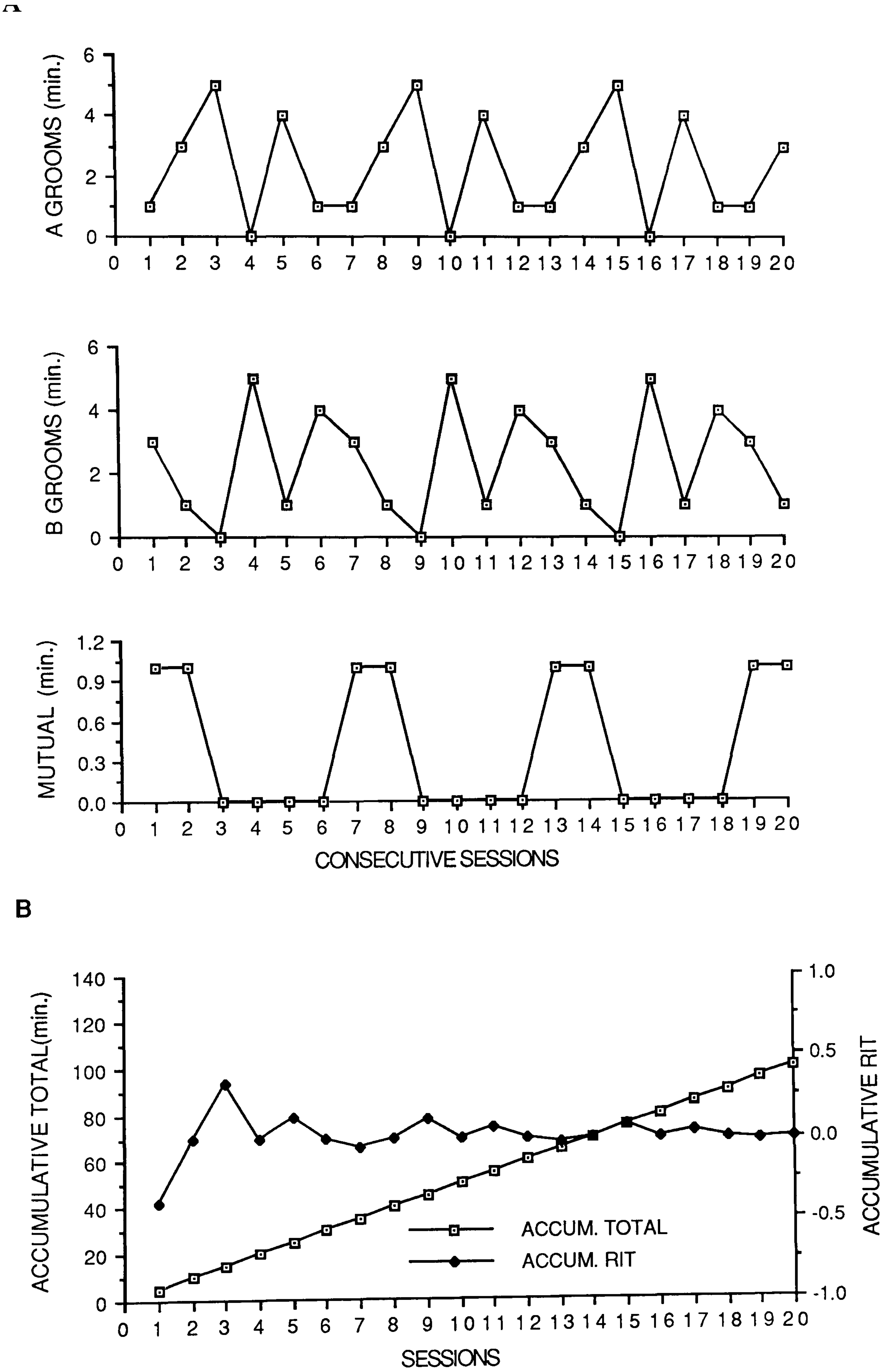


Fig. 7.6. a: Values of mutual and unilateral grooming for a sequence of 20 imaginary sessions, lasting 5 min. each. b: Accumulative total and accumulative RIT of these sessions.

A: Le-Da

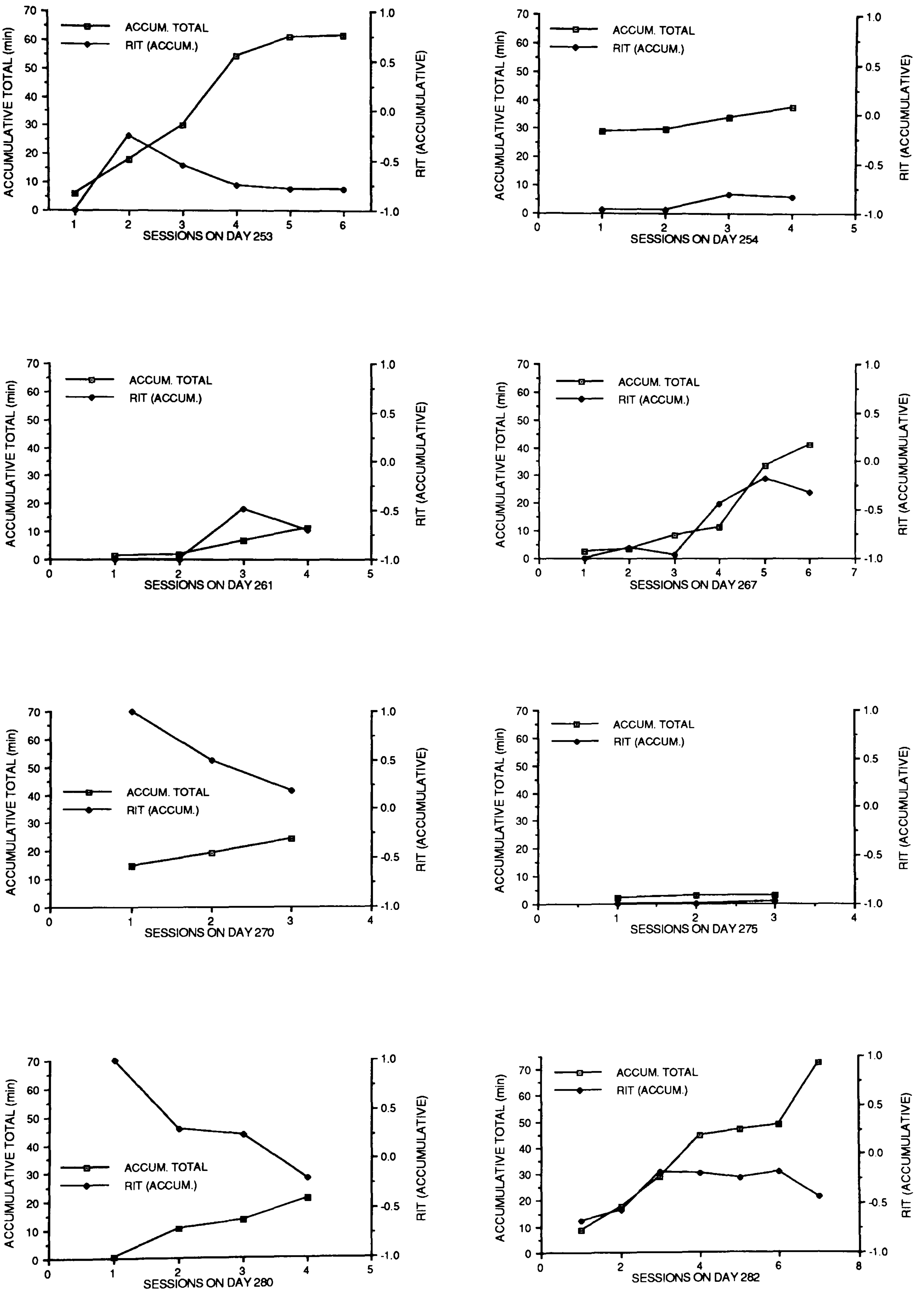
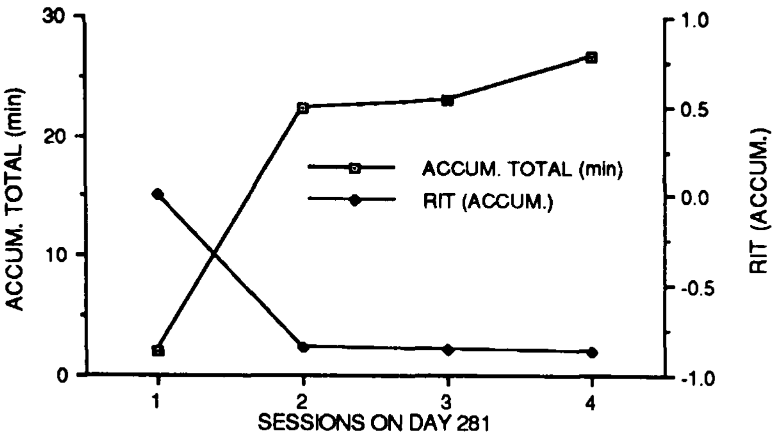
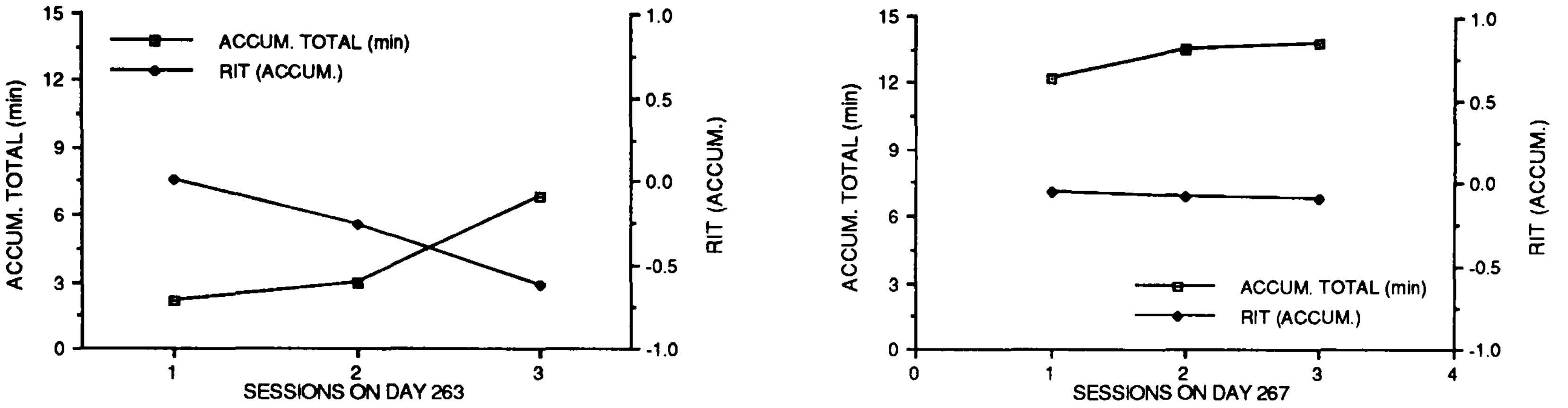


