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SOCIAL DOMINANCE IN A GROUP OF CAPTIVE MANDRILLS

SOCIAL DOMINANCE IN A GROUP OF CAPTIVE MANDRILLS (*MANDRILLUS SPHINX*): AN ANALYSIS OF BEHAVIOUR INDICES

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ABSTRACT

Social dominance has been defined and measured in various ways in studies of non-human primate social organization. In this project, dominance is defined operationally as an inter-correlated cluster of behaviours, one of which is the ability to aggress on an individual without that individual responding with aggression. Behavioural observations are conducted on a captive group of mandrills (*Mandrillus sphinx*) in order to determine whether dominance relationships are present and to examine the validity of traditional measures of dominance. A cluster of inter-correlated behaviours is identified which indicates dominance and ranks the animals into a linear hierarchy. The primary significance of the dominance hierarchy lies in conferring predictability to certain limited types of behavioural interactions, including agonistic encounters, non-agonistic approach-retreat patterns, and non-agonistic presenting. Delineation of such clear-cut dominance hierarchies is rare in non-captive situations, and possible reasons for this difference are discussed. An improved methodological approach to the study of dominance is proposed as a basis for comparative analysis utilizing the dominance concept.

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CHAPTER I

INTRODUCTION

Controversy surrounds the usefulness of the concept of dominance in the study of non-human primate social organization. In ordinary English usage, the word "dominance" implies notions of power, control and authority. What constitutes this power or control is not specified and presumably depends on the context in which the term is used. With the identification of pecking orders, or dominance hierarchies, in domestic barnyard fowl (Schjelderup-Ebbe 1922) the term dominance begins to acquire widespread usage in studies of animal behaviour. Unfortunately, definitions of dominance in this specialized context are rarely offered.

Dominance theory, that is the use of the concept of dominance for explaining social structure, had its origins in the early 1920s with the work of Schjelderup-Ebbe. Having observed the pecking orders established by chickens, Schjelderup-Ebbe equated dominance with the ability to aggress on an individual without having that individual respond aggressively. This ability was considered to form the basis of social structure, as was illustrated by the statement that the "social order among birds is

based on what has come to be called peck-right. The high ranking individuals are able to peck those of lower rank without themselves being pecked in return" (Allee 1942: 108). In fact, dominance or peck order was often used synonymously with social structure (Schjelderup-Ebbe 1922: 41).

Dominance relations were hierarchically arranged within the social groups observed by Schjelderup-Ebbe. In other words, an individual dominant over one animal might be subordinate to another. Theoretically, the agonistic behaviour characterizing dominance interactions could exist outside the context of a hierarchy. For example, in one situation individual A might aggress on individual B without B responding aggressively, while in a later encounter, individual B might aggress on A without A responding aggressively. However, rather than occurring in such a random fashion, direction of aggression was distributed in such a manner that individuals could be ranked on this criterion. This hierarchical arrangement, whether strictly linear or involving triangular relationships, was usually implied when the term dominance was used to describe the social structure of a group of animals.

Interest in the concept of dominance as a social structuring mechanism soon led other researchers to describe similar dominance hierarchies in a wide range of animal groups including lizards (Evans 1936), crayfish (Bovbjerg

1953), dairy cattle (Schein and Fohrman 1955), buffalo (McHugh 1958), goats (Klopfer and Klopfer 1973), mice (Ginsburg and Allee 1942), and non-human primates (Maslow 1940; Kummer 1957 cited in Gartlan 1968; Chance 1956). In these and related studies, terms that had been used interchangeably with "dominance hierarchy" included "peck order" (in chickens), "social dominance", "social rank", "social hierarchy", "rank order", "dominance order", and "dominance rank".

In its original context, dominance was measured by direction of aggression, but as primatologists adopted the concept, an expanding list of behaviours was used to measure it, including: priority to incentives (e.g., water: Boelkins 1967, Castell and Heinrich 1971; food: Dumond 1969, Mason 1961); agonistic behaviour (Baldwin 1968; Sade 1967; Struhsaker 1966; Plotnik et al. 1968); approach/retreat interactions (Rowell 1966; Simonds 1965; Richards 1974); mating success (Conoway and Koford 1965; Altmann 1962; Hall 1962); display behaviour (Baldwin 1968; Nishida 1970); non-sexual mounting behaviour (Altmann 1962; Simonds 1965); grooming behaviour (Sparks 1969; Buirski et al. 1973; Washburn and DeVore 1961); social spacing (Washburn and DeVore 1961; Emory 1975; Hall 1967); attention structure (Emory 1976; Chance 1967); and posture (Hinde and Rowell 1962).

