PRIMATES, 17(3): 257–290, July 1976

An Ethological Analysis of Types of Agonistic Interaction in a Captive Group of Java-monkeys (*Macaca fascicularis*)*

FRANS B. M. DE WAAL, JAN A. R. A. M. VAN HOOFF, and WILLEM J. NETTO
University of Utrecht

ABSTRACT. The primate literature provides many indications not only that the nature of dyadic interactions is to a large extent determined by the relations of the interacting animals with others and between these others, but also of the existence of polyadic interactions in which more than two individuals are simultaneously involved.

The objectives of the present study are to obtain a quantitative categorization of the agonistic interaction types of captive Java-monkeys and an analysis of their dynamics.

After having described the agonistic behaviour patterns of Java-monkeys we shall discuss the categorization of agonistic interaction types (depending on the number of involvees: "dyads", "triads" and "polyads"), the way in which these types can be further differentiated on the basis of the nature and the direction of the behaviours shown (*e.g.*, different types of alliances), and the existence of so-called "sub-directed" behaviours (*i.e.*, non-agonistic behaviours which are shown towards a dominant third animal more or less simultaneously with aggressive behaviour directed towards an opponent).

The analysis indicates that agonistic behaviour is different both in its form and its regulation in interactions of different complexity.

INTRODUCTION

The primate literature provides indications that the social relations which a primate maintains with a group member are partly determined both by their relations with third animals and by those among the third animals.

Thus the dominance relations between young japanese- or rhesus monkeys appear to correspond to a certain degree with those found between their mothers (KAWAI, 1958; IMANISHI, 1960; KOFORD, 1963a; SADE, 1967; MARSDEN, 1968). This is termed "dependent rank" as distinguished from the so-called "basic rank" (KAWAI, 1958).

Obviously the structure of relations within a group cannot be understood exclusively in terms of dyadic interactions (on which the studies of social behaviour focussed in the past). In order to do so one has to consider questions pertaining to the extent to which more complex interactions occur; to the form these interactions take behaviourally and to their dependence on age, sex, parent-offspring and peer relations of the involved individuals.

It is our aim to study the above mentioned questions with respect to the agonistic interaction behaviour and the structure of agonistic relations in caged groups of Java-monkeys (*Macaca fascicularis,* Raffles, 1821; also named crab-eating monkey).

*This research was supported in part by a government grant (i.e.: Beleidsruimte project: 16-21-06, "Brain and Behaviour") to the first author.

(a) LITERATURE

No doubt complex agonistic interactions are phenomena observable in many animal species. In jackdaws (*Coleus monedula*), for instance, an attacked individual can mobilize the whole colony against the aggressor by uttering the "jüp", a certain staccato call (LORENZ, 1931). In the Spotted hyena (*Crocuta crocuta*), according to KRUUK (1972; p. 255): "...one may sometimes see two hyaenas threaten a third by approaching in the attack posture, walking shoulder to shoulder while almost touching each other". In the Serengeti lion (*Panthera leo massaicus*): "Several lionesses may attack a male and put him to flight" (SCHALLER, 1972; p. 132).

Notably the publications concerning primate social behaviour offer descriptions of complex interactions, under headings like; "protection," "intervention," "redirection," "cooperative aggression," "coalitions," "alliances," etc.

Referring to rhesus monkeys ALTMANN (1962; p. 403), for instance, remarks: "Cooperative agression, *i.e.*, two or more monkeys simultaneously attacking or threatening another monkey, did not occur only when enlisted. Very often, an attack alone was sufficient to stimulate another monkey to join the fight. When he joined the attacked, these two often became the attackers." Similarly JAY (1965; p. 239) remarks about langurs (*Presbytis entellus*): "Male dominance is never contested by a female unless a male accidentally frightens an infant or a female with an infant. When this occurs he is liable to immediate attack from the mother of the infant and nearby females." HALL and DEVORE (1965; p. 64) state, with reference to baboons (*Papio ursinus; P. anubis*) that: "In its simplest form redirected aggression occurs when an animal threatens another, and the threatened animal redirects the aggression to a third party (···) or, rarely, to an inanimate object (···)". Often the term "redirection" is used in a broader sense. For instance, by KAUFMANN (1967; p. 79) writing about rhesus monkeys: "At least 10 to 20 percent of the attacks were redirected; that is a monkey attacked a lower ranking one when a higher ranking monkey approached" (see also ALTMANN, 1962; MICHAEL, 1971).

Detailed descriptions of behaviour patterns, characteristic for such complex agonistic interactions, are scarce. HALL and DEVORE (1965; p. 65) remark about baboons: "...an individual may sometimes seek support or "enlist" the threat behaviour of another individual. This is done by gestures like jerking the head rapidly from side to side." The best known example comes from KUMMER (1957, 1967) who defines "tripartite relations" in Hamadryas baboons as: "sequences in which three individuals simultaneously interact in three essentially different roles and each of them aims its behaviour at both of its partners." (1967; p. 64). A behaviour category shown specifically in this situation is the so called "Gesicherte Drohung": an aggressor places itself between its opponent and a dominant partner threatening at the first and more or less simultaneously presenting towards the second partner. KUMMER calls this a "Zweifronten-Verhalten" and supposes this behaviour to inhibit aggression by the dominant in the direction of the actor and to facilitate it in the direction of the opponent.

To these two German terms ALTMANN (1962) refers when he writes about "protect-

ed threat" and "two-frontal-behaviour"; commonly observed phenomena in his rhesus-monkeys. ANGST (1974; p. 59) described this phenomenon in Java-monkeys and supposed that in this species the social effects of protected threat may differ from those suggested by KUMMER for Hamadryas baboons. ANGST suggests that the main effect is a sexual contact with the dominant, which protects the presenting animal against (potential) aggressive opponents.

Some quantitative data, concerning complex types of agonistic interactions in primates, have been gathered in the wild situation (*e.g.*: for vervet monkeys by STRUHSAKER, 1967; for rhesus-monkeys by LINDBURG, 1971) and with experimental methods under laboratory conditions (*e.g.*, for rhesus monkeys by VARLEY & SYMMES, 1966, MASSERMAN et al., 1968, for pigtail macaques by TOKUDA & JENSEN, 1968).

Fieldworkers have recognized, however, that it is not usually possible under the prevailing conditions to note the responses of more than a few individuals involved in major agonistic interactions and thus to assemble sufficient reliable and representative quantitive material (see LINDBURG, 1971; p. 52). By contrast some of the laboratory workers reverted to experiments which in our opinion are of a rather artificial and simplistic nature.

Thus MASSERMAN et al. (1968) scored the number of aggressive and submissive interactions occurring in 40 groups of four rhesus monkeys in small cages, 20 of these groups were composed of three cagemates and one "stranger", the other 20 of non-cagemates. Before and after the tests the dominance relations between all pairs of animals involved were determined. The authors found that the rhesus monkeys showed more aggression and less submission towards dominant strangers, if cagemates were present to form alliances with. Although suggestive as to the importance of acquaintance relations, the experiments hardly provide insight into the social dynamics of macaque populations.

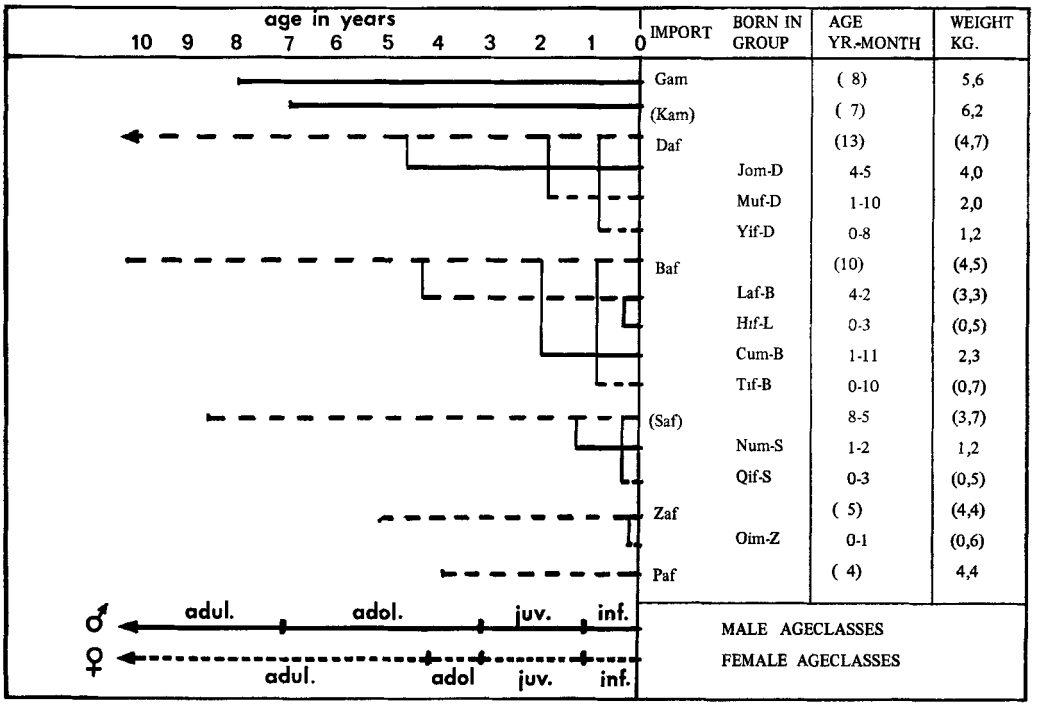
Except for the studies mentioned the analyses of agonistic behaviour have scarcely paid attention to the phenomenon of more complex interactions. Systematic descriptions and categorizations of types of agonistic interaction are still lacking. (N.B.: A footnote giving a short categorization can be found in TOKUDA and JENSEN, 1968).

(b) FORMULATING THE PROBLEM

After a first orienting study of the agonistic behaviour in a group of Java-monkeys in 1972, a more detailed study was performed on another group in 1973. It was designed to provide answers to the following questions:

(1) Which types of agonistic interactions can be distinguished with respect to:
   (a) the number of individuals involved, and
   (b) the nature and direction of the behaviour patterns shown by each of these. (Both aspects can reveal specific agonistic roles which characterize certain types of int raction.) Of special interest is an inventarization and a description of the so-called two-frontal-behaviours; *i.e.*, behaviour patterns that are simultaneously or intermittently directed at two or more interaction partners.

Table 1. Identification codes, ages, weights and genealogy of the individual members of group G.



(2) Which animals do figure in the different roles that can be distinguished within these interaction types; how are the patterns of the agonistic activities distributed over the group members?
How is the relation between the individual behavioural repertoires and age, sex, weight and genealogy of the individuals?
How is the nature of the performed behaviour related to these aspects in the receiver and in the other animals involved and their behaviour (*i.e.*, the social context)?
To what extent can the distribution of agonistic behaviour patterns be simply described in terms of some rank model (dominance hierarchy)?

As the studied group consists of 17 monkeys, the best method of behaviour recording would require 17 well-trained observers, whereas we have only one available. Of the behaviour occurring in the group, the observer tried to record the agonistic behaviours of all animals involved, in a manner as complete and detailed as possible, making use of an audio-recorder. The observer used a simultaneously recorded video-protocol as a control of his audio-protocol, realizing that: "for a group of 17 individuals it is impossible for one observer to record in detail all of the varieties of aggressive and submissive interactions" (SOUTHWICK, 1967; p. 190). The material thus gathered, is informative as to the above-mentioned questions: it falls short in

illustrating the relation of agonistic interactions with other categories of behaviour, or in revealing the fine-structure of agonistic behaviour.