Fig. 7.7. Accumulative total duration and accumulative Reciprocity Index by Time (RIT_C) of consecutive grooming sessions for each dyad (a-h). Only days with more than two grooming sessions are shown.

B: Le-Lo



C: Le-Ri



D: Le-To

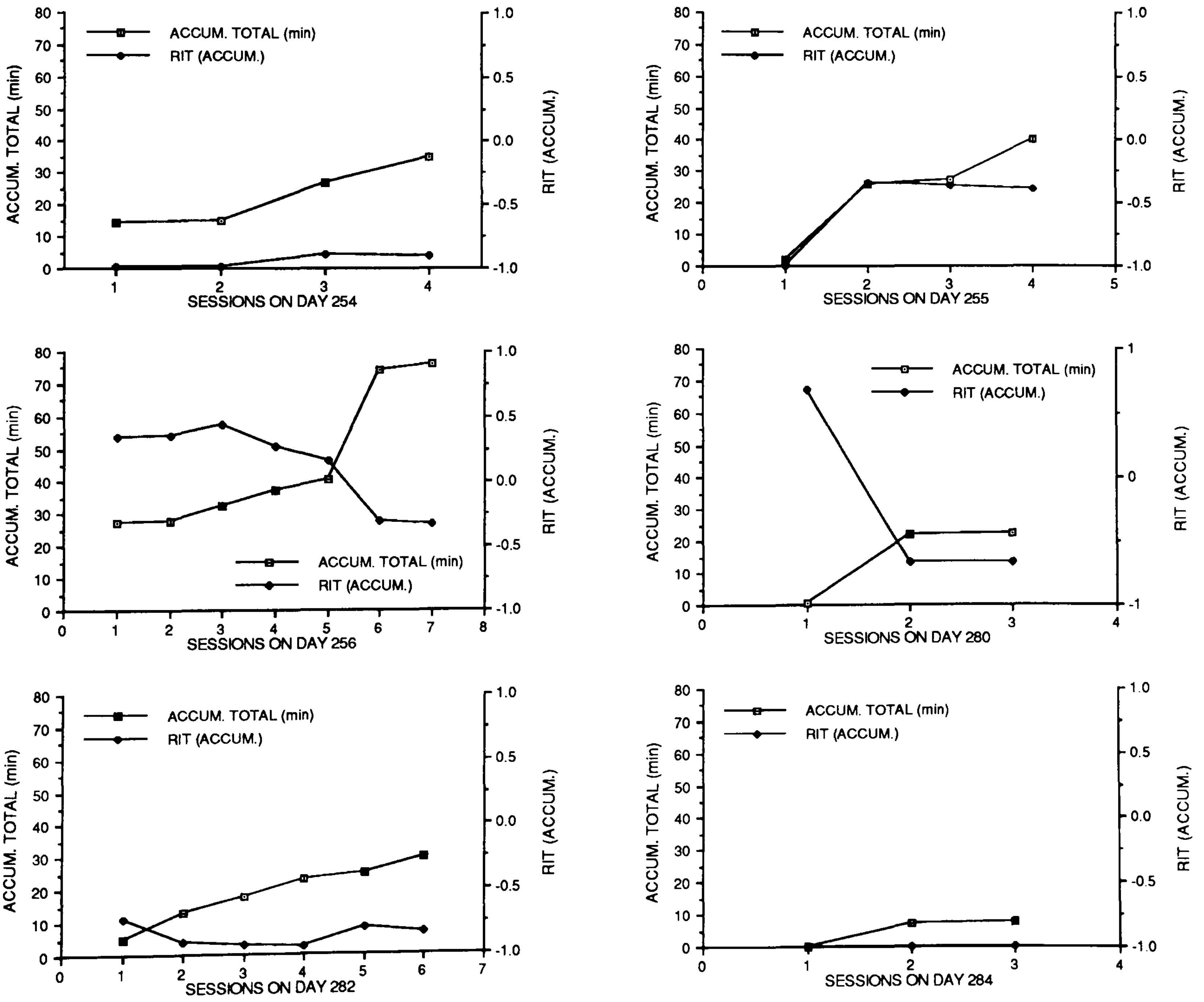
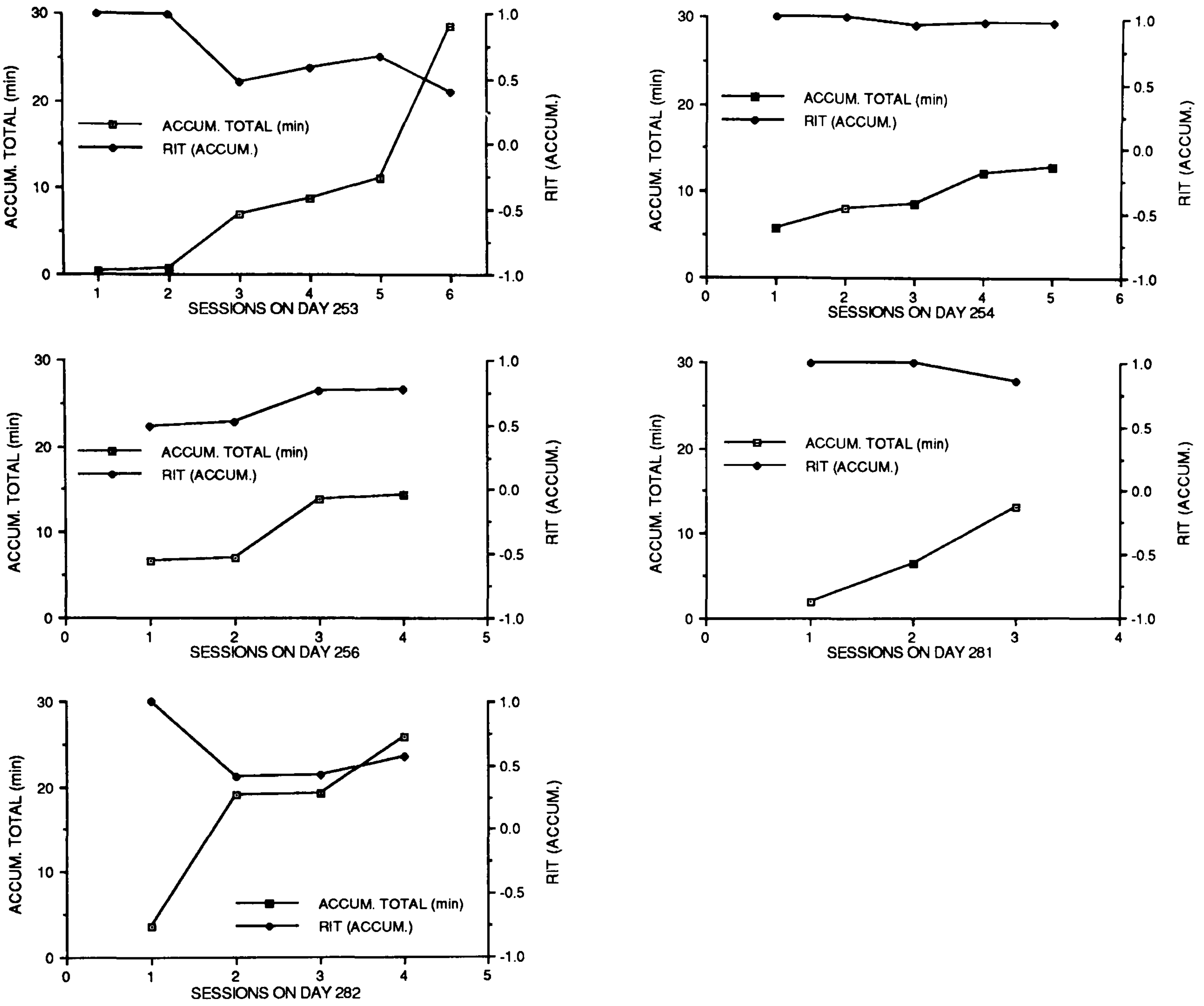
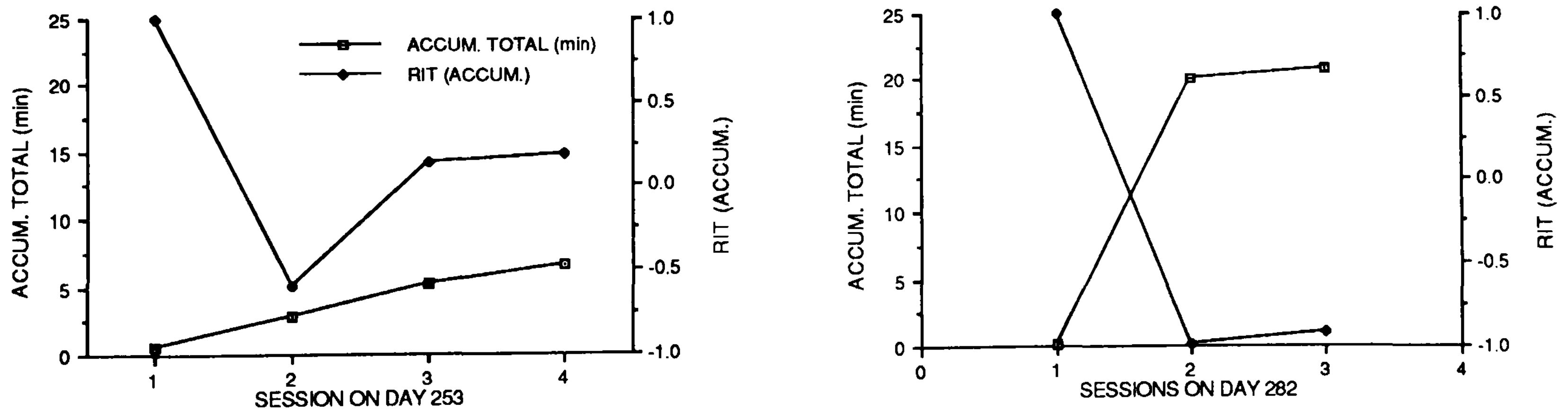