The growing list of behaviours used to measure dominance was a reflection of the expectation that dominance

order would explain or predict the outcome of a variety of behavioural interactions. In other words, if an individual attacked one member of a group but not another (i.e., was dominant over the first but not the second) this relationship could predict the outcome of subsequent interactions between the same individuals in other situations. The expectation that dominance order would explain a variety of behaviours was probably a direct outgrowth of the results from early studies of dominance hierarchies. Schjelderup-Ebbe, for example, found that access to food and nesting sites could be predicted by a chicken's position in the peck order or dominance hierarchy.

When used by primatologists, one often detects the implicit assumption that dominance explains the outcome of a wide variety of behavioural interactions, and thus that many behaviours may be used to assess dominance status. If indeed there are several behaviours that indicate dominance, these behaviours should be positively intercorrelated in the manner in which they rank the animals of a group. However, the concept of dominance is applied across species, genera and even families of primates without a demonstration of consistency in the number, type or correlation of behaviours that indicate dominance relationships. Different species, or the same species in different environments, may well exhibit different clusters of behaviour indicating a specific relationship (linear or otherwise) between animals. The fewer the behaviours

included in such a cluster, the less the explanatory power of dominance, since it would refer to a very restricted range of social interactions. This latter possibility has prompted some re-examination of dominance indicators, but it has not deterred the majority of primatologists from widespread application of the vaguely defined concept of dominance.

The fact that confusion persists over which behaviours indicate dominance is reflected in the following potentially conflicting statements taken from the same source:

> ...the dominance of one member of a group over another [is] measured by superiority in aggressive encounters and order of access to food, mates, resting sites, and other objects promoting survivorship and reproductive fitness (Wilson 1975:11).
>
> ...to dominate is to possess priority of access to the necessities of life and reproduction (Wilson 1975:287).

According to the first statement, superiority in aggressive encounters is a measure of dominance. The second statement, on the other hand, does not suggest that aggressive superiority is a dominance indicator (that is, as long as one does not assume that aggression is the only means of achieving priority of access). Nonetheless, most studies and casual references appear to assess dominance status primarily on the basis of outcomes of aggressive interactions (Bartlett and Meier 1971; Bern-

stein 1970:75; DeVore 1965:270). The fact that many of the behaviours used to measure dominance do not correlate with each other suggests that we should return to the original usage of the term in an attempt to define it operationally. For the purposes of this study, I operationally define dominance as <u>an inter-correlated cluster of behaviours, one of which is the ability to aggress on an individual without that individual responding with aggression</u>.

The implications of this definition are best illustrated by use of an example. Dominance is cited as explaining priority of access to food (Dumond 1969; Richards 1974) and mates (Conoway and Koford 1965; Altmann 1962). It is worth noting, however, that many other factors may be involved in determining priority of access. At a minimum, such factors may include kinship, friendship, and/or age/sex relations. Collectively, singly, or in combination, these factors may be as important as, or more important than, dominance in conferring priority of access. The operational definition of dominance given above requires that priority of access be correlated with direction of aggression. Without such a correlation, priority of access is not here considered an index of dominance, and alternate factors must be examined to account for its occurrence. While aggressive dominance may confer priority of access in some species or in certain situations, this does not necessarily apply to all species or all situations. In

such instances, the freeing of "priority of access" from "dominance" interpretations encourages examination of the rich complexity of primate social behaviour for alternate interpretations.

The study population for this project is a small group of captive mandrills in the Metro Toronto Zoo. Although few studies of mandrill behaviour exist in the literature, Emory (1975, 1976) makes a claim for strong rank order relations in this species based on observations of a captive group. Emory (1976:72) assesses dominance rank "on the basis of the patterns of locational supplanting of individuals, limited food tests of individual priority and age." Beyond this statement, no further elaboration of the assessment or significance of dominance in mandrills is offered.

Dominance hierarchies are frequently detected subjectively, rather than by clearly defined, quantitative techniques. Consequently, the observation and recording techniques employed in this study are chosen so as to reduce the subjective determination of dominance. Quantitative data on behavioural interactions are analyzed by computer in order to identify the cluster of inter-correlated behaviours that indicate dominance as defined in this thesis. The behaviours forming this cluster are compared with behaviours that have been claimed to measure dominance. The usefulness of the concept of dominance is assessed on

the basis of these results.