In this first publication we will present qualitative and quantitative descriptive data about agonistic behaviour patterns and interaction types (question 1.). Furthermore we will pay attention to the method and its reliability.

AGONISTIC BEHAVIOUR PATTERNS

(a) Definition

Previously we made an inventory of the elements of the social behaviour of Java-monkeys and empirically classified these with respect to their place in the behavioural organization on the basis of their temporal relationships. This was achieved by the application of a component-analysis to a matrix of correlations between these elements, which were assessed from a study of sequences of behaviour. This method which was first used in ethology by Wiepkema (1961), has in a slightly modified form been applied in a study on the structure of chimpanzee social behaviour by Van Hooff (1970, 1971). One is referred to the latter study for an extensive description of the method and its rationale.

Of the five most important factors found, two could be interpreted respectively as "aggression" and "submission and flight". For, behaviour elements of an obvious aggressive nature (*e.g., chase*) on the one hand, and obvious expressions of fear (*e.g., flight, crouch*) on the other hand turned out to be almost pure measures of these factors; they had high loadings on these factors, whereas their loadings on the other factors were negligible. All elements with a positive loading, sufficiently high to attribute significance to it, on one, or on both of these factors have been called *agonistic behaviour elements.*

After our first orienting study of agonistic behaviour we started distinguishing a few other patterns which we added to the category of agonistic behaviour. The decision to qualify them as such was not based therefore on results of the factor-analysis but it followed from specific later analyses concerning their temporal contingencies.

Recently Angst (1974) described the displays of Java-monkeys in detail and divided their behavioural sequences in "blocks" on the basis of a qualitative analysis. Although our studies were fully independent, the results accord well, particularly with respect to the behaviours with a typical display character.

(b) Description of Aggressive Behaviour

We distinguish between three principal categories of aggressive behaviour patterns:

Threat: Facial expressions, vocalizations and intention movements.

Chase: Quick and brusque movements towards the partner.

Physical assault: More or less violent physical contacts.

I. Threat

(1) *Staring*: fixedly looking at partner (Altmann, 1962; 32, "stares at").

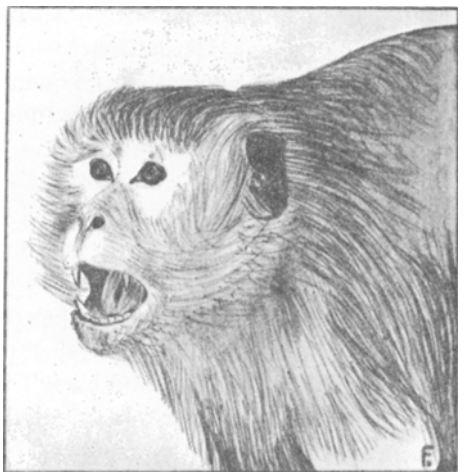


Fig. 1. Dominant male shows staring *open-mouth* (2).

(2) *Open-mouth*: staring with opened mouth (VAN HOOFF, 1967; Staring open-mouth face"). See Figure 1.
(3) *Grunt*: simple and rather soft vocalization; "hur" (ANGST, 1974; 4, "Drohgrunzen").
(4) *Head-bob*: Nodding head down- and forwards (ALTMANN, 1962; 30, "Bobs head towards").
(5) *Shoulder-bob*: Nodding shoulders down- and forwards (ALTMANN, 1962; 30, "Bobs thorax toward").
(6) *Ground-slap*: Slapping on the ground with hand(s) (ALTMANN, 1962; 28, "Slaps ground toward").

The following behaviour patterns can be considered as a separate subcategory, called "*two-frontal behaviour*" (or "appeal aggression"; see p. 272, c). These displays are distinct in that they are composed of aggressive and non-aggressive behaviour elements separately directed at different partners. These two partners are called respectively: the opponent and the dominant. The last term is used because the non-aggressive components of these "double displays' appeared to be directed only at dominants. The behaviours, which aggressors direct at the dominant partner, are called *sub-directed behaviours*. Most of these sub-directed behaviours seem to be adopted from other contexts of social behaviour; i.e., they occur mainly within sexual or socially positive sequences (*e.g., lip-smacking, presenting*). Two of these, however, command special attention, as their occurrence is restricted to agonistic sequences. These two specific sub-directed behaviours are *showlooking* and *frontal-pass*. *Showlooking:* an exaggerated, repetitive and stereotyped form of alternate threatening at the opponent and looking at the dominant, in which the head is jerked to and fro. Particularly the turn away from the dominant to the opponent is done abruptly and quickly. The aggressor's glance at the dominant is comparatively short. Photographs and video-images revealed that the eyelids, which are widely apart while threatening the opponent are lowered just before the turn towards the dominant; the aggressor animals do not stare but look at the dominant. The alternating movements of *show-*

looking occur in bouts and can be repeated so fast as to look mechanical (we have video-recordings of a monkey performing 16 *showlooks* within 30 seconds.)

Showlooking is distinguishable from "*looking*" mainly by the brusqueness of the head movements, which makes it very conspicuous. In addition, "*looking*" was never seen to occur in a repetitive manner. The spatial distribution of the three involvee determines the angle of rotation of the head movements in *showlooking*. But the pattern varies less as would be expected solely from this. It occurs mainly when the aggressor finds itself in a position somewhere between the opponent and the dominant, aggressors seem to manoeuvre themselves actively in such a position.

Frontal-pass: walking just in front of the dominant, passing him once or several times. *Frontal-passing* is accompanied by threats towards the opponent and preceded by approaching the dominant (in a rather quick, sleek manner). It may be followed by approaching the opponent (sometimes in a peculiarly slow and "stiff" way; pattern (9). Figure 2 gives a schematic representation of these locomotion patterns.

N.B.: Aggressors approaching and passing dominants at distances exceeding 2 meters are not considered as frontal-passers. KUMMER (1957; pp. 52, 53) described similar patterns of hamadryas baboons.

Some non-specific sub-directed behaviours are:

- *Touching* the dominant with the hand, which may be followed by embrace (the latter is always carried out by the dominant).
- *Lip-smacking* (see under 7, *pointing*).
- Raising the tail and *presenting the hindquarters* towards the dominant (KUMMER, 1957; "Gesicherte Drohung"; ANGST, 1974, 55, "Präsentieren", 2).

  This is mainly done by female aggressors and may result in a short mount by the dominant, during which the aggressor continues threatening the opponent (ANGST, 1974; 50, "Imponier begatten", 1).

The following three threat displays seem to be reserved especially for two-frontal behaving aggressors; *i.e.*, they are rarely directed at an opponent without being accompanied simultaneously or intermittently by sub-directed behaviours towards a dominant (see pp. 272–274, c).

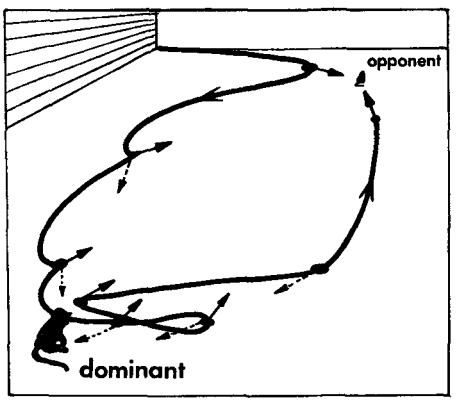


Fig. 2. *Frontal-pass* by an aggressor (route indicated by thick solid line) which threatens the opponent (solid arrows) and *showlooks* towards the dominant (broken arrows).

(7) *Pointing*: Facial expression composed of the following elements: eyes—fixedly looking, though less widely opened as in *staring*; eye brows—lifted; scalp—pulled backward; ears—flattened; mouth—nearly closed; lips—tensely closed; mouth-corners—in normal position or slightly pulled forward; chin—lifted up and thrusted forwards (Shirek-Ellefson, 1972; "white pout threat" and ANGST, 1974; 6, "Stummes Hetzen"). See Figure 3.

The mouthparty strongly thrusted forwards and the scalp pulled backward render the *pointing face* a "stream-lined" appearance. It seems a big living arrow, indicating precisely in whose direction the aggression is meant. This impression is even stronger in the cases that *pointing* is combined with *showlooking* or *stiff-approach* (9).

An expression resembling the *pointing face* is the *lip-smacking face*, in which the mouth and lips are rapidly opened and closed, resulting in audible smacks (VAN HOOFF, 1967). This may alternate with *pointing* but in a different female: *pointing* towards the opponent and *lip-smacking* towards a dominant third animal. In these cases of sub-directed *lip-smacking* the head movements are as brusque as in *show-looking*.

(8) *Serial-grunt*: vocalizations of the "grunt type" but louder, more rasping and mostly rapidly repeated (ANGST, 1974; 7, "Hetzgrunzen"). Sometimes this vocalization alternates with screamlike vocalizations (ANGST, 1974; 43, "Offensives Keifen").

(9) *Stiff approach*: a slow approach, step by step, with rigid legs and high borne back and shoulders (ANGST, 1974; 7, "Straffen der Gliedmaszen"). This may pass into *chase* or *physical assault* (cf., 16, *nosepush* and 17, *breast-push*).

Finally we should note that two-frontal behaviour is not necessarily restricted to aggressive monkeys. Aggressees may show (21) *flight-visiting* and/or (29) *bark-*

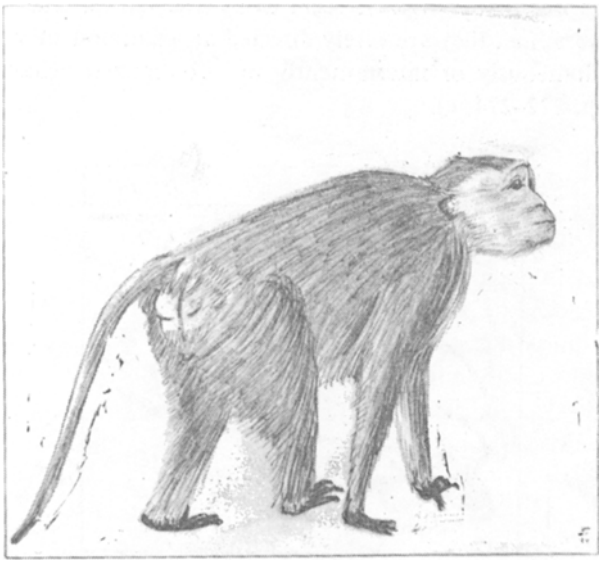


Fig. 3. *Pointing* (7) and *stiff approach* (9) shown by an adult female.

screaming which are of a two-frontal nature as well (see the description of fear behaviour).

II. Chase

(10) *Lunge*: short rush towards the partner (maximum 2 meters) (ANGST, 1974; 5, "Scheinangriff").

(11) *Chase*: Long run towards, or pursuit of the partner.

(12) *Missing strike*: Brusque hand movement towards the partner without touching it (although the partner may be within reach).

III. Physical assault

(13), (14), (15). *Strike, Catch* and *Tug*: Three types of vigorous hand contacts.

(16) *Nose-push*: a short and weak push by the aggressor, during a nose-nose contact with the opponent.

(17) *Breast-push*: can be regarded as an intenser form of the *nose-push* (16). The aggressor puts forth much more strength and pushes with face and breast. If the opponent does not flee it might be showen through the cage over several meters. This pattern and pattern (16) were only recorded from *pointing* aggressors.