Fig. 7.7. Contd.

E: Da-Lo



F: Da-Ri



G: Da-To

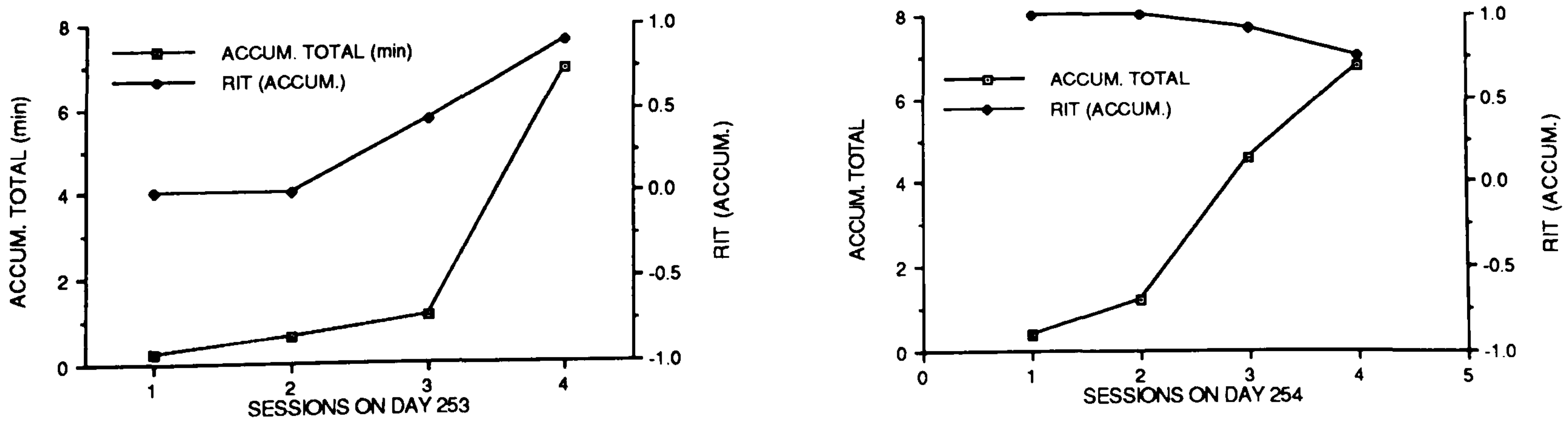
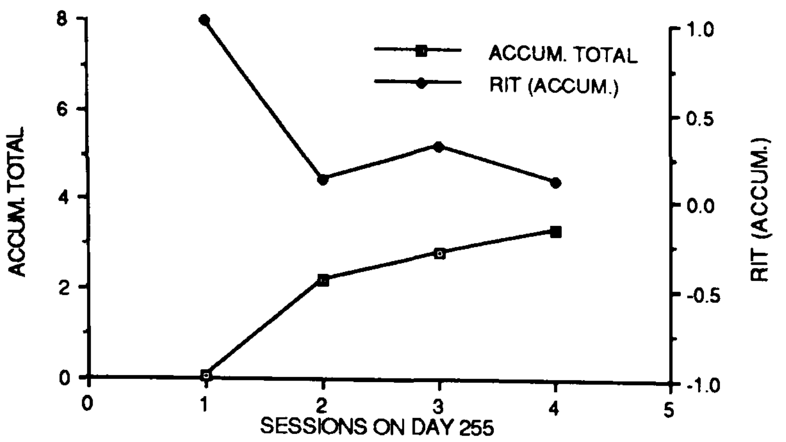


Fig. 7.7. Contd.

G: Da-To contd.



H: Lo-Ri

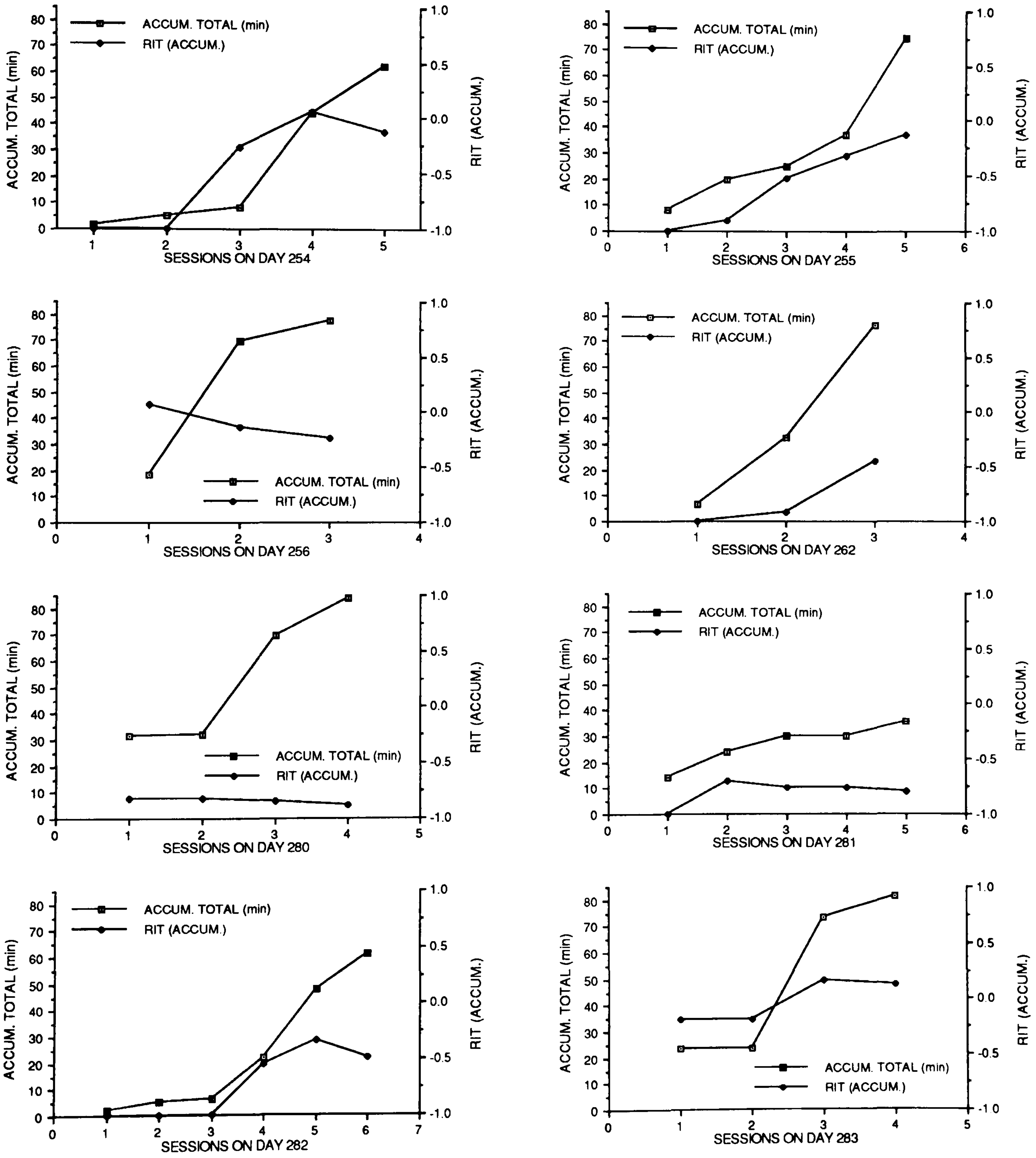
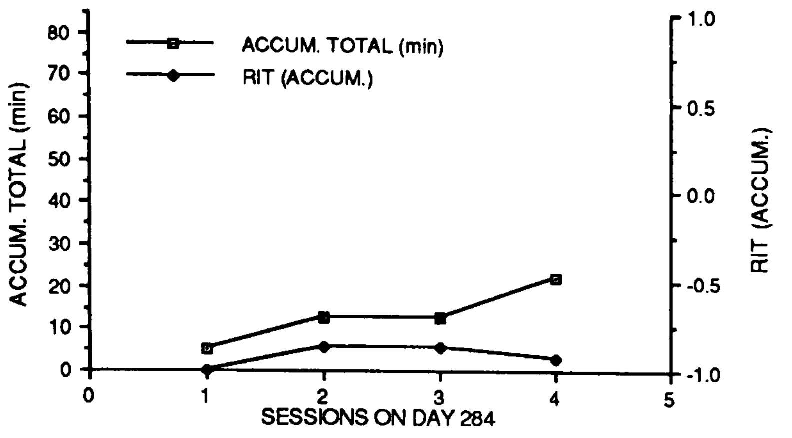