The anticipated significance of this study is as follows. First, the identification of a behavioural cluster indicating dominance in a captive group of mandrills would corroborate objectively the existence of a social ordering mechanism that has been claimed to exist in this species. This would constitute a contribution to the limited information available on mandrill behaviour and would be a general contribution to the literature on social dominance in primates.

Second, whatever the outcome of the analysis, a methodologically improved, systematic approach to the study of dominance is presented. The benefits of this approach over others, including increased objectivity and reliability, may provide the basis for doing comparative analysis utilizing the dominance concept. No such comparative basis exists as of yet since: (a) the literature on non-human primate dominance hierarchies reflects a variety of non-comparable methodological approaches; and (b) many people do not specify how they measure dominance.

Finally, on the theoretical level, the usefulness of social dominance as a descriptive and analytical device is considered. This assessment focuses on the results obtained from correlation analysis of the traditional measures of dominance and questions whether the overall classification of these measures as dominance indicators is

warranted. Because social dominance often is considered to be a significant social structuring mechanism, a critical assessment of its influence is appropriate.

CHAPTER II

METHODOLOGY

Introduction

Confusion surrounding the concept of dominance derives from the following: (a) lack of explicit definition; (b) use of different behaviour patterns by different researchers for measuring dominance; (c) lack of correlation between behaviour patterns used to measure dominance; and, (d) subjective determination of dominance hierarchies. The following steps and research objectives attempt to remedy these sources of confusion.

First, an operational definition of dominance is provided as a baseline for common understanding. For the purposes of this study, dominance is operationally defined as a cluster of inter-related behaviours, one of which is the ability to aggress on an individual without that individual responding with aggression (see supporting discussion, Chapter I).

Second, in response to the fact that different researchers use different behaviour patterns to measure what they call (but often fail to define as) dominance, I observe and record a variety of behaviour patterns from daily

interactions in a captive mandrill group. Some of these behaviours have been used by other researchers to measure dominance, while other recorded behaviours have not been used previously as dominance indicators.

The third research objective is designed to deal with the confusion created by a demonstrated lack of correlation between behaviour patterns that supposedly measure the same phenomenon, i.e., "dominance". Correlation analysis is performed in order to establish whether or not significant correlations exist between behaviours that have been used (or might be used) to measure dominance. In accordance with the operational definition, dominance may be measured by direction of aggressive interactions. Statistical analysis reveals which other behaviour patterns are significantly inter-correlated with direction of aggressive interactions, and hence may also be considered measures of dominance as it is defined here.

Finally, the observation and recording techniques employed in this study are chosen so as to reduce or eliminate subjective detection of dominance hierarchies. Such data then may be compared objectively with comparable information on other groups. The methodological procedures employed to meet these objectives are described more fully after a brief discussion of background information on mandrills, the species chosen for this study.

Mandrills: Background Information

Mandrills frequently have been classified with *Papio* (Buettner-Janusch 1966), but current taxonomy tends to regard drills and mandrills as generically distinct and to refer to them as *Mandrillus* (Jolly 1967,1970; Napier 1967). Furthermore, the two forms are accorded full specific status: *Mandrillus sphinx* (the mandrill) and *Mandrillus leucophaeus* (the drill).

Physically, mandrills are large and show well-marked sexual dimorphism (Jolly 1967, 1970; Napier 1967). Massive muzzles with longitudinal swellings on both sides of the nose appear in both sexes. The nostrils and nose of the male are bright red, and the longitudinal paranasal swellings are bright royal blue. The nasal coloration of the female is much less intense with the blue coloration of the paranasal swellings being either very faint or absent. Both sexes have white cheek tufts and yellow to orange beards. Body hair is dark brown to dark grey with yellow and orange fringes.

The geographical range of the genus is restricted to the western section of the Cameroun-Gabon forest between the Niger and Congo Basins (Grubb 1973). Poor visibility in the dense tropical rain forests inhabited by *Mandrillus* has severely hampered the two field studies which have been carried out on this genus to date (Gartlan 1970, for drills; Jouventin 1975, for mandrills). Consequently, the genus

Mandrillus is characterized by a scarcity of data regarding ecology, reproduction and development, and social behaviour in the wild. Jouventin's (1975) socio-ecological field study suggests that mandrills live in the lower forest layers. Large adult males exploit ground level food supplies while females, infants and juveniles rely more on resources found in the undergrowth and branches of lower and middle forest layers. The basic social unit in the wild consists of a single adult male "leader", perhaps a second younger adult male, 5-10 females with or without infants, and about 10 juveniles. Several such one-male units have been observed to associate together, forming troops of up to 200 or more individuals. Adult males living a solitary existence have been encountered several times in the forest. Jouventin (1975) postulates that such animals may be excess males rejected from the one-male units upon reaching sexual maturity.