(18) *Open-mouth push*: The opened mouth is pressed against the partner; the jaws remain opened. Before, during and after this "pseudo-biting" the *open-mouth threat face* (2) is shown. *Open mouth pushing* was observed only in adults and adolescents towards infants and juveniles.

The patterns mentioned above are called *light physical assaults* because they never cause injuries. Only *biting* (19) is considered a *heavy physical assault* since it may injure the partner.

(19) *Biting*: meaning obvious. *Biting* between members of an established group was never seen to result in deep wounds, whereas *biting* between strangers caused extensive and deep wounds on a few occasions.

(c) DESCRIPTION OF FEAR BEHAVIOUR

We distinguish between three principal categories of fear behaviour-patterns:

I. *Flight*: Fast withdrawing locomotion.

II. *Flight-intention*: Postures or movements expressing a tendency to flee.

III. *Submission*: Facial expressions and vocalizations.

I. Flight.

(20) *Flight*: fast running away from a partner.

(21) *Flight-visiting*: fast running away from one partner which is simultaneously directed towards another partner, resulting in non-aggressive physical contact with the latter.

II. Flight intention

(22) *Shrink*: bending away of the upper part of the body. This may be extended with one step backward.

Fig. 4. *Barkscreaming* (29) by a juvenile male.

(23) *Blocked-flight*: locomotion patterns directed away from the partner, who prevents flight by *catching* (14).
(24) *Crouch*: pressing the body against the floor (ANGST, 1974; 37, "Stummes Pressen") or creeping away in a corner with head and ventral side hidden.

III. Submission
(25) *Bared-teeth*: lips and mouth-corners are retracted thus showing incisors, canines and molars and mostly a large part of the gums (VAN HOOFF, 1967; "Silent bared-teeth face").
(26) *Teeth-chattering*: Rapidly opening and closing of the jaws with bared teeth (VAN HOOFF, 1967; "Teeth-chattering face").
(27) *Teeth-smacking*: id. with tongue protrusion. Intermediate between (26) and *lip-smacking*.
(28) *Screaming*: Loud, high-pitched vocalizations, shrill sounding and drawn-out, accompanied by *bared-teeth* face and an opened mouth. (ANGST, 1974; 40, "Kreischen"; cf., "Bared-teeth scream face", VAN HOOFF, 1967).
(29) *Barkscreaming*: very loud screaming, strongly modulated in frequency and shorter than (28). This may be associated with aggressive as well as fear behaviour-patterns. The accompanying posture may show a forward tendency and clearly expresses an ambivalence between the tendency to attack and to flee (see Figs. 4 and 5) (Shirek-Ellefson, 1972; "scream threat" and ANGST, 1974; 42, "Verkreischen"; cf., "Staring bared-teeth scream", VAN HOOFF, 1967).
Barkscreaming individuals do not usually aim their behaviour solely at one partner, but may intermittently *barkscream* shortly towards dominant third animals; it often is a "double directed" display.
(30) *Barking*: vocalizations resembling barking of dogs, accompanied by *staring* at the partner. The teeth may be bared (ANGST, 1974; 44, "Protest Schrei").

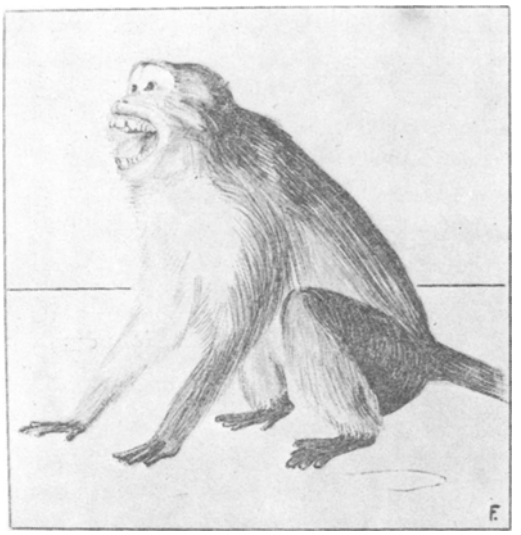


Fig. 5. *Barkscreaming* (29) by an adolescent male.

In all observed cases *barking* was directed at a dominant partner attacking a third group member. Thus adult females might *bark* and *present* their hindquarters towards the α-male when it bit their screaming child.

(d) Discussion of This Section

As early as 1957 Kummer offered a detailed description of subdirected behaviour-patterns of hamadryas baboons. He focussed primarily on what might be called "bipolar simultaneous two-frontal behaviour" in that the aggressive and sub-directed displays are distributed over the two body poles and shown at the same time to both partners; *i.e.*, the *protected threat* ("Das bipolare Verhalten"; Kummer, 1957, p. 52). Aggression together with sub-directed *presenting* is only one type of two-frontal behaviour; however, it should be distinguished from "monopolar alternating two-frontal behaviour"; like aggression accompanied by *showlooking* or *lip-smacking* in another direction. Here the displays are "packed together" primarily in the head and shown in alternation to the opponent and the dominant. This is, by far, the most common type of two-frontal behaviour in Java-monkeys and besides our observations confirm its presence in other catarrhine primate species; *e.g.*, *Macaca mulatta*, *M. fuscata, Papio hamadryas* and *P. anubis* (for the latter species see also Hall & DeVore, 1965, p. 64).

Sub-directed behaviours and the aggressive patterns associated with them (*e.g.*, *pointing* and *serial-grunt;* see pp. 272–274, c) give the impression of a "sollicitation for aid". This impression is st engthened by the fact that the sub-directed behaviours are exclusively directed at dominant group members. As the most dominant member, the α-male, is by definition devoid of a more powerful partner it stands to reason that we do not expect him to show sub-directed behaviours. Indeed, one of the α-males ("*Aam*") of our two groups of monkeys never has been observed to perform *showlooking, presenting, lip-smacking* or *frontal-passing* towards a third animal during his

aggressive actions, nor *pointing* and *serial-grunts* towards his opponent. The other α-male ("*Gam*"), however, sometimes showed *pointing* and *showlooking* when a large number of aggressors jointly attacked a group member, which stood under his protection at that time (for instance: an oestrous female). So, in cases where, so to speak, "high demands were made upon his authority". But this male was never seen to direct the two behaviour patterns at group members; he *pointed* at an imaginary opponent and *showlooked* at an imaginary dominant behind him (as if he hallucinated a Super α-male to which he "prayed" for aid).

Finally, it is worth noting that intermediates between *showlooking* and *looking* may occur, which cannot be labelled as one of the two patterns in a satisfactory way. And not only between these two, but between many behaviour patterns smooth transitional forms have been observed. Splitting up monkey behaviour in elements is like giving names to points on a continuum (HINDE, 1966; VAN HOOFF, 1971). A certain arbitrariness in the categorization is therefore unavoidable.

THE GROUP

During the period of study (17 May–15 August, 1973) the group concerned (group G) included 17 monkeys. Here "G" refers to the dominant male *"Gleuf"*, further denoted here as *"Gam"*, according to an identification code, in which the four letters subsequently refer to:

(1) First letter of the animal's daily name.
(2) Age class: a=adult; o=adolescent; u=juvenile; i=infant.
(3) Sex: m=male; f=female.
(4) Descent: first letter of the name of the animal's mother (if present in group).

The group consisted of two adult males, six adult females, one adolescent male, three juveniles and five infants. In Table 1 the individuals are listed with age, weight and further particulars.

The term "import" means that the animal has been imported via the R.I.V. (State Institute of Public Health) directly from Indonesia. (*Kam* we received from a private person and *Saf* was born at the R.I.V. The monkeys arrived in this order: *Daf* (1965); *Baf*, *Saf* (1966); *Gam* (1969); *Kam*, *Zaf* and *Paf* (1971). Ages apply to May 1973. Estimated ages are placed between parentheses. Weights apply to 13 November 1973. (The youngest children are weighed together with their mothers. The weight of the mother is the difference between this total and the estimated weight of the child). *Daf* was pregnant during the study and gave birth to a son just afterwards. The other adult females (except *Zaf*) showed normal oestrous cycles. *Paf* began cycling during the study.

The group was lodged in a cage placed inside a building. Till 20 July its dimensions were 20 m^2 surface and 2 meters high; after that the surface was enlarged to 40 m^2. The walls of the cage were made out of eternite and wire netting. The cage contained metal bars, eternite platforms and a big water basin. In periods without observation, the monkeys had access also to a (smaller) cage outside. They were fed twice a day (9.00 and 16.00).

Doubtlessly this group lives in circumstances quite different from those of feral

groups. The restricted space available excludes, for instance, periferilization processes. Time sampling methods revealed that the group members devote most of their time to social positive behaviour, play and solitary activities and much less to sexual and agonistic interactions (to the latter an average of 2%).

METHOD

(a) Observation Procedure

The observations consisted of episodes, each lasting half an hour and always recorded by one and the same observer, who simply sat in front of the cage. He named the observed behaviours in the form of the triplet complex: "Who does what to whom" and spoke these data into a microphone connected either with an audio- or with a video-recorder. Priority in the observation was always given to agonistic behaviours. These were, moreover, recorded in greater detail than other patterns of social behaviour, for we used a list of 60 behavioural codes, from which 30 represented agonistic patterns. In some instances the maximal speed of speaking appeared to be insufficient to record all observed agonistic behaviour. Immediately after such an outburst of agonistic activity, the recording was supplemented from the observer's memory. The spoken protocols were recorded on a sound-track of either an audio-recorder (51 episodes) or a video-recorder (29 episodes). In case of video-recording a second observer handled the camera. On both audio- and video-recorder a second audio-channel was used to record simultaneously the vocalizations of the monkeys, permitting a more detailed description of these. By playing back the video recording slowly and repeatedly we could determine the exact sequence, duration and frequency of certain behaviour patterns. These data have been transcribed as the *video-protocols.* Our basic material was formed by the *audio-protocols;* i.e., the transcriptions of the spoken protocols both from the audio-recorder and from the audio-channel of the video-recorder. From the latter these transcriptions were made without seeing the pictures (monitor off) and before the video-protocols were transcribed. These audio-protocols, of which there were 80 (51+29), provided much more fragmentary information about thh agonistic events, however. Thus these cannot give r liable answers to questions like: "how often and how long did individual A *stare at* individual B?" But we expected a trustworthy answer to questions like: "within how many interactions did A *stare at* B at least one time?" or, still less detailed: "...did A show *threat elements* towards B?". As our analysis is mainly directed at the questions formulated in the introduction (pp. 259–261, b), the audio-protocols were expected to be sufficiently reliable to supply the data, necessary for that purpose. This was investigated by comparing the corresponding 29 audio- and video-protocols (see pp. 285–286).

(b) Observation Episodes

Observations were carried out in the mornings (36 protocols b.tween 9.00 and 12.00) and afternoons (44 protocols between 14.00 and 17.00) during the period of 15 May–17 August 1973, except for the first three weeks of July, however, on account of the enlargement of the cage (see The Group). This was the only radical change in the

group's environment within the period of study. Although not planned within the framework of our study, this change was treated as an experiment. Contrary to our expectations, however, the change hardly appeared to affect the agonistic activity of the group during the following period.