Fig. 7.7. Contd.

H: Lo-Ri contd.



I: Lo-To

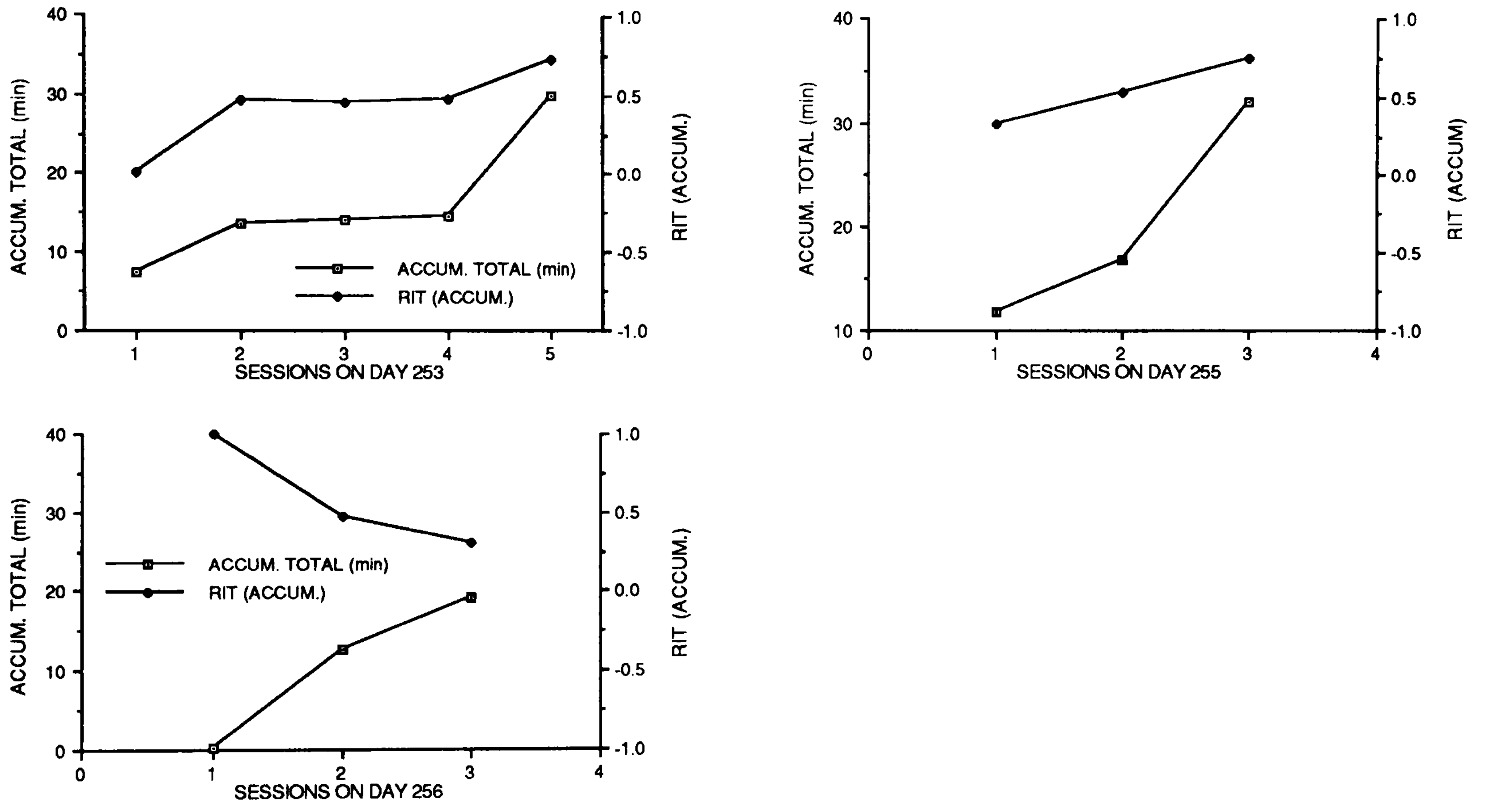


Fig. 7.7. Contd.

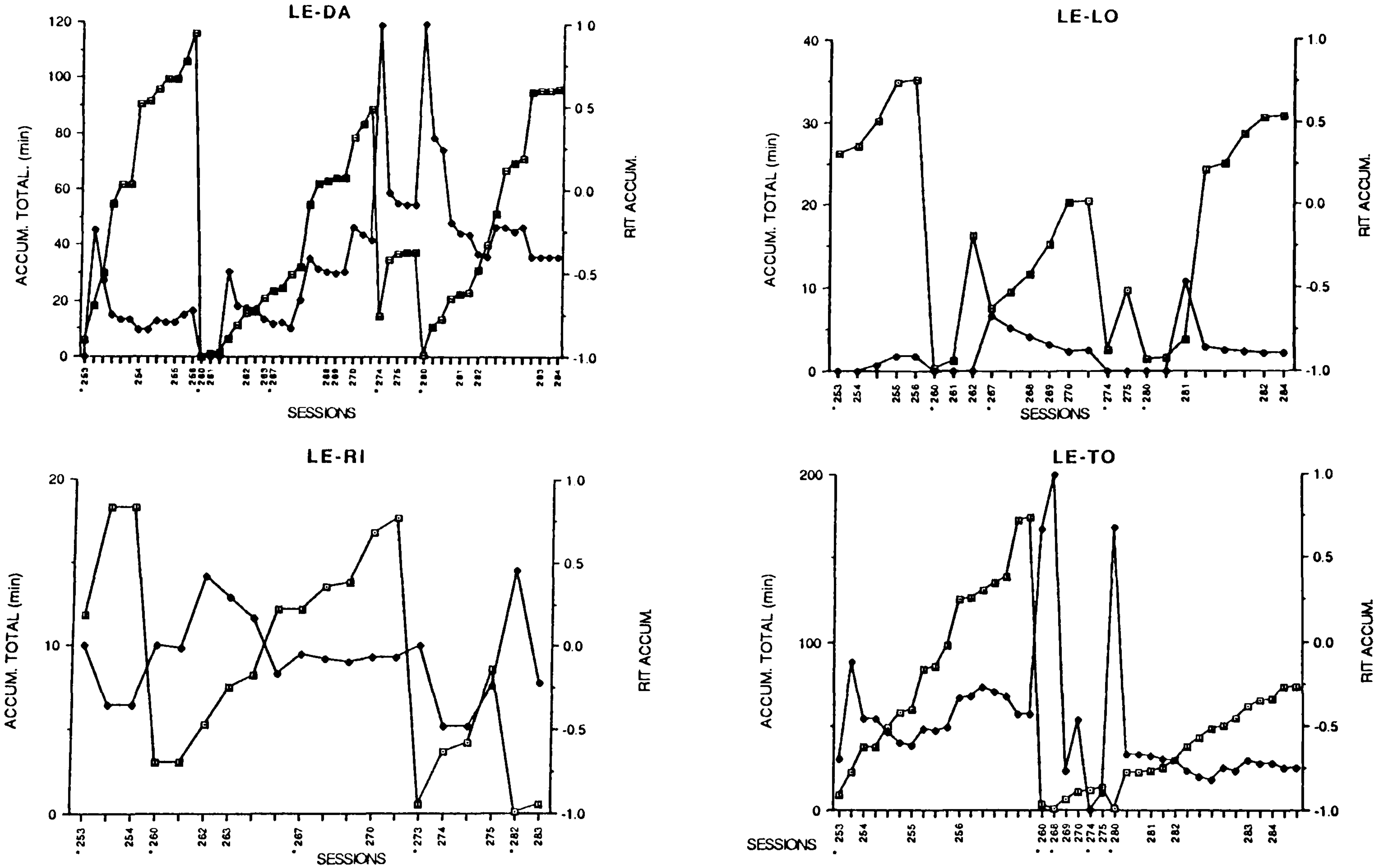


Fig. 7.8. Accumulative duration and accumulative RIT of grooming sessions over the five observation periods within phase six. Numbers on x-axis are days from 1 Oct. 1991 (see Table 6.I). Each dot represents one grooming session. Asterisks indicate first day of observation period.