A fairly large home range of ten square kilometers was estimated for a one-male mandrill unit (Jouventin 1975). A variety of fruit and vegetable food was collected in this area, and the most prevalent and dangerous predators, aside from humans, were leopards and the crowned hawk-eagle.

The Research Population

The study population for this project is a captive group of mandrills (Mandrillus sphinx) housed at the Metro

Toronto Zoo. The eight members of the group, one adult male, four adult females, one juvenile female, one infant female and one infant male, are identified by name in Table 1.

The captive environment of the mandrills forming the research population for this study is radically different from the dense tropical rain forest that is the natural habitat of Mandrillus sphinx. However, since these research results apply only to adaptations employed by this group in the captive situation and make no pretense of being applicable to "natural living conditions", the altered environment does not affect conclusions drawn from the data.

Mandrills are a particularly suitable species for this project because of the high frequency of social interactions within this group. An adequate sample of the behaviour patterns used to measure dominance must be obtained in order to test reliably for correlations between these behavioural measures. Considerably more observation hours are required in order to determine social rank reliably in a group of animals who interact relatively infrequently.

Physical Setting

The mandrill group lived in an indoor enclosure in the zoo's African Pavillion, a floorplan of which appears in Figure 1. The African Pavillion was maintained at

TABLE 1. Members of the Mandrill Group as of May 1, 1978.

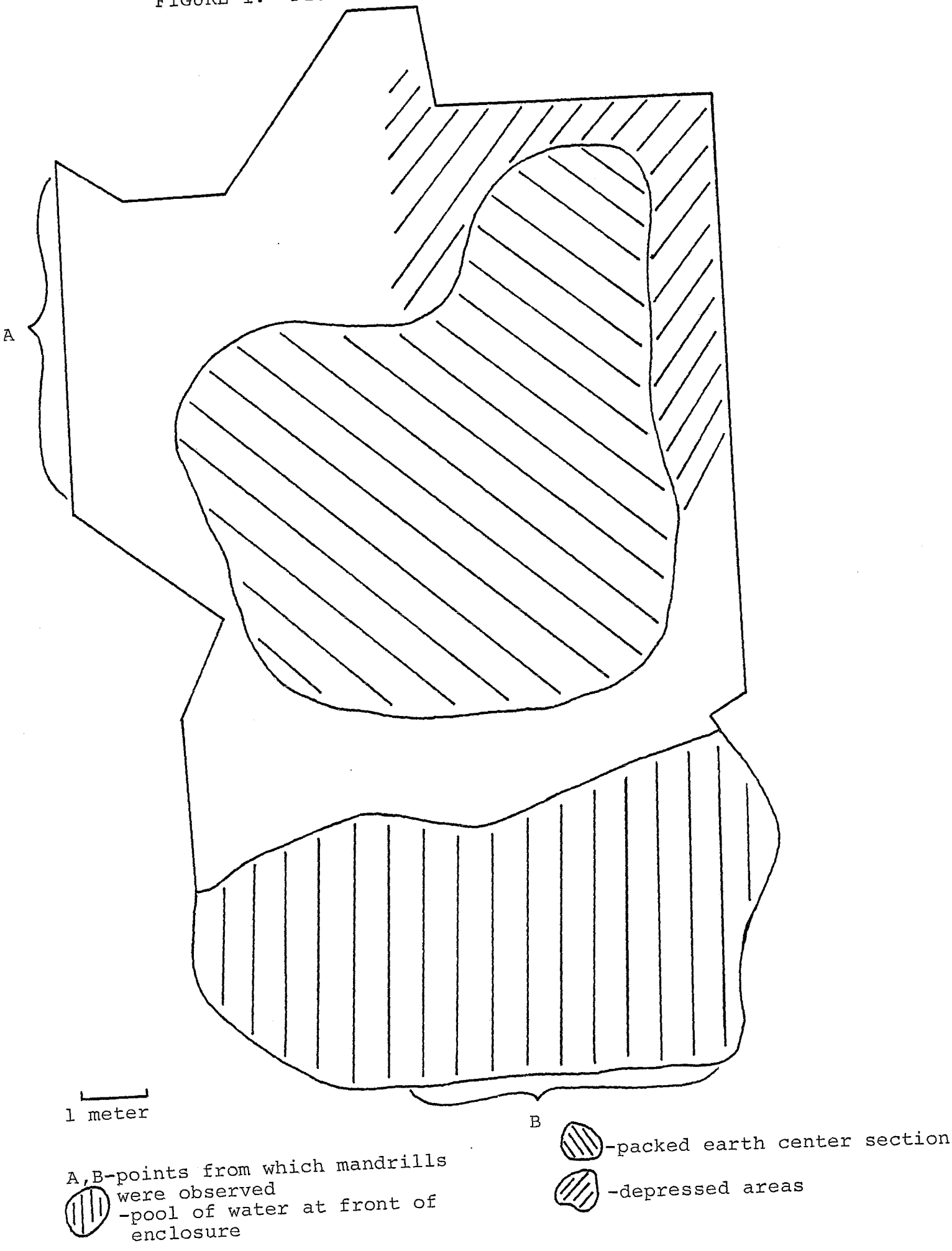
NAME*	I.D.#	AGE/SEX CLASS	SOURCE	ARRIVAL DATE	APPROXIMATE AGE
Willy	1	adult male	IAE**	July 1973	10 years
Mandy	2	adult female	Riverdale Zoo	Nov. 1972	10 years
Bertha	3	adult female	IAE	Nov. 1973	7 years
Chigan	5	juvenile female	Portland Zoo	Nov. 1975	3 years
AO32	6	adult female	IAE	July 1973	10 years
Jake	7	infant male	born MTZ***	Feb. 1978	2½ months
Bitch	8	adult female	IAE	July 1973	10 years
Suzie	9	infant female	born MTZ	Nov. 1977	5 months