AGONISTIC INTERACTIONS AND ROLES

(a) GENERAL CLASSIFICATION AND DEFINITIONS

In "Agonistic Behaviour Patterns" we gave a classification of the social behaviour patterns, namely:

1. Aggressive behaviours (threat, chase, light- and heavy physical assault).
2. Fear behaviours (flight, flight-intention and submission).
3. Sub-directed behaviours.
4. Other social behaviours (sexual-, play- and social positive behaviours).

Categories 1 and 2 are taken together as "*agonistic behaviour*". The behaviour patterns of category 3 are distinguished as such, whenever these occur in sequences containing agonistic elements; otherwise these are considered to belong to category 4.

An *agonistic interaction* is each confrontation between group members in the course of which agonistic behaviour patterns are performed, and which is not interrupted by a pause longer than 15 seconds. Those individuals which show and/or receive agonistic behaviours we shall call the *involvees*. Dependent on the number of involvees, we speak of *dyadic-, triadic- or polyadic interactions*. Sub-directed behaviours are not classified as agonistic and as a consequence individual A, receiving those patterns, but neither showing nor receiving agonistic behaviours, is not considered an involvee in the interaction. In such a case, however, the respective interaction is characterized as an *impure dyad, triad,* etc., thus taking account of the impure involvement of individual A. The same procedure is applied to cases where group members had contact with the interaction partners by means of other social behaviour categories (for instance, if a non-involvee *grooms* an involvee). By doing so we obviate to some extent the disadvantages carried with the one-sided character of our pragmatic definition of involvement.

Pure dyads are thus defined as agonistic interactions in the course of which the two individuals involved were not observed to have any form of contact with third animals. The purity of these dyads goes of course by comparison. These are unlikely to be pure in the sense of "not affected by the presence of third animals and not affecting these". It is to be expected that in a group of monkeys the interaction partners will always reckon with the presence of the others and their possible interference and that this may influence the course and outcome of confrontations.

The delimination of an agonistic interaction by a pause of minimally 15 seconds is based on our impression that after more prolonged intervals the chance of resumption is decreased till about the level of the chance of starting agonistic behaviour. At the moment we verify the correctness of this assumption (c.f., NELSON, 1964). The use of this time-limit can be illustrated by the following examples; in which A, B and C stand for group members and the exchange of agonistic behaviour is indicated by a connecting dash between them:

Table 2. Frequencies of types of agonistic interaction.

I	1. Dyads "impure" because of		
	(a) sub-directed behaviour	109	
	(b) other behaviour	458	
	2. "pure" Dyads	217	
	Total number of Dyads		784
II	Total number of Triads		147
III	Polyads with		
	4 animals involved	50	
	5 " "	20	
	6 " "	13	
	7 " "	10	
	8 " "	3	
	9 " "	2	
	10 " "	3	
	11 " "	4	
	Total number of Polyads		105
Total number of agonistic interactions			1036

A–B	10 sec. interruption	A–B:	1 dyad A, B
A–B	20 sec. interruption	A–B:	2 dyads A, B
A–B	10 sec. interruption	A–C:	1 triad A, B, C
A–B	20 sec. interruption	A–C:	2 dyads A, B and A, C

Within the 80 half hours recorded 1036 agonistic interactions were observed. In Table 2 one finds the frequencies of the different types of interactions. (The polyads are classified according to the number of individuals involved and the dyads according to their "purity").

(b) DYADS

In 489 of the 784 agonistic dyads aggressive actions were shown by at least one of the involvees. An *aggressive action* is defined as a bout of agonistic behaviour patterns:
(a) without interruptions longer than 15 seconds,
(b) of which at least the first pattern is aggressive and which is
(c) directed at one and the same group member. (In practice it appears that such bouts rarely contain fear elements; this was observed in only 25 of the 489 dyads with aggressive actions; *i.e.*, 5.1%). The first, and often the only involvee to show aggression is called the *aggressor*.

Dyads in which the aggressive actions occurred can be divided into three types on the basis of the responses of the aggressee:

1. *Aggressive reaction*: an aggressive action given by the aggressee after it has received aggression and which is directed at the aggressor.
2. *Fear reaction*: a bout of agonistic behaviour patterns starting with a fear element and directed at the aggressor. (In practice such bouts only very rarely appear to contain aggressive elements; this was observed in only 11 of the 290 fear reactions shown in dyads; *i.e.*, 3.8%).
3. *Non-agonistic reaction*: the aggressee does not react by means of agonistic behaviour.

In the remaining 295 agonistic dyads no aggressive actions did occur. In this type

Table 3. Frequencies of types of agonistic dyadic interaction.

I	Dyads with aggressive action (total 489)	
	Aggressee gives (1) Aggressive reaction	15
	(2) Fear reaction	290
	(3) Non-agonistic reaction	184
II	Dyads without aggressive action	
	(4) "Unprovoked" fear	295
	Total number of agonistic Dyads	784

of dyad an animal shows fear behaviour towards a partner that is not behaving overtly aggressively, *e.g.*, just *looked* or *approached.* We shall take this type in our list of types of agonistic dyads as the fourth, namely 4, *"unprovoked" fear.* Table 3 gives the frequencies of the four types of agonistic dyads.

(c) STRAIGHT-AGGRESSION AND APPEAL-AGGRESSION

From Table 2 we have learned that 109 of the 784 dyadic interactions were "impure", in the sense that one or both of the involvees showed *sub-directed behaviours* to a third party. We asked ourselves whether the form of the aggressive action shown is different when at the same time *sub-directed* behaviour is performed towards a third

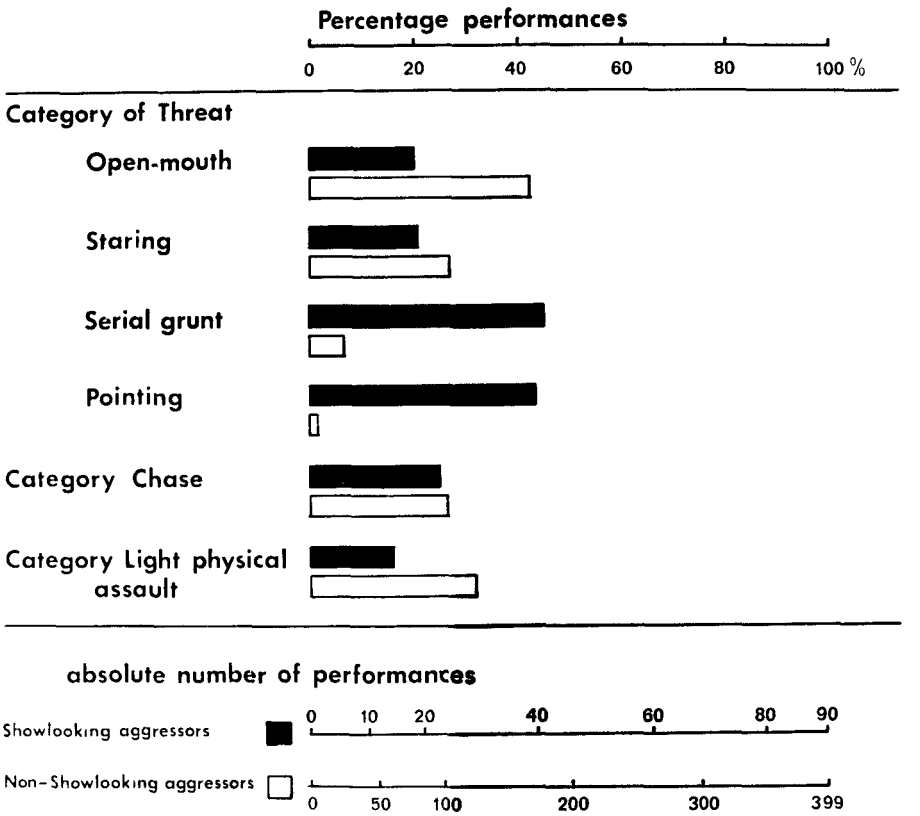
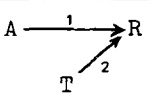
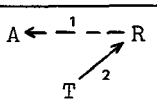
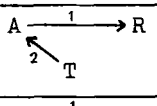
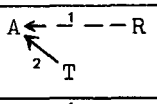
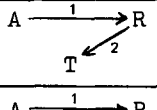
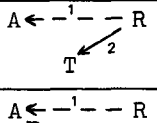
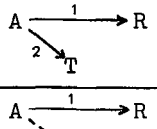
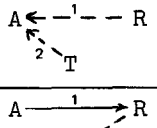
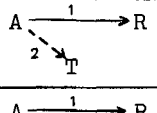
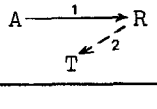
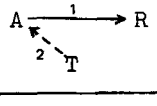


Fig. 6. Percentage of aggressive actions comprising particular elements and categories of agonistic behaviour, for *showlooking* and *non-showlooking* aggressors respectively.

Table 4. Frequencies of types of agonistic dyadic interaction-components of triads and polyads.

I	Dyadic components with aggressive action (total 593)	
	Aggressee gives (1) Aggressive reaction	11
	(2) Fear reaction	379
	(3) Non-agonistic reaction	203
II	Dyadic components without aggressive action	
	(4) "Unprovoked" fear	210
	Total number of agonistic dyadic components	803

animal. By far the most frequently observed element of *sub-directed* behaviour appeared to be *showlooking* (for a definition see pp. 262–263). It accompanied 90 of the 489 aggressive actions performed within dyads. How is the composition of these 90 aggressive actions as compared with the remaining 399? For this purpose we determined the number of aggressive actions during which *showlooking* resp., *non-showlooking aggressors* performed the following elements or categories of behaviour at least once: *open-mouth, staring, serial-grunt, pointing, chase,* and *light physical assault.* These variables are selected on the basis of their relatively high frequencies of occurrence within dyads (for descriptions see pp. 262–265). The results are presented in Figure 6.

interaction scheme	category frequency	interaction scheme	category frequency
	a) 25		g) 6
	b) 11		h) 5
	c) 13		i) 17
	d) 14		j) 13
	e) 11		k) 15
	f) 7		

Explanation : The direction of aggressive actions and "unprovoked" fear is indicated by arrows between the involvees A, R and T :

A ——→ R : aggressive action by A towards R
A ←- - - - · R : "unprovoked" fear by R towards A

The order in which these bouts of agonistic behaviour subsequently began is indicated by the small figures.

Scheme I. Categories of triadic agonistic interactions.

These data indicate that the elements *pointing* and *serial-grunt* are performed almost exclusively by aggressors which intermittently *showlook* at third animals, whereas *open-mouth* and the elements of the category *light physical assault* occur relatively more often as part of the aggressive actions of *non-showlooknig* aggressors. Thus a distinction between two main types of aggressive actions that can occur in dyadic interaction, namely between *straight aggression* and *appeal-aggression,* as suggested already by ANGST (1974), seems justified. A further argument is revealed by a video-analysis of dyads. This revealed that 17 aggressive actions accompanied by *show-looking* had an average duration of 22.6 seconds, whereas 77 actions without *show-looking* lasted an average 3.2 seconds (The Mann-Whitney U test was employed to compare the two samples; $p<0.1\%$, two-tailed). This great difference in duration of the respective actions suggests differences in the controling factors as well.

(d) DYADIC COMPONENTS OF COMPLEX INTERACTIONS

Agonistic triads and polyads may be considered as composed of dyads. Table 4 gives the frequencies with which the different types of dyadic interactions occurred as components of triads and polyads. (The total number is smaller than the maximum possible number, because not all involvees in complex interactions exchange agonistic behaviours).