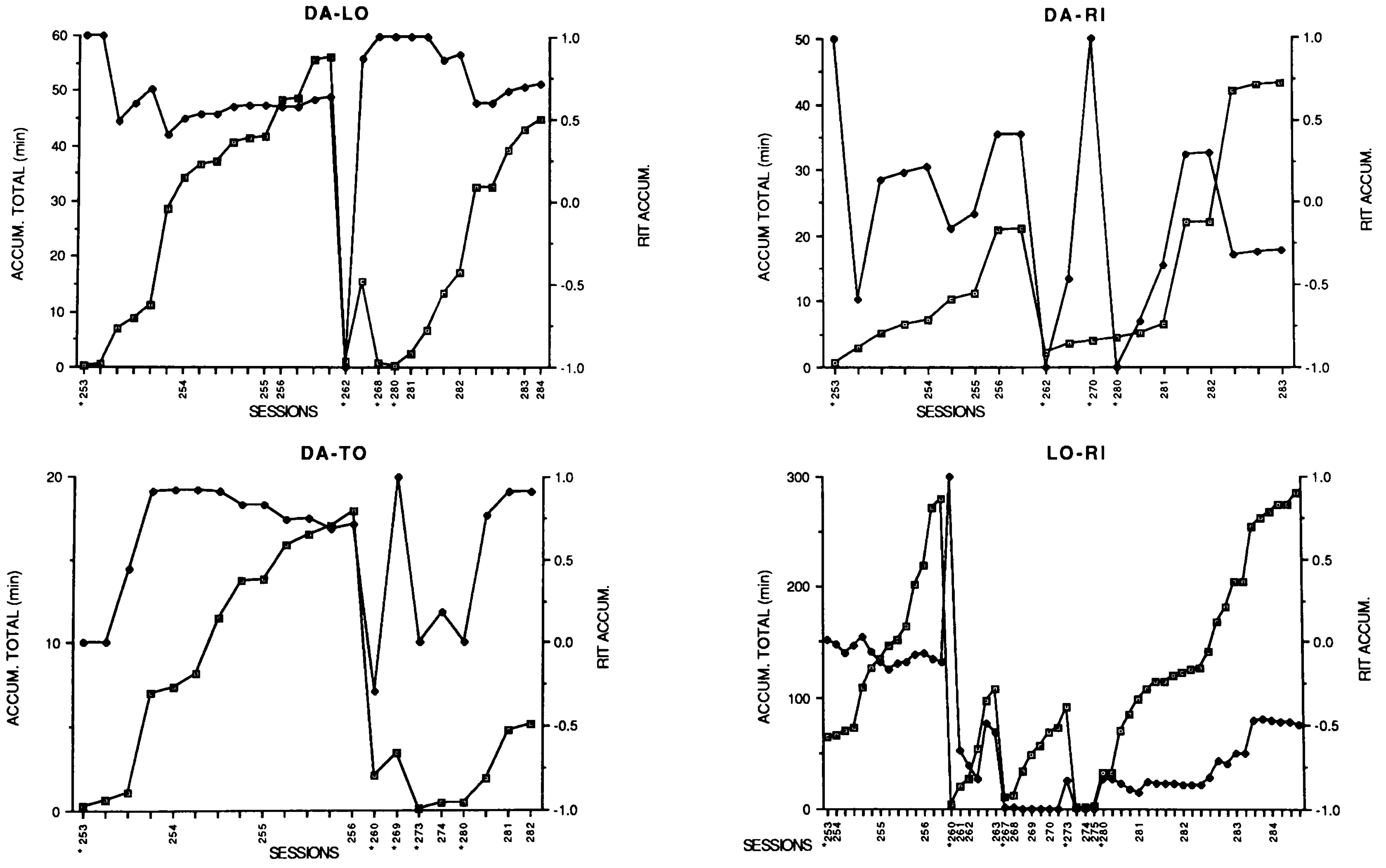

DA-LO
ACCUM. TOTAL (min)
0
10
20
30
40
50
60
RIT ACCUM.
-1.0
-0.5
0.0
0.5
1.0
SESSIONS
•253
254
255
256
•262
•268
•280
281
282
283
284
DA-RI
ACCUM TOTAL (min)
0
10
20
30
40
50
RIT ACCUM.
-1.0
-0.5
0.0
0.5
1.0
SESSIONS
•253
254
255
256
•262
•270
•280
281
282
283
DA-TO
ACCUM. TOTAL (min)
0
10
20
RIT ACCUM.
-1.0
-0.5
0.0
0.5
1.0
SESSIONS
•253
254
255
256
•260
•269
•273
274
•280
281
282
LO-RI
ACCUM. TOTAL (min)
0
100
200
300
RIT ACCUM.
-1.0
-0.5
0.0
0.5
1.0
SESSIONS
•253
254
255
256
•260
261
262
263
•267
268
269
270
•273
274
275
•280
281
282
283
284

Fig. 7.8. Contd.

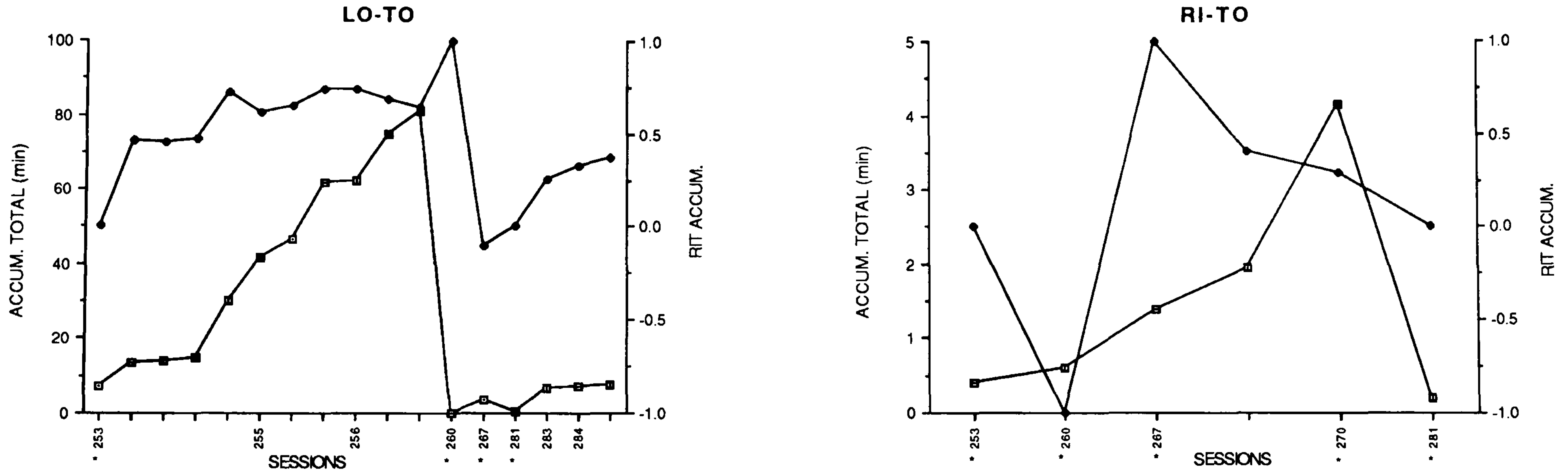

LO-TO
ACCUM. TOTAL (min)
0
20
40
60
80
100
RIT ACCUM.
-1.0
-0.5
0.0
0.5
1.0
• 253
255
256
• 260
• 267
• 281
283
284
SESSIONS
RI-TO
ACCUM. TOTAL (min)
0
1
2
3
4
5
RIT ACCUM.
-1.0
-0.5
0.0
0.5
1.0
• 253
• 260
• 267
• 270
• 281
SESSIONS

Fig. 7.8. Contd.