* House names as recorded in zoo records.

** IAE = International Animal Exchange, Ferndale, Michigan.

*** MTZ = Metro Toronto Zoo.

FIGURE 1. Floor Plan of Mandrill Enclosure



temperatures and humidities appropriate for the growth of abundant lush tropical plants. A flat, packed earth area occupied the center of the enclosure. All other floor surfaces were made of poured concrete and gravel. Large boulders, tree stumps and branches were scattered on the earthen area. Along the back and right peripheries, the central earthen area sloped downwards to a maximum of three feet. A large pool of water in front of the enclosure separated the mandrills from the public and provided an unobstructed view of activity within the enclosure. The enclosure measured approximately 10.1 meters and 13.7 meters at the greatest width and length, respectively.

The right wall of the enclosure was concrete topped with an inward sloping log palisade, while the right half of the rear wall was completely concrete. The rest of the rear wall and most of the left wall were made of chainlinked fence, thus providing the public with a good view of the mandrill enclosure. The first 5.5 meters of the left wall were made of transparent plexiglass. Dense vegetation growing behind the plexiglass visually blocked the mandrill enclosure from the neighbouring crocodile enclosure.

I made all observations from locations A and B (see Figure 1). Although visibility was good from both of these locations, the entire enclosure was not visible from either because of the depressed areas along part of the back and right walls. Consequently, I split the observations equally

between locations A and B, yielding an equal distribution of observation time at each location throughout the day and on all types of data collection.

Keepers transferred the mandrills from the viewing enclosure to a holding area each evening. The holding area was a room containing cages located behind the viewing enclosure. While in the holding area for the night, the mandrills received a main meal, and their viewing enclosure was thoroughly hosed down and cleaned. Each morning, after the mandrills returned to the viewing enclosure, the holding area was likewise hosed and cleaned.

Keepers scattered monkey chow on the floor of the viewing enclosure each morning in quantitities greater than were ever consumed during the course of a day. In addition, the mandrills received one or two fresh vegetable snacks during the day. These snacks, which were thrown into the enclosure in a scattered fashion rather than a concentrated lump, were highly prized by the animals.