We do, however, oversimplify the structure of complex interactions by dissecting them into dyadic components. Thus the "unprovoked" fear occurring within complex interactions is "unprovoked" in the sense that fear is shown towards a partner from which no aggression has been received, but aggression receipt from another partner is not excluded, as in dyads (compare Scheme I; triad category K).

It makes more sense to have a look at the intact interaction structures, therefore.

(e) TRIADS

Each triad develops out of a dyadic interaction, or, at any rate, one dyadic component is always observed at first. The three individuals involved are, therefore, named the *actor* (A), *reactor* (R)—constituting the first dyad, and the *third involvee* (T). In the beginning we classified the 147 triads according to the occurrence and direction of aggressive-, fear- and sub-directed behaviour patterns. On that basis we distinguished 67 triadic interaction types. One of these was observed 13 times, all other types 7 times or less. So, it appears that triadic interactions are far from stereotyped. By restriction of the distinguishing criteria, the 67 types could be classified within more global categories. This classification is solely based on the direction and order of the aggressive actions shown by the involvees and on the fact whether "unprovoked" fear behaviour is shown. In this manner we found 17 categories of triadic interaction types. Categories which were observed 5 times or more, are listed in Scheme I.

We will pay special attention to three of these categories.

I. *Actor Alliances* (AA): the third partner shows aggression into the same direction as the first aggressor does or just did (Scheme I; category a). Thus the third

involvee joins the actor against the reactor. This type of interaction is not confined solely to triads; often it develops into polyads, in which many more individuals direct aggression jointly to a single opponent. It seems useful to distinguish between these aggressive actions and those which are not performed within the frame-work of alliances.

1. *Solo-aggression*: aggressive actions of a single individual against a group member (i.e., all aggressive actions within dyads and those within triad categories b till and including i, and k from Scheme I).
2. *Start-aggression*: aggressive actions which start off an aggressive interaction, in which one or more individuals join aggressively as well (Scheme I; category a, action 1).
3. *Join-aggression*: aggressive actions by third, fourth etc., individuals into the same direction as the start-aggression (Scheme I; category a, action 2).

II. *Reactor Alliances* (RA): the third partner shows aggression towards the first aggressor (Scheme I; category b) and may thus operate as a defender of the reactor. This aggressive role in this interaction is called:

4. *Protective aggression.*

III. *Redirections* (Rd): the aggressee of the first dyad shows aggression towards a third animal (Scheme I; category c). This we call,

5. *Pass-on-aggression*: This type of interaction is not always confined to two aggressors but may develop into "chains" involving a third, fourth, etc. Furthermore, *pass-on-aggression* may be directed at the observer, a bird or other moving objects. A very remarkable version has been observed several times, namely, that involvees of an extended agonistic interaction jointly ran to the waterbasin and threatened at their own reflections.

All aggressive actions occurring in dyads, triads and polyads could be classified under the five types distinguished above (the "aggressor roles"); this is done in Table 5.

(N.B.: Not all these aggressor roles are mutually exclusive, as will be shown in part f of this section).

The triad categories g, h and i differ from respectively a, b and c by the absence of

Table 5. Frequencies of types of aggressive actions; this Table comprises all aggressive actions observed.

I	Solo-aggression	(1) Pass-on-aggression	36	
		(2) Protective aggression	44	764
		(3) Other types	684	
II	Start-aggression	(1) Pass-on-aggression	13	
		(2) Protective aggression	9	110
		(3) Other types	88	
III	Join-aggression			208
	Total number of aggressive actions			1082

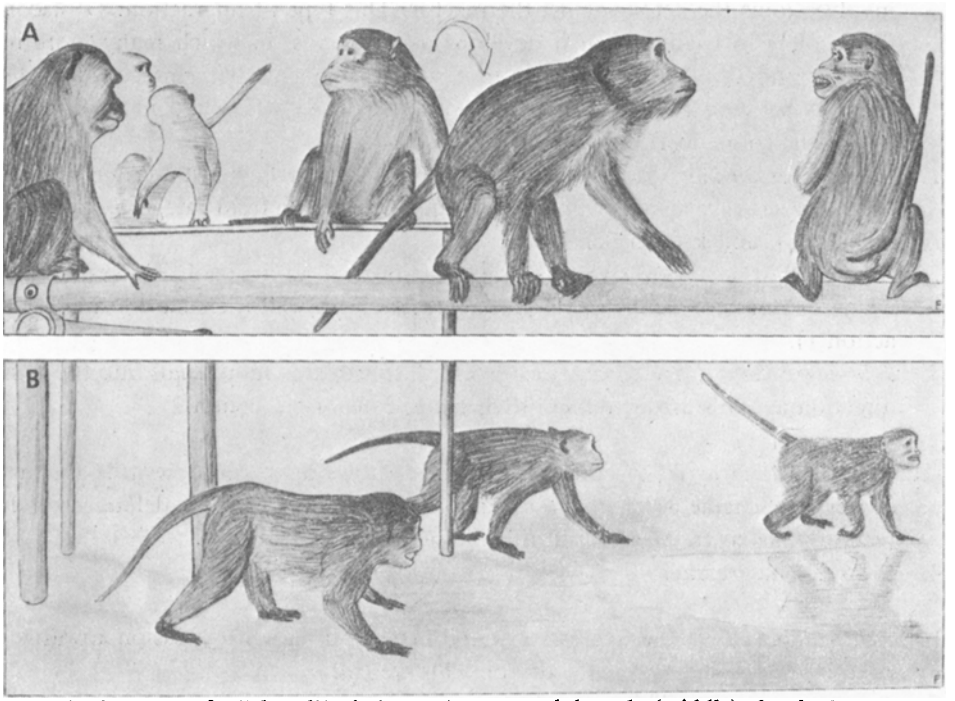
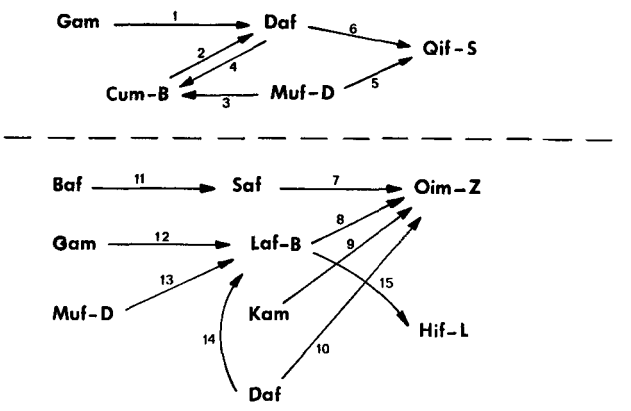


Fig. 7. An instance of a "closed" triad. **a.** A young adult male (middle) *showlooks* at the α-male (left) after which he jumps at the bar (arrow) and *points* (7) at his opponent, which *shrinks* back (22) with *bared-teeth* (25) and tail in upright position (right). **b.** After this the opponent *flees* (20) with *bared-teeth* (25), (right) from the two males. The α-male (foreground) approaches with *open-mouth* (2) threat, thus joining the start-aggressor which shows *pointing* (7) with *stiff approach* (9), (background).

aggression and the occurrence of "unprovoked" fear between the first two partners. We use for these categories the same names as used for a, b and c, but with the prefix "unprovoked" added. (So, abbreviated, resp.: UAA, URA and URd).

Very rarely triadic interaction types were observed in which each partner exchanged agonistic behaviours with *both* others. (Because of their rarity these more complex triads have not been represented in Scheme I). Sub-directed-, sexual- or social positive behaviours, however, often occur between duo's of involvees which do not exchange agonistic behaviours. An example of such a "closed" triad, in which each involvee aims behaviour at both of its partners, is represented in Figure 7. To KUMMER (1967) this "closedness" was one of the necessary criteria for "*tripartite relations*" (see pp. 258–259, a). We used neither this, nor his other criteria in defining triadic interactions. As a consequence there are only a few triadic types which can be considered as real "tripartite relations" in KUMMER's sense.

Interestingly enough we observed interactions in which *presentation* of the hindquarters was used in a sense contrary to those of the *protected threat* (KUMMER, 1957; see 258–259, a). A third partner interfered with an agonistic dyad by *presenting* towards the aggressor and walking in front of him with the apparent intention to hinder him in reaching his opponent. In some instances this behaviour had been preceded by



Scheme II. Instance of a complex agonistic interaction (polyad *No. 89*). The direction of aggressive actions is indicated by arrows between the involvees. The order in which these actions subsequently began is indicated by small figures (further explication see text).

barking (see 261–265, b) and followed by a protective aggressive action against the original aggressor.

(N.B.: We possess video-recordings of such interactions).

(f) POLYADS

A satisfactory classification of polyads appeared to be impossible because of the vast variety of interaction structures observed. One can describe, however, the aggressor roles of the involvees in the same terminology as applied to indicate aggressor roles in dyadic and triadic interactions. We will illustrate this with a concrete example: polyad *No. 89* (Scheme II).

The 15 aggressive actions performed within this polyad have been classified as follows:

Solo-actions (11, 15); start-actions (1, 3, 5, 7, 12); join-actions (2, 4, 6, 8, 9, 10, 13, 14); protective-actions (3, 11, 12) and pass-on-actions (15). So, within this polyad, actor- alliances were started two times by protective aggressive actions (3 and 12), whilst both receivers of these actions performed join-aggression within other actor-alliances (2, 8) and one of them showed pass-on-aggression afterwards (15). Such an extensive interweaving of the three interaction types AA, RA and Rd occurs within many polyads. Nevertheless these take place in a relatively short time (*e.g.*; for this case video-analysis revealed that the whole interaction lasted 2 minutes and that the last part—the interval between the onset of action 8 and of action 15—lasted only 34 seconds). Extensive polyads often unroll in phases. Thus in polyad *No. 89* a new phase had come when *Saf* started an actor-alliance against *Oim-Z*, whilst her child *Qif-S* still received threats of *Daf* and *Muf-D* (one could call this *parallel-aggression* by *Saf*). Some time later *Daf* joined the new actor-alliance. It is tempting (and maybe right) to see this action of *Saf* as an intended manoeuvre to liberate her child by attracting its enemies to aim aggression at another individual.

FACTORS INFLUENCING ALLIANCE-FORMATION

Comparison of Table 3 with Table 4 shows that more than half of the agonistic contacts within the group occurs in interactions with more than two involvees. It is evident that the monkeys are attracted to agonistic interactions between others. We should like to know which features do mark those interactions which attract outsiders to associate themselves.

In this connection we are concerned with the two types of active association with agonistic interactions; *i.e.*, *protective-* and *join-aggression* (for definitions, see pp. 274–276, e). We shall confine ourselves here to the following three questions:

(a) Does the tendency to join aggression covary with the number of aggressors with whom joining is possible?

(N.B.: It is useless to pose a corresponding question with respect to reactor-alliances, because group members never protected more than one aggressee at the same time).

(b) Do monkeys, involved in an agonistic interaction, influence the chance of association by outsiders by *showlooking*, or by uttering loud vocalizations like *serial-grunt*, *scream* or *barkscream*?

(c) If there is such an influence, does it vary with the ages of the animals that perform the *showlooking* and vocalizing?

With respect to the first question we did not have a clear *a priori* hypothesis. With respect to the second, however, we expected that *serial-grunt* and *showlooking* do attract join-aggressors and that *screaming* and *barkscreaming* do aid reactors in receiving protection. The same has been supposed, independently from us, by ANGST (1974, p. 16, 17 and 50). Question (c) is posed because the big difference in frequency of *screams* and *barkscreams*, uttered by young monkeys as compared with elder ones, suggests that the social effectiveness of these vocalizations may depend on the age-class of the performers.