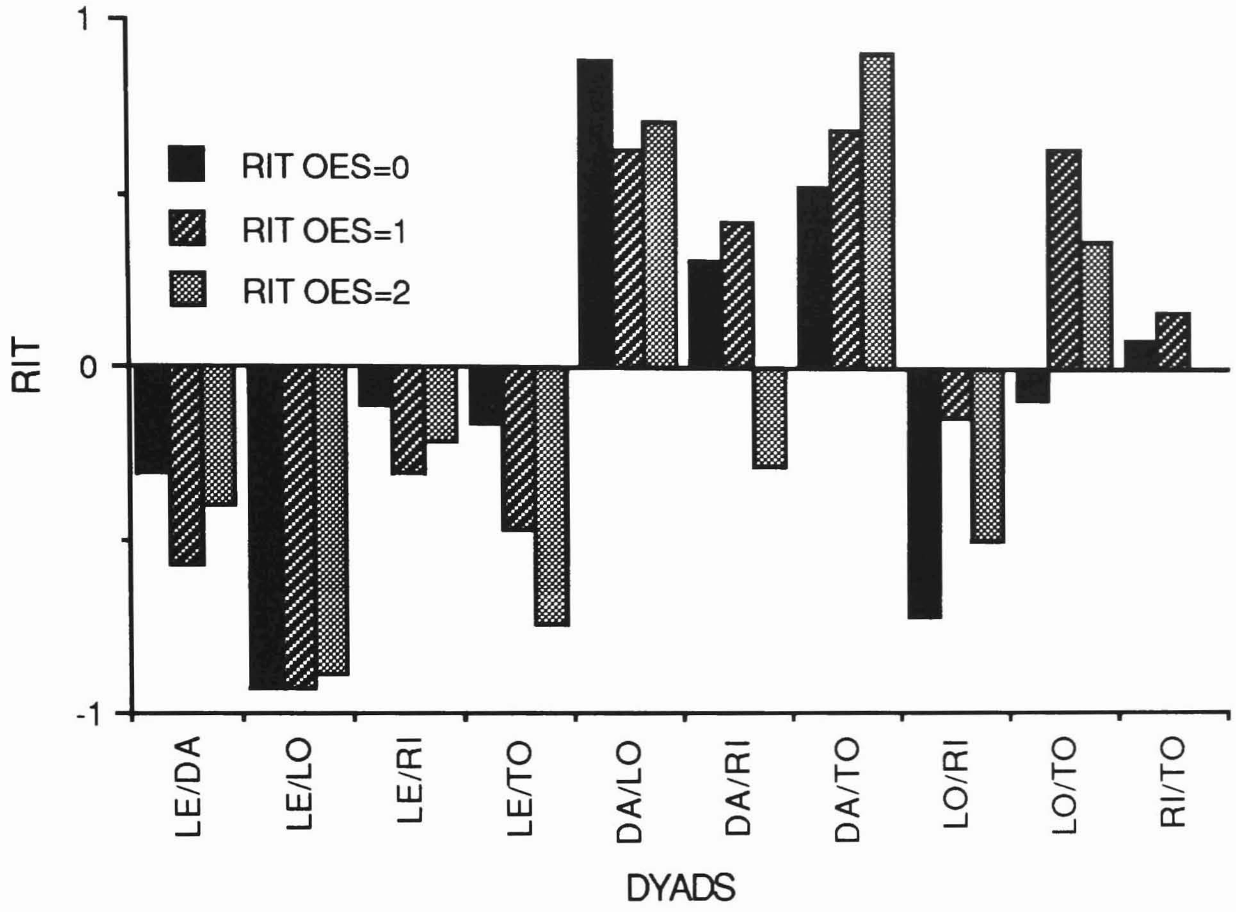


Fig. 7.9. RIT values for each dyad in the presence and absence of oestrous females during phase six.

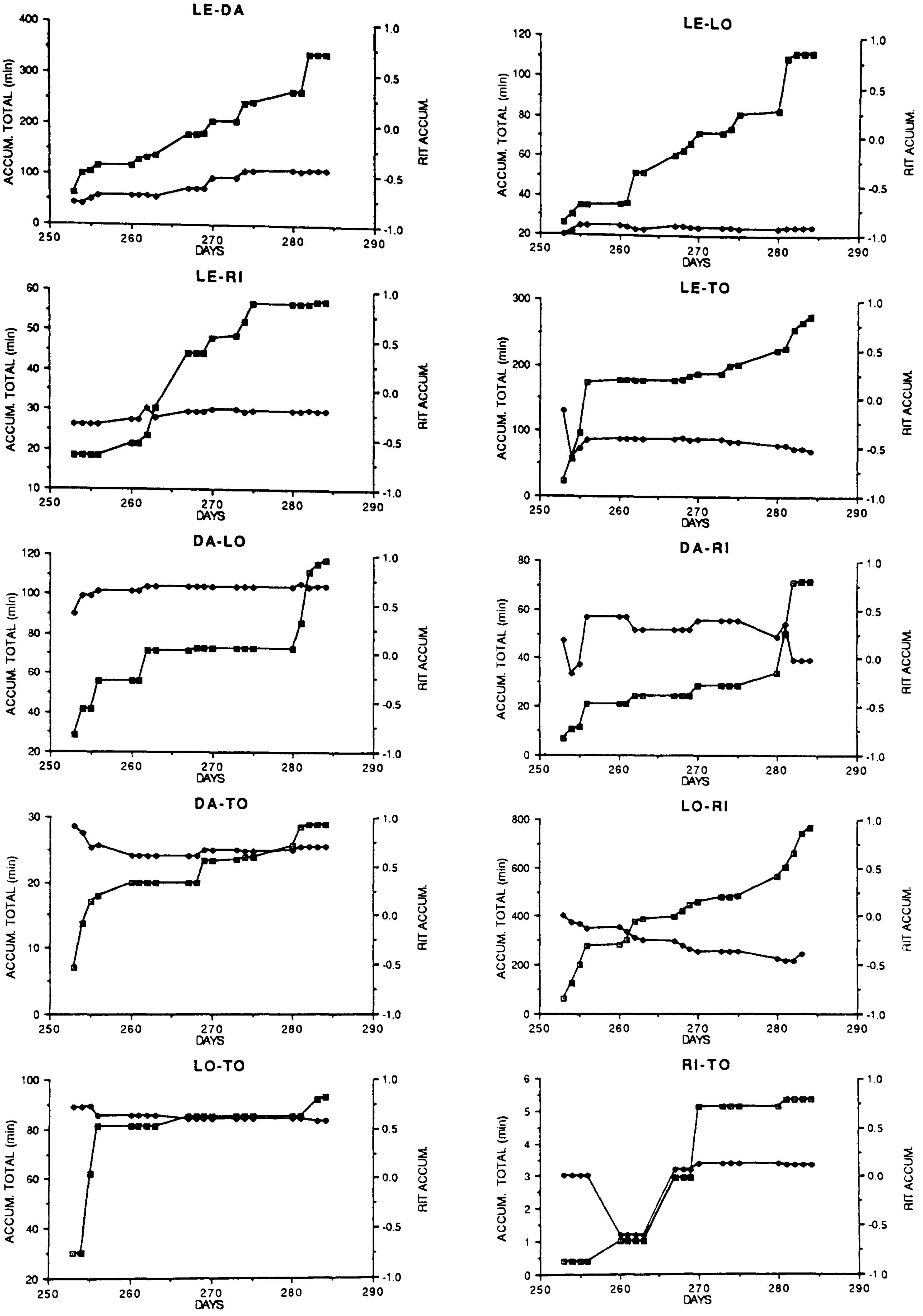


Fig. 7.10. Accumulative total and accumulative RIT for each dyad over the whole of phase six.

CHAPTER VIII

NO EVIDENCE FOR TIT-FOR-TAT WITHIN GROOMING SESSIONS

In the previous chapters it has become evident that some male-male dyads of chimpanzees groomed on a reciprocal basis, and the individuals in these dyads adjusted the amount of grooming they gave to the amount they received, at least in the absence of oestrous females. There was no strong evidence that grooming was reciprocated on the basis of TIT-FOR-TAT on consecutive sessions, but reciprocation of grooming occurred primarily within sessions in which both males adjusted the duration of their unilateral grooming to mutual grooming. These 'DSM' (or 'UUM') sessions were very long, and can be viewed as highly cooperative.

Therefore, to gain a better understanding of the dynamics of reciprocation within these session, those of phase two will be analysed here in terms of grooming bouts and interruptions in grooming. Additionally, a sequential analysis of grooming configurations will be used.

RESULTS

The term grooming 'configuration' will also refer to interruptions in grooming here. There were 33 'DSM' sessions in phase two, 30 (91%) of which involved Le. It would be statistically wrong to analyse all the 'DSM' sessions together, because dyads did not have equal numbers of these sessions. Therefore, only the two dyads with most 'DSM' sessions (Le-Da: 16 (17 minus one for which only total duration was available; Le-To: 10) were analysed, and treated separately.

Table 8.I gives for both Le-Da and Le-To the median, total number, and total time of grooming bouts of each configuration, and of interruptions (>10 s.) in grooming. At this level of analysis (i.e. bouts instead of sessions) there was no difference between the duration of the grooming configurations (Kruskal-Wallis One-Way Analysis of Variance by Ranks: Le-Da: df=3, N=211, KW=1.14; Le-To: df=3, N=84, KW=5.38).

It is assumed here that Le was dominant to Da and To. Therefore, Le's grooming and To's and Da's grooming will be compared. If Da would be dominant to Le, then Le's grooming in Da-Le should be compared with To's grooming in Le-To, and Da' grooming in Da-Le with

Le's grooming in Le-To.

Table 8.II gives the matrices with frequencies of the different sequences of the configurations within DSM sessions, for Le-Da and Le-To. For both dyads, Le's unilateral grooming followed on, and was followed most often by mutual grooming. Also, both Da's and To's unilateral grooming were followed most frequently by interruptions in grooming, and interruptions in grooming were followed most frequently by unilateral grooming by To (Le-To), and by Le (Le-Da), and least by mutual grooming (Le-Da). Unilateral grooming by one was least often followed by unilateral grooming by the other (both dyads), and mutual grooming was followed (both dyads), and preceded (Le-Da) least often by interruptions

The two dyads differed in the relative durations of their grooming configurations (Table 8.III). Unilateral grooming bouts by Da and To had the longest median duration when they were preceded by mutual grooming and Le's unilateral bouts, the shortest duration when preceded by Le's unilateral bouts and mutual bouts respectively (Table 8.III). Pauses in Le-Da's grooming were longest when preceded by Da's grooming, and shortest when preceded by mutual grooming, and in Le-To's grooming pauses were longest when preceded by To's grooming, and shortest when preceded by Le's grooming. However, these differences were non-significant.