Besides their own social interactions and whatever distraction they derived from watching the antics of the human "zoo-goers", the mandrills received a certain variety of other live stimuli. Part of the gorilla enclosure could be seen from the left side of the mandrill enclosure, making these animals mutually visible. Neither species appeared to pay any particular attention to the other except when extremely loud and noisy behaviour attracted auditory and

visual attention. Adjacent to the mandrill enclosure on the right, although visually separated by the concrete wall, was an enclosure containing birds that occasionally emitted high-pitched, piercingly loud calls which prompted the mandrills to jump onto the wall, cling to the palisade, and peer with forward directed ears between the small chinks in the logs.

Schools of fish inhabited the pool at the front of the enclosure. The mandrills often grabbed at the fish, but I never saw them catch any. A variety of small birds flew freely throughout the African Pavillion. The mandrills grabbed at birds that flew close enough, but again I never saw them succeed in such attempts. Mice lived under the logs and boulders inside the mandrill enclosure, and when they ventured very far from the protection of their burrows, mandrills stalked them. During the course of this study, I observed two successful attempts at catching mice, both by the same mandrill. Over the course of five years, zoo personnel had never observed the successful catching of any live animal by a mandrill; hence, these mice-catching incidents are believed to be the first of their kind in this group. Although the mice were caught and dismembered, mandrills did not eat any portion of them in either instance.

Observation and Recording Procedures

One reason for the confusion surrounding the term "dominance" is that it so frequently has been described subjectively rather than in clearly defined, quantitative terms. It is my view that delineation of dominance hierarchies should be based on quantification of interaction patterns between identified individuals. Such data then may be compared objectively with comparable information from other groups.

One of the first objectives of this study was to obtain a comprehensive and systematic description of daily social interactions within the mandrill group. This description provided the necessary context to which any discussion of dominance ultimately had to relate. After assessing several methodologies, I decided that BEVRECS, an observational behaviour stream recording system, would yield the most valid and reliable records of the behaviour stream. In addition, this approach provided a great deal of flexibility in analyzing the data and searching for patterns in the frequency and distribution of behaviour by means of electronic data analysis.

BEVRECS (Denham 1975) was initially developed by Ruth A. Bobbitt for the laboratory study of mother/infant behaviour in pigtail macaques (Bobbitt, Jensen and Gordon 1964). Subsequently, it has been used in field studies of

monkeys (Kurland 1977) as well as in field (Denham 1975) and laboratory (Kogan and Wimberger 1966) studies of human behaviour. At a minimum, each BEVRECS entry provides information on who did what, in relation to whom/what, where and when (Denham 1979:5). Thus, each entry represents the occurrence of one behaviour by one monkey at a particular moment.

Each BEVRECS entry consists of a number of variables allowing any behaviour to be recorded. Although all versions of BEVRECS share a basic set of core variables, other appropriate variables may be added to meet specific research objectives. For the purposes of this study, each BEVRECS entry contains 12 variables. The variables and their definitions are as follows:

ACTOR: the individual monkey whose behaviour is recorded

BEHAVIOUR UNIT: an "activity or change relative to the environment" (Denham 1975:163)

AVOID FLAG: indicator that the accompanying BEHAVIOUR UNIT was in response to a non-agonistic approach by the ACTOR

ORIENTATION: "an identifiable and relevant component of the ACTOR'S environment" (Denham 1975:163)

OBJECT: the item through which an ACTOR and an ORIENTATION interact

CONTINUATION: indicator that an entry is not complete in a single row of the recording form

TERMINATION: indication of the conclusion of a BEHAVIOUR UNIT, which enables the behavioural record to contain dura-

tion information on chosen activities

TIME: the hour, minute and, in some cases, second at which the recorded activity occurred

DRINK FLAG: indicator of the number of interruptions accompanying the "drink" value for the BEHAVIOUR UNIT variable

DAY: day of the study on which the behavioural entry was made

BEVRECS TYPE: indicator of whether observer's attention is focused on one individual or the group as a whole

INDIVIDUAL: which particular monkey is the focus of observer attention

Each of these 12 variables can assume a specific set of values defined by the researcher. These values are numerically coded to facilitate electronic data analysis. Figure 2, a sample recording sheet used for making daily behavioural observations, illustrates the application of the 12 variables defined above.

Two separate, but structurally similar, BEVRECS data sets were compiled. These were the Group BEVRECS Data Set and the Individual BEVRECS Data Set. Group BEVRECS data and Individual BEVRECS data were collected in separate sessions. In Individual BEVRECS recording sessions, I followed the activities of one particular monkey, whereas in Group BEVRECS recording sessions, I focused on the group as a whole. Both BEVRECS Data Sets provided temporal and behavioural data. However, temporal and behavioural

Figure 2. Sample recording sheet for daily behavioural observations. Sentences to the right of each entry translate the numerical values for reader's benefit. All entries in this sample took place on the fifth day of observation while the observer focused on one individual, Willy.