(a) *Is the join-tendency related to the number of aggressors to join with?*

The 110 actor-alliances (AA's) observed, can be classified according to the number

Table 6. Actor-Alliances classified according to the number of aggressors involved.

	AA2	*AA3*	*AA4*	*AA5*	*AA6*	*AA7*	Total
frequency	58	28	13	4	3	4	110

Table 7. The tendency to join, in relation to the number of aggressors to join with; data of 11 group members taken together.

Aggressors to join	Opportunities to join	Observed joins	Tendency to join
1	8348	107	1.3%
2	1005	52	5.2
3	432	24	5.6
4	170	11	6.5
5	65	7	10.8
6	35	4	11.4
7	16	0	0.0

of aggressors involved (resp., AA2, AA3, AA4, etc.). The frequencies of these classes are given in Table 6.

In order to answer question (a), we counted for each group member the number of times it joined respectively a single aggressor, two aggressors, three, etc. and expressed this frequency as a percentage of the number of respective opportunities it could do so. This percentage is called the tendency to join resp., 1, 2, 3, etc. aggressors. Thus *Daf*, for instance, could join all solo- and start-actions (for definitions, see pp. 274–276, e) performed by and directed at other group members than herself. Actually *Daf* appeared to have 753 opportunities to join a single aggressor, while she utilized 17 of these (2.3%). *Daf* could join two aggressors in those of the 110 recorded AA's which were not directed at herself (1) and in which she herself did not already operate as a starter (11) or first joiner (17). She utilized three of these 81 opportunities to join two aggressors (3.7%).

The data thus computed for 11 group members have been taken together and presented in Table 7 (of the six remaining group members three never showed join-actions and three only once). For each of these 11 individuals Table 8 presents the average join-tendency and the specific tendencies to join 1, 2 or 3 aggressors.
(N.B.: In all cases the number of opportunities exceeded 20).

It appears that every group member which joins relatively frequently is attracted stronger to join two aggressors rather than a single one (Table 8). The data summarized in Table 7 seem to indicate that the attractiveness still increases with higher numbers of aggressors up to a certain number. It is not clear, however, whether this trend is representative for all group members; already with respect to the relative attractiveness of three compared with two aggressors Table 8 reveals big inter-individual differences (compare *Kam, Gam* with *Daf, Muf-D*). It is our impression that these differences reflect consistent individual traits. However, the present numerical data are insufficient to establish this.

We want to emphasize here that the quantitative analysis of complex interactions presents many sorts of snags, because of the big number of interdependent variables playing a role. New light may, for instance, be shed on the data concerning join-

Table 8. The average join-tendency and the specific tendencies to join 1, 2 or 3 aggressors; data for 11 individual group members.

Individual	Total opport. to join	Total observ. joins	Average tendency to join	Tendencies to join one-	two-	three aggressors
Laf-B	693	33	4.8%	2.3%	15.8%	13.5%
Muf-D	718	31	4.3	2.2	7.9	18.0
Kam	831	33	4.0	2.4	9.1	5.9
Daf	753	30	4.0	2.2	3.7	15.1
Gam	735	22	3.0	1.8	7.4	6.9
Saf	643	18	2.7	1.1	6.9	5.4
Jom-D	796	11	1.4	0.4	4.1	2.3
Cum-B	745	8	1.1	0.5	2.1	2.4
Num-S	849	8	0.9	0.5	1.9	2.1
Yif-D	780	6	0.8	0.5	1.0	0.0
Baf	807	5	0.6	0.4	1.0	0.0

tendencies if we take into consideration which group members received the join-aggression. Suppose that most join-actions are directed at only a few group members (call these "scapegoats") and that these animals are not as strongly "preferred" as objects of single aggressors. Then the tendency to join a single aggressor may appear to be lower than the tendency to join two or more aggressors, because of the relatively few opportunities to join single aggressors against those "scapegoats" whereas the opportunity to join two aggressors mostly concerns aggression against the "scapegoats".

This example has not been given without reason. For we found indeed indications that this group contains "scapegoats" as defined above. As the structure of agonistic relations will be treated extensively in a separate paper, we may restrict ourselves here to showing that *Paf* and *Oim-Z* can be considered as the "scapegoats"; together they received 104 of the 208 join-actions (50.0%), but only 147 of the 774 solo- and start-actions (19.0%). If we compare the tendencies to join aggression against *Paf* and *Oim-Z* with such tendencies against the other group members (see Table 9), we learn that the stronger inclination to join two or more aggressors rather than a single one is present with respect to both the "scapegoats" and the other group members. It is therefore a fundamental aspect of join-aggression and is not the effect of the presence of "scapegoats", in spite of the hypothetical possibility of the latter explanation.

(b) *Do showlooking and serial-grunts influence the formation of actor-alliances?*

When *showlooking* (*sl*) and *serial-grunts* (*sg*) occur, these form part of aggressive actions. We can distinguish between four types of aggressive actions, namely those comprising[1] *sl*, *sg*, *sl & sg*, and actions comprising neither *sl* nor *sg*. Now we want to know which percentage of aggressors, performing these respective types of actions

Table 9. Comparison between the tendencies to join aggression against *Paf* and *Oim-Z* with such tendencies against the other group members; data of 11 group members taken together.

	Aggressors to join	Opport. to join	Observ. joins	Tendency to join
Against *Paf* and *Oim-Z*	1	1487	45	3.0%
	2	411	27	6.6
	3	120	14	11.7
	4	88	8	9.1
	5	49	6	12,2
	6	31	4	12.9
	7	16	0	0.0
Against other individuals	1	6861	62	0.9%
	2	594	25	4.2
	3	312	10	3.2
	4	82	3	3.7
	5	16	1	6.3
	6	4	0	0.0

1) Comprising: i.e., the elements in question have been observed at least once during the aggressive action. N.B.: In case an actor- or reactor-alliance was started the elements should have been observed before.

released join-aggression and thus started an actor-alliance or received protective aggression from a group member defending the opponent. In other words: what are the percentages of "choices pro" and "contra" these types of aggressors.

Thus *Cum-B*, for instance, performed 39 aggressive actions, of which eight were join-actions. The remaining 31 actions were potential start-actions. On the other hand, all 39 actions could have led to counter aggression of a protector. Hence the percentages of choices pro and contra aggressors are based on different numbers of actions. The data of eight young group members (infants and juveniles), respectively nine older members have both been taken together in Table 10.

These data show that both young and older group members, performing aggressive actions which include *serial-grunts*, started significantly more actor-alliances than those not giving *serial-grunts* (see Table 10; comparison by χ^2-test, $p<0.1\%$, one-tailed). This trend had been found, more or less pronounced, in the data of 10 group members, whereas two showed an opposite trend (the remaining five group members never performed *serial-grunts* or even aggression). This does not necessarily mean, however, that the join-aggressors have been attracted mainly to the *serial-grunts*. There may be other variables of which the occurrence is closely associated with *serial-grunts*. It will be difficult to determine such variables and isolate them, as has been possible with respect to *showlooking*. This behaviour element does not influence the chance of being joined, which is demonstrated by Table 10. This was contrary to our expec-

Table 10. 'Choices pro' and 'contra' aggressors performing showlooking (*sl*) and/or serial-grunts (*sg*).

Aggression classes	Potential starters of AA's	Actually did start AA's	Percentage choices PRO	
sl	9	1	11.1%	Choices 'pro'
sl & sg	44	11	25.0	8 young
sg	28	10	35.7	group members
neither *sl* nor *sg*	55	4	7.3	
sl	116	7	6.0%	Choices 'pro'
sl & sg	76	27	35.5	9 older
sg	24	10	41.7	group members
neither *sl* nor *sg*	527	38	7.2	

Aggression classes	Potential receivers of protective aggression	Actually did receive	Percentage choices CONTRA	
sl	12	0	0.0%	Choices 'contra'
sl & sg	57	5	8.8	8 young
sg	39	0	0.0	group members
neither *sl* nor *sg*	82	7	8.5	
sl	164	10	6.1%	Choices 'contra'
sl & sg	115	6	5.2	9 older
sg	39	2	5.1	group members
neither *sl* nor *sg*	582	23	4.0	

tations, however, the effects of *showlooking* may be restricted to the dominant receiving *showlooking*. Since the number of joinings by the dominant are relatively scarce, the data are insufficient to establish such specific effects. Moreover, the aggression classes distinguished do not seem to produce different chances of receiving protective aggression. Anyway, we expected the occurrence of protective actions to depend rather on behaviours of the aggressee, especially on conspicuous behaviour patterns like *barkscreams* and *screams*.

(c) *Do screams and barkscreams influence the formation of reactor-alliances?*

In order to check this, we distinguished between aggressees performing *barkscreams* (*bs*), *screams* (*sc*) and those performing neither *bs* nor *sc* (by the way, aggressees were never observed to perform *bs* and *sc* during one interaction). For each class we computed both the percentage of protection and of actor-alliances received (*i.e.*, the "choices pro" and "contra" these reactors). Of course we considered only those *sc* and *bs* which had been performed before possible actor- respectively reactor-alliances arose from the interactions. As a consequence, the percentages of choices pro and contra are based on different numbers of reaction classes. They are presented in Table 11.

Although adolescent and adult Java-monkeys are known to perform *barkscreams*, it is illustrative as to its rarity that the older members of this group never did so during the 40 hours recorded. Whereas the young members *barkscreamed* 35 times, from which 19 in reaction at aggression. *Cum-B* performed 13 of these latter ones, five of which were followed by protection. Hence, the relatively high percentage of protected young *barkscreamers* (Table 11) reflects mainly the "success" of *Cum-B*'s *barkscreams*. The almost complete lack of the *barkscreams* in the behavioural repertoires

Table 11. 'Choices pro' and 'contra' aggressee's uttering scream (*sc*) or barkscream (*bs*).

Reaction classes	Potential receivers of protection	Actually did receive	Percentage choices PRO	
bs	19	8	42.1%	Choices 'pro'
sc	65	6	9.2	8 young
neither *bs* nor *sc*	415	21	5.1	group members
bs	0	—	—	Choices 'pro'
sc	36	1	2.8%	9 older
neither *bs* nor *c*	344	17	4.9	group members

Reaction classes	Potential receivers of AA's	Actually did receive	Percentage choices CONTRA	
bs	17	2	11.8%	Choices 'contra'
sc	58	3	5.2	8 young
neither *bs* nor *sc*	424	37	8.7	group members
bs	0	—	—	Choices 'contra'
sc	19	9	47.4%	9 older
neither *bs* nor *sc*	361	57	15.8	group members

of older group members suggests that conspicuous reactions to aggression do not yield them any profit. Maybe even the opposite is true; *screams* of older aggressees may even attract aggressors to join against them (Table 11; comparison by χ^2-test, $p<1\%$, two-tailed; this trend has been found in the data of three older group members, whereas of the remaining six adults two never screamed and four never received actor-alliances after the few screams they gave). If this really would be a by-product of *screaming* by older Java-monkeys, one wonders why they do not always keep their mouth. Maybe they try, however, for their *screams* sometimes sound restrained.