It should be kept in mind that the duration of a bout of unilateral grooming is sometimes determined by when the groomer stops grooming, and sometimes by when the partner starts grooming, as the latter results in a new bout of mutual grooming. Similarly, the duration of mutual grooming and the duration of interruptions in grooming depend on both partners. It is, therefore, of interest to compare the duration of each configuration when it preceded each other configuration. For example, if subordinates are more likely to reciprocate grooming (Oberski, in press), then interruptions in grooming should be shorter before unilateral grooming by the subordinate than before unilateral grooming by the dominant.

There were non-significant differences in the median duration of configurations dependent on which configuration followed it. For both Le-Da and Le-To, the median duration of mutual grooming bouts was longest when followed by unilateral grooming by Da or To, and shortest when followed by an interruption in grooming. Interruptions in grooming were longest when followed by mutual grooming, and shortest when followed by unilateral grooming by Da or To.

For Le-Da, Le's unilateral bouts were longest when followed by mutual bouts, shortest when followed by Da's unilateral bouts. Da's unilateral bouts were longest when followed by mutual bouts, shortest when followed by Le's unilateral bouts. For Le-To, Le's unilateral bouts were longest when followed by To's unilateral bouts, shortest when followed by a pause. To's unilateral bouts were longest when followed by a pause, shortest when followed by a mutual bout. Again, these differences were all non-significant.

There was a strong positive correlation between the duration of Le's unilateral grooming of To, and mutual grooming following it ($N=13$, $r_S=0.769$, $0.005>p>0.002$). However, all other correlation between durations of consecutive bouts were non-significant, or could not be carried out due to small sample sizes.

DISCUSSION

The results presented in this chapter confirm the earlier finding that grooming was not reciprocated within 'DSM' sessions by grooming in turns, that is by an alternation between unilateral grooming by the two grooming partners. Instead, most grooming in 'DSM' sessions was reciprocated by alternating unilateral with mutual grooming. Interruptions in grooming followed less often on the unilateral grooming by Le, than by Da and To.

There was, on the whole, no relationship between the duration of consecutive grooming configurations. All configurations were similar in duration when analysed as bouts. Thus, the long duration of DSM sessions, as discussed in Chapter IV was not the result of longer bouts of mutual and/or unilateral grooming, but rather of a greater number of such bouts in these sessions.

Also, pauses tended to be longer before Le's grooming than before Da's or To's grooming. These results indicate that Da and To generally were more likely to reciprocate grooming, and tended to reciprocate sooner than Le. That mutual grooming tended to be longest before unilateral grooming by Da or To suggests that, in addition to being more likely to reciprocate grooming, Da and To also stopped sooner during mutual grooming than Le.

Table 8.I. Details of unilateral and mutual grooming bouts and of interruptions in grooming in the DSM sessions of Le-Da (A) and Le-To (B).

A

Configuration	Total duration (min.)	Total number	First quartile (min.)	Median dur. (min.)	Third quartile (min.)
Le unilateral	131.01	61	0.43	1.10	3.12
Da unilateral	134.02	44	0.40	1.35	3.41
Mutual	176.60	57	0.52	1.10	3.41
Interruption	165.25	49	0.58	1.00	4.06

B

Configuration	Total duration (min.)	Total number	First quartile (min.)	Median dur. (min.)	Third quartile (min.)
Le unilateral	22.38	24	0.28	0.94	1.36
To unilateral	46.99	20	0.41	1.11	3.19
Mutual	53.65	26	0.85	1.61	2.38
Interruption	62.10	14	0.42	0.78	7.37

Table 8.II. Frequencies of configuration sequences within DSM sessions of Le-Da (A) and Le-To (B).

A

Followed by Configuration	Le unilateral	Da unilateral	Mutual	Interruption
Le unilateral	-	1	39	17
Da unilateral	4	-	8	24
Mutual	30	15	-	8
Interruption	23	19	7	-

B

Followed by Configuration	Le unilateral	To unilateral	Mutual	Interruption
Le unilateral	-	3	13	5
To unilateral	1	-	6	8
Mutual	17	6	-	1
Interruption	3	8	3	-

Table 8.III. Median durations of consecutive grooming configurations in DSM sessions of Le-Da (A) and Le-To (B).

A

	When preceded by			
Median dur. of	Le unilateral	Da unilateral	Mutual	Interruption
Le unilateral	-	3.02	1.05	0.62
Da unilateral	0.32	-	2.17	1.15
Mutual	1.08	1.57	-	3.08
Interruption	1.00	1.16	0.72	-

	When followed by			
Median dur. of	Le unilateral	Da unilateral	Mutual	Interruption
Le unilateral	-	0.18	1.17	0.72
Da unilateral	0.29	-	2.54	1.34
Mutual	1.28	1.40	-	0.81
Interruption	1.00	0.83	1.53	-

B

	When preceded by			
Median dur. of	Le unilateral	To unilateral	Mutual	Interruption
Le unilateral	-	0.88	0.85	1.20
To unilateral	2.65	-	0.24	1.59
Mutual	1.48	1.44	-	1.82
Interruption	0.28	3.15	0.90	-

	When followed by			
Median dur. of	Le unilateral	To unilateral	Mutual	Interruption
Le unilateral	-	1.20	1.03	0.28
To unilateral	0.50	-	0.24	1.11
Mutual	1.48	1.57	-	0.37
Interruption	0.90	0.47	4.13	-

CHAPTER IX

GENERAL DISCUSSION AND CONCLUSIONS

This study presented an empirically derived definition of a grooming session, and offered a new method for the analysis of grooming in chimpanzees at the dyadic level. Fundamental to this method was the distinction between unilateral and mutual grooming, and how these forms of grooming were employed in grooming reciprocation. Subsequently, grooming reciprocation was investigated in the absence and presence of oestrous females, by studying the distribution over session types. Additionally, the effects of aggression and provisioning on the reciprocation of grooming were analysed.

Although this project was concerned with one small captive group of chimpanzees only and should, therefore, perhaps primarily be seen as a preliminary study, several points have emerged, the most important of which will be discussed here.

Grooming occurs in 'units', or sessions, the criterion for which can be determined empirically. However, the length of this criterion changes with different social situations (e.g. the presence of oestrous females), and probably varies between dyads as well. Moreover, the resolution of the log-survivorship analysis depends partly on the duration of observation sessions, a fact not always recognized (e.g. Slater & Lester, 1982). This raises problems concerning the methods that should be used in analysing grooming sessions. For example, is it better to use the appropriate bout criterion, with the consequence that several different criteria may have to be used for different observation periods, or to use the same criterion for all periods. In any case, an empirically determined session criterion is probably a better reflection of how chimpanzees pattern their grooming in time, than an arbitrarily chosen one (as in Pusey, 1978; Goodall, 1986a; Nishida, 1988; Takahata, 1990b). This study provided the first example of the application of log-survivorship analysis to grooming behaviour.

A method was presented for the analysis of grooming sessions, and was based on the presence or absence of unilateral and mutual grooming. This method distinguished between seven types of grooming session (or five types, if dominance was not taken into account), which were found to have different characteristics in terms of their duration and frequency of occurrence. The differences between the session types did not seem to attributable to chance or to be an artefact of the categorisation method. A direct comparison of the results obtained in this study with those in the literature is difficult, as no report has used a similar method of analysis, and as there are no studies available on male-male grooming that discriminate between unilateral and mutual grooming, and analyse at the dyadic level. Nishida (1988) and Goodall (1968b) took account of mutual grooming in their analyses of grooming reciprocation between mother and offspring only.

The results of this study indicate that, in general, there was no evidence that grooming between the males complied with a TIT-FOR-TAT strategy, as grooming was reciprocated by mutual *and* unilateral grooming, but never by just mutual or just unilateral grooming. This is not surprising when the limitations of the Prisoner's Dilemma Game are considered (e.g. Noë et al., 1991), keeping in mind the complexity of chimpanzee social behaviour, and the likelihood that two grooming chimpanzees are engaged in a continuous flow of communication with each other. It may well be more fruitful to interpret chimpanzee grooming as a coalition game, but this alternative was not investigated here. At most, grooming could be said to be an example of a combination strategy of reciprocal altruism and mutual cooperation (Rothstein & Pierotti, 1988).

It has become evident that, for chimpanzees, mutual grooming is distinctly different from unilateral grooming, and should be treated separately. It is insufficient for studies of reciprocity to consider only the totals of grooming given and received (i.e. unilateral grooming added to mutual grooming; e.g. Simpson, 1973; Hemelrijk & Ek, 1991), because the dynamics of reciprocation are different for different kinds of session, depending on the presence or absence of unilateral and mutual grooming.

As the median duration of sessions in which only one individual groomed ('D', 'S', or 'U') was short, it may be concluded that chimpanzees only like to groom for longer when they are also being groomed in the same session (see also Simpson, 1973), implying that they prefer to be groomed, rather than to groom. If chimpanzees prefer to be groomed rather than to groom, it may be justified to assume that grooming is altruistic (e.g. Falk, 1958; Mason et al., 1962). However, if grooming can be exchanged for other favours (such as support in a fight, or access to females in oestrus), it might well become more advantageous to groom, than to be groomed.

Wild chimpanzees groom longer, the longer they are being groomed within sessions (Simpson, 1973), and sessions (as defined by each author) were longer if there was either mutual or sequential grooming (Pusey, 1978; Ghiglieri, 1984; Goodall, 1986a). In this study, sessions with mutual and unilateral grooming by both, in the absence of oestrous females (Chapter IV), were the longest sessions. These sessions represent a complicated interaction, in which each male assesses the other's motivation to groom, on the basis of mutual grooming. A male adjusted his own unilateral grooming on the basis of mutual grooming, and not on the basis of unilateral grooming by his partner.This seemed especially true for dyads that groomed a lot.

Even though mutual grooming was proportionally less important in dyads that groomed more (in the absence of oestrous females), males still groomed more unilaterally, when there was more mutual grooming. The stronger a grooming relationship is, the more likely mutual grooming will function as an indication of the motivation to reciprocate, regardless of its duration. It is as if there is an 'exchange rate' between mutual and unilateral grooming: dyads with a strong grooming relationship groom more unilaterally for less mutual grooming than dyads with weaker relationships.

Mutual grooming was not the result of a chance overlap of the grooming, and dyads with strong grooming relationships groomed more mutually than expected by chance. There was a positive correlation between grooming total and the proportion of grooming that was mutual in dyads that groomed only little. This could mean that these dyads used mutual grooming to further reduce the time they spent in grooming.

Although mutual grooming obviously results in perfect reciprocity, it is an inefficient form of grooming in chimpanzees (in contrast to lemurs; Barton, 1987) because it gives limited access to a partner's body. Thus, it is suggested here that mutual grooming also has a communicative function, and may be interpreted by a chimpanzee as an indicator of his partner's motivation to groom him back (at least for dyads that groomed a lot). Possibly, mutual grooming is even used actively, to communicate a willingness to continue grooming unilaterally, after the partner has stopped grooming. Mutual grooming could have evolved as an effective means of assessing the likelihood that grooming given will be reciprocated in the same session, thereby avoiding having to keep track of many grooming relationships at the same time. This means that even the actor-receiver model, in which individuals give back most to those from whom most was received (implying that grooming partners are ranked by ego according to how much they groomed ego) does not need to be invoked (cf. Hemelrijk, 1990b). If this is so, mutual grooming could have become ritualised, for example in the form of a 'grooming hand-clasp', as observed at the Mahale mountains (McGrew & Tutin, 1978). Less obvious ritualised forms of mutual grooming may well have gone unnoticed.

The general effect on grooming of the presence of oestrous females was a reduction in reciprocity, both at the group level and the dyadic level. In the absence of oestrous females, there was a positive correlation between total grooming, and the proportion of the total that was spent in reciprocal grooming sessions. However, this relationship became negative in the presence of oestrous females, indicating that the more a dyad was involved in grooming, the less it groomed reciprocally. Accordingly, the grooming balance shifted in the direction of the dominants, with more unilateral grooming by the subordinates, and less by the dominants, and less mutual grooming than in the absence of females in oestrus. Finally, the nature of cooperative sessions with mutual grooming and unilateral grooming by both males changed. Instead of adjusting their unilateral grooming to mutual grooming, males now groomed more unilaterally in these sessions the more their partner groomed unilaterally. This could be interpreted as a loss of 'trust' between grooming partners: instead of relying on the communicative value of mutual grooming, males now only reciprocate grooming after it has been received.

As the relationship between unilateral and mutual grooming within the cooperative grooming sessions did not hold in the presence of oestrous females, it can be suggested that the function of grooming changes with the social context in which it occurs. At Arnhem, grooming sessions between the males were longer when an oestrous female was present (de Waal, 1982). At Edinburgh, however, only certain types of grooming session became longer when there were females in oestrus. The observed changes provide at most indirect support for a 'sexual bargaining' theory (de Waal, 1982), where subordinates have to groom dominants to gain access to oestrous females. However, caution in the interpretation of these results is appropriate, as a sequential analysis of grooming and sexual behaviour was not done here (cf. de Waal, 1989b). It is more parsimonious to explain the effect of oestrous females on grooming as the indirect result of polarised dominance relationships under the pressure of sexual competition, especially as the rate of aggression increased in the presence of oestrous females. This would have resulted in a more clearly defined dominance hierarchy, reflected in the grooming relationships, in which higher-ranking males are groomed more by lower-ranking males than vice versa (Simpson, 1973).

The direct effect of aggression was for dominants to groom subordinates more unilaterally, which is in accordance with observations at Gombe, where a dominant will often groom a subordinate after a conflict, probably as a reassuring gesture (Goodall, 1986a)

Provisioning had no effect on the reciprocation of grooming in this study, probably because competition for food was virtually absent. Although there are some reports on grooming in the context of feeding in wild chimpanzees (Reynolds & Reynolds, 1965; Goodall, 1968b; Nishida, 1970; Ghiglieri, 1984; Kano 1980), these are not concerned with the reciprocation of grooming. De Waal's (1989b) study on the relationship between grooming and food-sharing involved an experiment in which a limited amount of food was provided after observations of grooming had been recorded. It was found that a chimpanzee was more likely to share food with someone from whom grooming had been received, than with someone to whom grooming had been given. However, provisioning at Edinburgh usually did not invoke competition for food, and it is, therefore, not surprising that it had no effect on grooming.

There was great variation between dyads in the time they spent in grooming, and in how they distributed their grooming over different session types, both with and without oestrous females. However, some general patterns of grooming reciprocation were found, for example, the grooming balance at the end of the day often reflected the overall grooming balance for the whole period with zero, one, or two females in oestrus. There was some evidence of reciprocation over longer time-spans than a session, especially between the alpha and beta males, who followed an 'investment' strategy, in which an initial 'investment' in grooming was paid back in the course of several consecutive sessions. Tracing the grooming balance over the whole of phase six suggested that in some dyads this balance is static, whereas in others it is dynamic. It seemed that the balance of grooming in each dyad depended on a balance between dominance (which polarised the relationship) and cooperation (which balanced the relationship), so that dyads with a strong dominant-subordinate relationship showed a gradual decrease in the grooming balance towards grooming by the subordinate. Dyads with a more cooperative relationship, however, showed an increase in the grooming balance towards equilibrium. There are no reports of similar results in the literature.

A sequential analysis of grooming configurations within the DSM sessions (in which there was mutual grooming and unilateral grooming by both males) provided no evidence for TIT-FOR-TAT (Axelrod, 1990), but interruptions in grooming tended to be shorter before unilateral grooming by subordinates than before unilateral grooming by dominants, implying that the former were more motivated to reciprocate. This would be expected, as dominants are more valuable as a 'resource' than subordinates (e.g. as allies during aggressive incidents, as possessors of food, as monopolisers of oestrous females), and subordinates thus express the value of the relationship by grooming them more (Simpson, 1991). However, this analysis was based two dyads only.

This study has revealed some previously unknown aspects of grooming reciprocation with the aid of a method for analysis at the dyadic level and an original approach to the dynamics of grooming generally. However, as the study concerned one small captive group of chimpanzees only, it should be considered as a preliminary study of grooming reciprocation in chimpanzees, and as a generator of new hypotheses about the dynamics and functions of grooming.

Many aspects of grooming in chimpanzees (and primates in general) need still to be investigated in detail (Chapter I). However, in the context of the present study, future studies could make comparisons of the distribution of grooming over session types and over mutual and unilateral grooming between different captive and wild groups, as well as comparisons between different primate species. Interesting cultural differences could be discovered in the use of mutual grooming by different chimpanzee populations. Also, a detailed study of mutual grooming is needed, which evaluates the two basic hypotheses about the cause and function of mutual grooming across different species. Finally, changes in the dynamics of grooming reciprocation with changing social contexts (female oestrus, aggression, eating) should be investigated in more detail.

APPENDIX A

LITERATURE SCAN FOR DATA ON MUTUAL GROOMING

Mutual grooming is only mentioned rarely in the primate literature. This could mean that most primate species do not groom mutually, or that researchers have assumed that mutual grooming is meaningless. A scan was made for data on mutual grooming through 35 research articles by different authors, that had the word 'grooming' in the title. These articles are listed below, an asterisk indicating those with data on mutual grooming. There were only 3 reports that presented values for mutual grooming. One of these was concerned with lemurs (Barton, 1987), one with Indian langurs, Presbytis entellus, (McKenna, 1978), and one with chimpanzees. Reports without 'grooming' in the title but with data on mutual grooming all concerned chimpanzees (Huffman, 1990; Kawanaka, 1989; McGrew & Tutin, 1973), but of course this could have resulted from the authors bias toward his own study subject. Otherwise it may indicate that mutual grooming has attracted most attention in chimpanzee researchers, implying that chimpanzees groom more mutually than other primate species!

Abordo et al., 1975.
Ahumada, 1992.
Aureli et al., 1992.
*Barton, 1987.
Bauer, 1979.
Boccia, 1989.
Borries, 1992.
Buettner-Janusch & Andrew, 1962.
Coelho et al., 1983.
D'Amato et al., 1982.
Daschbach et al., 1983.
Defler, 1978.
Drickamer, 1976.
Dunbar, 1991.
Goy et al., 1988.
Falk, 1958.
Freeland, 1981.
Furuya, 1965.
Goosen, 1974.
Hemelrijk & Ek,1991.
Hosey & Thompson, 1985.
Hutchings & Barash, 1976.
Koyama, 1973.
*McKenna, 1978.
Mehlman & Chapais, 1988.
Merrick, 1977.
Muroyama, 1991.
*Nishida, 1988.
Reiss, 1984.
Seyfarth, 1977.
Silk, 1982.
Simpson, 1973.
Sugiyama, 1988.
Terry, 1970.
Tsukahara, 1990.

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