Viewed in this light, the way *Kam* has been observed to initiate two agonistic interactions with *Paf,* seems very interesting. Stealthily he approached her from behind, jumped on her back and stood immediately after that in front of her, *show-looking* at *Gam* and directing *pointing* with *serial-grunts* at *Paf.* The frightened *Paf screamed* short, but loud. These two unusual interactions gave the impression that *Kam* "evoked *screaming* in *Paf* in order to attract *Gam* to join his aggression." (one time *Gam* actually joined).

KUMMER (1957, p. 56) described two almost identical interactions between adult female Hamadryas baboons, under the heading "Schwanzzerren" (tail tugging). He suggested that aggressors performing *protected threat* have a much higher chance to be joined by the dominant, if their opponents show fear-reactions.

SUMMARY OF THIS SECTION

As to the factors influencing alliance-formation we presented quantitative data suggesting, more (++) or less (+) convincingly that the Java-monkeys of the captive group studied:

(1) had a higher tendency to join several aggressors rather than a single one (++).
(2) did start relatively many actor-alliances after they performed aggression with *serial-grunts* (++).
(3) have been protected relatively often against aggression, if young and after *bark-screaming* (+) or *screaming* (very weakly indicated).
(4) received relatively many actor-alliances, if they were old and *screaming* in reaction to aggression (+).

More data concerning alliance-formation, provided by this same study, will be presented in a later paper on the structure of agonistic relations between the group-members. Those data suggest that there exist interindividual "preferences" (and "aversions") with respect to join-aggression and protection.

AGGRESSION WITHIN ACTOR-ALLIANCES

When aggression was directed against adult and adolescent group members, it appeared that the aggressive actions performed within actor-alliances more often comprised elements of *physical assault* than did actions within dyads (see Fig. 8, χ^2-test, $p<1\%$, two-tailed). By contrast *physical assault* aginst children and juveniles occurred, less often within actor-alliances than within dyads (see Fig. 8, χ^2-test, $p<0.1\%$, two-tailed).

These two trends in the data can be considered representative as none of the

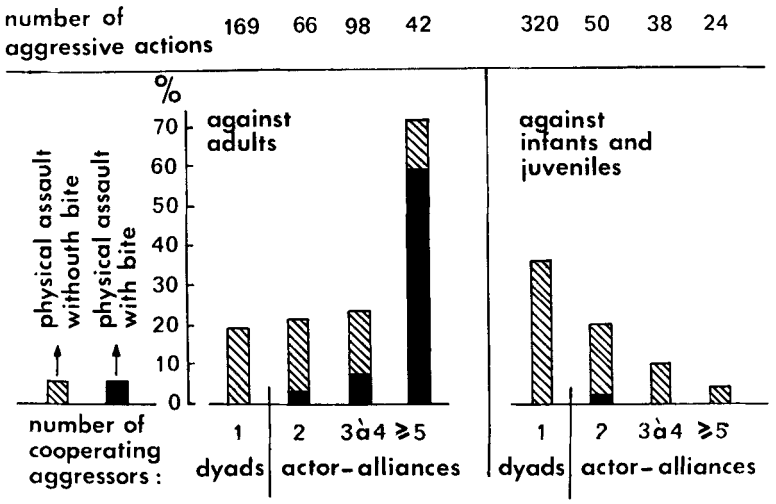


Fig. 8. Relation between percentage of aggressive actions comprising *physical assault* and the number of aggressors joined together, against young and elder aggressees respectively.

group members showed opposite trends. It should be noted, however, that the first trend (*i.e.*, more frequent and greater violence in *AA's* against adults and adolescents) is strongly marked only with respect to aggression against some of the older group members and particularly in actor-alliances with many participants. This is obvious from the data concerning *heavy physical assault:* all 34 aggressive actions observed to comprise *biting* occurred within actor-alliances and of these only one had been directed at a young group member; however, of the 33 actions with *biting* against older individuals 28 had been received by *Paf* or *Zaf*. We are still far from an understanding of the mechanisms underlying the intensification of aggression within actor-alliances. There may be other factors playing an important role, besides (or even instead of) the age class and social position of the aggressee and the number of aggressors joined together. Our data revealed, for instance, that of the 34 aggressive actions with *biting* only two occurred within actor-alliances which lacked the participation of the α-male and from those 32 cases only two took place before the α-male joined the aggressors (the α-male, *Gam*, himself started 16 and joined 22 of the 110 AA's and bit during eight of these interactions). This suggests that his aggression against certain group members facilitated *physical assault* by others in the same direction. This hypothesis certainly needs a closer investigation, preferably carried out with several groups of monkeys. For, it contrasts strongly with the current opinions about the role of the α-male in controlling aggressive behaviour in a monkey group (*e.g.*, TOKUDA & JENSEN, 1968; KOFORD, 1963b, p. 146; SMITH, 1973; BERNSTEIN & SHARPE, 1966). The latter couple of authors (p. 101) wrote about the α-male *A* of their captive rhesus-monkey colony: "Male *A* also served to terminate intragroup fighting by attacking any animals in a disturbance with certain animals, by substituting himself for the aggressor animal or by attacking another animal." and "...this served to limit both the duration and *intensity* of intragroup conflicts." (our italics)

Finally, with respect to the rarity of *heavy physical assault* against young group members it is important to note that there are indications for this in natural groups of rhesus monkeys as well; LINDBURG (1971) found that "over the observation period adult males received 1.56 wounds per animal, and adult females 1.35. Juveniles and infants, by contrast, were recipients at a mean rate of 0.29 wounds per animal" (p. 73).

THE RELIABILITY OF THE METHOD

(a) INTRODUCTION

Most studies of primate social behaviour focus on dyadic interactions. It is evident, however, from the data on agonistic behaviour presented in this paper that more complex interactions are of equal, if not greater interest fot the understanding of the social organization of a species. Moreover, these phenomena occur often enough to allow their analysis. Presumably every ethologist familiar with primate behaviour was already aware of this and we suppose therefore that the scarcety of investigations concerning complex agonistic interactions is due mainly to the difficulties in recording these; the major agonistic incidents may happen with "lightning" speed and complex interactions seem to be chaotic happenings at first sight. It is no luxury, then, that we investigated the reliability of our method of recording agonistic behaviours.

Of the 80 observation episodes recorded 29 have been transcribed twice, each resulting in an independent *audio-* and *video-protocol* (see pp. 269–270, a). These comprised 354 agonistic interactions, of which 265 had been video-recorded in a way enabling us to recognize the involvees and their behaviours from the monitor. We are concerned here with the lacks and errors in the audio-protocols of those 265 interactions as revealed by a comparison with the corre-sponding video-protocols.

(b) NATURE OF THE ERRORS MADE

Scoring incorrectly: Behaviour patterns or involvees had been recorded incorrectly (*i.e.*, by misnaming these) only three times. This number is negligible on a total of *ca.* 4000 element recordings.

Missing an involvee: According to the video-protocols group members were involved as participants 691 times. In 12 cases of these a participant was not mentioned as such in the audio-protocols (*i.e.*, 1.7%).

Mistaking an involvee's role: Missing an involvee or noticing its agonistic behaviour too late may lead to the misjudgement of the role of another involvee. Such is the case, for instance, when the start-aggressor of an actor-alliance remains unmentioned and, as a consequence, the join-aggressor has been considered a solo-aggressor.

This type of error had been made with respect to 30 involvees. (4.3%). It occurred in connection with dyadic interactions (2.3%) but particularly in connection with triads (6.1%) and polyads (6.8%).

Missing behaviours: A considerable part of our data was tabulated as *one-zero scores* (see pp. 269–270, a; see also ALTMANN, 1974, who discussed this type of processing). This implies that during the analysis a certain element or category of behaviour was

Table 12. Degrees of incompleteness of the audio-protocols with respect to the different categories of behaviour.

	Dyads			*Triads*			*Polyads*			Total		
Category of behaviour	N	not	%	N	not	%	N	not	%	N	not	%
Threat	82	4	4.9	71	3	4.2	145	2	1.4	298	9	3.0
Chase	32	2	6.3	17	3	17.6	71	4	5.6	120	9	7.5
Physical assault	41	2	4.9	26	1	3.8	45	2	4.4	122	5	4.1
Sub-direct. behaviour	35	2	5.7	27	3	11.1	89	5	5.6	151	10	6.6
Flight-int.	25	3	12.0	13	2	15.4	7	1	14.3	45	6	13.3
Flight	76	4	5.3	42	2	4.8	72	5	6.9	190	11	5.8
Submission	67	3	4.5	47	1	2.1	61	2	3.3	175	6	3.4

N=number of (re)actions comprising the behaviour (video-protocol). not=number of these cases missed in audio-protocols.

scored either as present or not present, depending on either whether it was performed by an involvee *once or several times* within an interaction or whether it did not occur at all. Hence the missing, for instance, of two out of three *headbobs*, shown by an aggressor, will be acceptable, but not the missing of all three *headbobs*.

All agonistic and sub-directed behaviour patterns appeared to remain unobserved more or less often, except for the vocalizations (which were recorded separately; see pp. 269–270, a) and for the behaviour pattern *biting*. Let us give a few examples. *Tugging* was missed in the audio-protocols four of the 105 cases recorded on video (*i.e.*, 3.8%); *Showlooking* in 10 of 132 cases (7.6%) and *shrink* in six of 40 cases (15.0%). Table 12 shows the degrees of incompleteness of the audio-protocols with respect to the different categories of behaviour when occurring in dyads, triads and polyads.

(c) DISCUSSION OF THIS SECTION

It appeared that our audio-protocols yield 85 till 100% of the data, important to us, with hardly any errors; the remaining data are not incorrect recordings but these are lacking. In other words: the audio-reports on agonistic interactions had been incomplete but scarcely incorrect.

The audio-protocols appeared to be incomplete especially with respect to the category *flight-intention* (see Table 12). Of the behaviour patterns belonging to this category, *shrink* is the most common one and it certainly can be called inconspicuous. Although "inconspicuous" elements had a higher chance of remaining unnoticed it is not clear whether this is the only factor involved. The extent to which the observer expects certain patterns might be another important factor. This is indicated by the fact that the most frequently shown category of behaviour—*threat*—had been recorded the best, and indeed better than, for instance, the much more conspicuous category of *chase* which had been performed much less frequently.

It, finally, seems useful to remark once more that it was sufficient with regard to our methods that a pattern or category of behaviour was scored *once* during an interaction, irrespective of its actual frequency or duration of occcurrences. As a consequence the degree of completeness of the audio-recordings will be "favoured" for those behaviours which are repeated often during an interaction (like *threat behaviours*) and for those interactions which last relatively long (like *polyads*). So, the fact that the audio-protocols of polyads did not appear to be less complete than those

of dyads and triads is—in view of our *one-zero* way of scoring—less surprising than it seems to be at first sight.

DISCUSSION

Aggressors showing sub-directed behaviours towards a dominant third animal; i.e., the *appeal-aggressors,* generally aim characteristic aggressive elements at their opponent, which are shown rarely by aggressors paying attention solely to an opponent; i.e., the *straight-aggressors.* The occurrence of at least one of these elements of appeal-aggression, namely *serial-grunt* is associated with a higher chance of the occurrence of actor-alliances. It is likely, therefore, that it is an effective element that facilitates the formation of actor-alliances. This raises the question whether the purpose of appeal-aggression is the starting of an actor-alliance. This is a question of interest as aggression of a violent nature occurs almost exclusively in the context of actor-alliances. Maybe appeal-aggressors "wait for a social approval to turn violent", which approval might come from joining group members and, as it seems, especially from the α-male (see Aggression within Actor-Alliances). Something to that effect is also suggested for rhesus-monkeys by REYNOLDS (1962) when he writes about one form of appeal-aggression; *i.e., protected threat;* "Its significance is tied up with the fact that aggressive behaviour is a breach of tolerance of the dominant male" (p. 154). Be that as it may, it seems obvious anyway that appeal- and straight-aggression do not only differ with respect to their form but also with respect to their controling factors (see Agonistic Interactions and Roles, c). Investigations concerning these differences in causation and function are of great importance since these may differentiate the current opinions about the role of aggression in social groups, which mostly ignore the existence of appeal-aggression.

We prefer to use the term "appeal-aggression" here, in stead of "two frontal behaviour" (KUMMER, 1957; translated by ALTMANN, 1962) or "compound activities" (REYNOLDS, 1962) because aggressive elements do not form part of all displays which are characterized by a two-directional performance. There exist many different types of such displays and even some in which social behaviours are shown in only one of the two directions. Thus, of the following four examples of two-directional behaviour in different animal species only the last one might be called "appeal-aggression" and only the last two are "compound-activities" in REYNOLDS's sense (*i.e.*: "They may further be distinguished from behaviour units in that they necessarily involve three animals," 1962, p. 154):

1. Hamadryas baboons sometimes show *notifying,* in which an adult male faces another one, followed by walking away in a certain direction, while presenting the anal field. One of its effects seems to be the release of a following response in the receiving male. Thus this behaviour may play an important role in the coordination of travel (KUMMER, 1968).
2. A display analogous to *notifying* is *Wedeln* in jackdaws (*Coleus monedula*): a jackdaw flies just over its (sitting) partner and shows quick fanning movements with its tail while flying away in a certain direction. LORENZ (1931), which described this display, interprets it as an invitation to accompaniment.

3. DEAG and CROOK (1971) described *agonistic buffering* in *Macaca sylvana* L: an adult male picks up a baby and "presents" it towards another male. This gesture often results in a non-agonistic contact between the two males during which they both hold the baby (see also WHITEN & RUMSEY, 1973).

(N.B.: We observed this behaviour in Java-monkeys as well; we named it the *sandwich*).

4. The oldest and best known example of two-directional behaviour is *Hetzen* as shown by the females of many genera of *anatidae* towards their sex partner and another conspecific male (LORENZ, 1941). She noisily threatens the latter one, meanwhile swimming or walking in front of her partner possibly to enlist his aid against the "enemy".

The short- and longterm effects of the display listed above, as supposed by the respective investigations, are:

(a) Social facilitation of behaviour of the same kind in the same direction (respectively: (1) walking; (2) flying; (3) taking the baby; (4) aggression).

(b) A positive contribution to the relationship between the two males (in example 1 and 3) or between the female and her male (in example 4).

In connection with the latter hypothesis we wonder whether appeal-aggression in Java-monkeys might serve to strengthen the bond between the aggressor and the dominant receiving its sub-directed behaviour. Maybe, however, such a positive influence on the relationships results mainly from those interactions in which social facilitation took place (*i.e.*: in which the dominant joined the appeal-aggressor) and not simply and solely from the occurrence of sub-directed behaviours. Still another possibility, hardly separable from the one above, is that joining an aggressor does not have a bond-strengthening effect so much, but generally occurs between individuals which are already "good friends", Thus LINDBURG (1971) observed "coalitions" within groups of free-ranging rhesus monkeys to occur mainly between group members which often joined each other in grooming and sleeping as well. About feral langurs (*Presbytis entellus*), however, JAY (1965, p. 239) remarks: "Since most adult females do not display patterns of individual preference for each other, chance dictates the nearness of a female which might join in a combined threat or alliance."

Research aimed at solving the kind of problems discussed above should start, like ours, with a description and categorization of types of social interaction (see HINDE, 1974; KUMMER et al., 1974). In studies about primate aggression, especially in experimental studies, it has been usual, however, to focus on dyadic interactions or to dissect complexes into dyadic components. Generalizations based on such studies should be regarded with caution as this analysis shows that aggressive behaviour may be different both in its form and its regulation in interactions of different complexity.

REFERENCES

ALTMANN, S. A., 1962. A field study of the sociobiology of Rhesus monkeys, (*Macaca mulatta*). *Ann. N.Y. Acad. Sci.*, 102: 338–435.

ALTMANN, J., 1974. Observational study of behavior: sampling methods. *Behaviour*, 49: 227–267.

ANGST W., 1974. Das Ausdrucksverhalten des Javaneraffen, (*Macaca fascicularis* Raffles). *Fortschritte der Verhaltensforschung*, Beiheft 15, Zeitschr. f. Tierphyschol, pp. 90.

BERNSTEIN, I.S. & L.G. SHARPE, 1966. Social roles in a Rhesus monkey group. *Behaviour*, 26: 91–103.

DEAG, J. & J. CROOK, 1971. Social behaviour and "agonistic buffering" in the wild Barbary macaque (*Macaca sylvana* L.). *Folia primat.*, 15: 183–200.

HALL, K.R.L. & I. DEVORE, 1965. Baboon social behavior. In: *Primate Behavior*. I. DEVORE (ed.), Holt, Rinehart & Winston Inc., New York, pp. 53–110.

HINDE, R.A., 1966. Ritualization and social communication in rhesus monkeys. *Phil. Trans. Roy. Soc. Lond.* Series B, 251: 285–294.

———, 1974. Interactions, relationships and social structure. In: *Abstracts, Fifth Cong. Int. Primat. Soc. Nagoya, Japan*, 90.

HOOFF, J.A.R.A.M. VAN, 1967. The facial displays of the catarrhine monkeys and apes. In: *Primate Ethology*, D. MORRIS (ed.), Weidenfeld & Nicholson, London, pp. 7–68.

———, 1970. A component analysis of the structure of the social behaviour of a semi-captive group of chimpanzees. *Experientia*, 26: 549–550.

———, 1971. Aspecten van het sociale gedrag en de communicatie bij humane en hogere niet-humane primaten. Thesis, University of Utrecht. Bronder offset N.V., Rotterdam.

IMANISHI, K., 1960. Social organization of subhuman primates in their natural habitat. *Current Anthrop.*, 1: 393–407.

JAY, P., 1965. The common langur of North India. In: *Primate Behavior*, I. DEVORE (ed.), Holt, Rinehart & Winston, Inc., New York, pp. 197–249.

KAUFMANN, J.H., 1967. Social relations of adult males in a free ranging band of rhesus monkeys. In: *Social Communication among Primates*, S.A. ALTMANN (ed.), Chicago Univ. Press, pp. 73–98.

KAWAI, M., 1958. On the system of social ranks in a natural group of Japanese monkeys. I. Basic rank and dependent rank. *Primates*, 1: 111–130, English translation in: *Japanese Monkeys*, K. IMANISHI & S.A. ALTMANN (eds.), Emory Univ. Atlanta, Georgia (1965), pp. 66–86.

KOFORD, C.B., 1963a. Rank of mothers and sons in bands of rhesus monkeys. *Science*, 141: 356–357.

———, 1963b. Group relations in an Island Colony of rhesus monkeys. In: *Primate Social Behavior*, C.H. SOUTHWICK (ed.), D. van Nostrand Company Inc., Toronto & London, pp. 136–152.

KRUUK, H., 1972. *The Spotted Hyena: A Study of Predation and Social Bahavior*. Chicago Univ. Press.

KUMMER, H., 1957. Soziales Verhalten einer Mantelpavian-Gruppe. *Beih. Schweiz. Zeitschr. Psychol.*, 33.

———, 1967. Tripartite relations in Hamadryas baboons. In: *Social Communication among Primates*, S.A. ALTMANN (ed.), Chicago Univ. Press, pp. 63–71.

———, 1968. *Social Organization of Hamadryas Baboons: A Field Study*. Chicago Univ. Press.

———, W. GÖTZ, & W. ANGST, 1974. Triadic differentiation: an inhibitory process protecting pair bonds in baboons. *Behaviour*, 49: 62–87.

LINDBURG, D., 1971. The rhesus monkeys in North India, an ecological and behavioural study. In: *Primate Behavior*, Vol. 2, L. ROSENBLUM (ed), New York Acad. Press, pp. 1–106.

LORENZ, K., 1931. Beitrag zur Ethologie sozialer Corviden. *J. f. Ornithol.*, 79: heft 1.

———, 1941. Vergleichende Bewegungsstudien an Anatiden. *Suppl. J. Ornith.*, 89: 194–294.

MARSDEN, H., 1968. Agonistic behaviour of young rhesus monkeys after changes induced in social rank of their mothers. *Anim. Behav.*, 16: 38–44.

MASSERMAN, J., S. WECHKIN, & M. WOOLF, 1968. Alliances and aggressions among rhesus monkeys. In: *Sci. & Psychoanalysis*, 12: 95–100.

MICHAEL, R.P., 1971. Hormonal factors and aggressive behaviour in the rhesus monkey In: *Influences of Hormones on the Nervous System. Proc. Int. Soc. Psychoneuroendocr.*, Brooklyn, 1970, Kargel, Basel. pp. 412–423.

NELSON, K., 1964 The temporal patterning of courtship behaviour in the glandulocaudine fishes. *Behaviour*, 24: 90–146.

REYNOLDS, V., 1962. The social life of a colony of rhesus monkeys (*Macaca mulatta*). Thesis, University of London.

SADE, D.S., 1967. Determinants of dominance in a group of free-ranging rhesus monkeys. In: *Social Communication among Primates*, S.A. ALTMANN (ed.), Chicago Univ. Press, pp. 99–114.

SCHALLER, G.B., 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. Chicago Univ. Press.

SHIREK-ELLEFSON, J. 1972. Social communication in some old world monkeys and gibbons. In: *Primate Patterns*, P. Dolhinow (ed.), Holt, Rinehart & Winston, Inc., 297–311.

SMITH, E.O., 1973. A further descriptive analysis of the control role in pigtail macaques (*Macaca nemestrina*). *Primates*, 14: 413–419.

SOUTHWICK, C.H., 1967. An experimental study of intragroup agonistic behaviour in rhesus monkeys (*Macaca mulatta*). *Behaviour*, 28: 182–209.

STRUHSAKER, T., 1967. Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour*, 29: 83–121.

TOKUDA, K. & G.D. JENSEN, 1968. The leader's role in controlling aggressive behavior in a monkey group. *Primates*, 9: 317–320.

VARLEY, M. & D. SYMMES, 1966. The hierarchy of dominance in a group of macaques. *Behaviour*, 27: 54–75.

WHITEN, A. & T.J. RUMSEY, 1973. Agonistic buffering in the wild Barbary macaque, *Macaca sylvana*, L. *Primates*, 14: 421–425.

WIEPKEMA, P.R., 1961. An ethological analysis of the reproductive behaviour of the bitterling. *Arch. néerl. Zool.*, 14: 103–199.

The investigation was supported by a grant from the Beleidsruimtemiddelen Hersenen en Gedrag to the first author.

—Received *February 1, 1975*; Accepted *April 11, 1975*

Authors' Address: FRANS B. M. DE WAAL, JAN A. R. A. M. VAN HOOFF, and WILLEM J. NETTO, *Laboratory of Comparative Physiology, University of Utrecht, Jan van Galenstraat 40, Utrecht, The Netherlands.*