Actor	Behaviour Unit	Avoid Flag	Orientation	Object Continuation Termination	Time	Drinking Flag	Day	BEVRECS Type	Individual	
1	100		8		101500		5	1	1	- Willy walks toward Bitch
8	105	1	1		101500		5	1	1	- Bitch walks backwards away from (avoiding a non-agonistic approach) Willy
1	100		2	1	101500		5	1	1	- Willy walks toward Mandy, and at the same time,
1	100		3		101500		5	1	1	- Willy walks toward Bertha
3	101	1	1		101600		5	1	1	- Bertha walks away from (avoiding a non-agonistic approach) Willy
2	241		1		101600		5	1	1	- Mandy presents to Willy
1	312		2		101615		5	1	1	- Willy grooms Mandy
1	312		2	1	101650		5	1	1	- Willy stops grooming Mandy (total duration of grooming bout: 101650-101615=35 seconds)
1	101		2		101650		5	1	1	- Willy walks away from Mandy
1	513				101700	1	5	1	1	- Willy drinks with one interruption
1	312		65	65	101700		5	1	1	- Willy hits a rock with another rock

resolution were finer in the collection of Individual BEVRECS Data since the focus on a single individual allowed fore more detailed observation. In the group sessions, behaviour was recorded continuously with time marked off in one minute intervals. In the individual sessions, behaviour was also recorded continuously, but the occurrence of certain behaviours was noted to the nearest second in order to capture more precise duration information.

The techniques of focusing on an individual or on the whole group each had advantages and drawbacks. Focusing on each individual for the same amount of time in different Individual BEVRECS recording sessions maximized the possibility of obtaining a proportionally even distribution of observations on each animal. This even distribution of observation time per individual increased the reliability of results based on interindividual comparisons of behaviour frequency. In addition, in order to test certain hypotheses, it was necessary to obtain duration information on such activities as "grooming" and "sitting together". Focusing on the activities of a single animal rather than the group yielded the extra time necessary to note and record behaviour to the nearest second instead of just to the nearest minute. Also, to capture rapidly occurring behaviour patterns observer attention could not be distracted by the attempt to record the behaviour of more than one group member at a time.

On the other hand, the primary disadvantage of individual-based recording sessions was that infrequently occurring behaviours might not be recorded often enough to warrant the frequency and correlation analysis demanded by this study. For example, if aggressive behaviour occurred relatively infrequently, it would be recorded even less frequently if I were limited to recording only the behaviour of the individual I happened to be focusing on (and the aggressive interactions were taking place between other group members).

Focusing on the group as a whole maximized the chance of recording infrequently occurring behaviour. In group-focused sessions, I did not waste a great deal of time observing one animal who was often inactive. However the primary disadvantage of this technique, when compared to individual-focused sessions, was that it did not provide the same degree of assurance of even distribution of observation time per individual. Observer attention might unconsciously focus more often on the activities of a particular individual rather than continuously scanning and noting the behaviour of "less noticeable" group members. Thus, the behaviour of certain individuals might be proportionally under- or over-represented in the behaviour record due to observer bias.

A combination of individual-focused and group-focused behaviour recording sessions was employed in this

study. This approach utilized the advantages of both techniques as well as partially compensating for the disadvantages of using only one or the other. Over the course of Individual BEVRECS recording sessions, which averaged an hour and a quarter each in length, every individual received a total of 24.75 hours of observation. Total time devoted to Group BEVRECS sessions, which also averaged an hour and a quarter each in length, was 24.75 hours.

Observations of infant-infant and adult-infant interactions were not recorded. The detection of dominance was based on observations of adult behaviour not fully developed in infants, so it was not possible to rank infants on these criteria. Since infants lacked a fully adult behaviour repertoire and were often shown a great deal of tolerance by other group members, I decided not to record data on infants for the purposes of this research.

Most non-interactional behaviour patterns, such as "self-grooming", "climbing a fence", "manipulating a stick", etc., are not recorded in this study. Such behaviours are undeniably important in understanding social organization; however, most assessments of dominance depend on observations of inter-individual interactions. Therefore, recording inter-individual interactions exclusively (with a few exceptions related to specific hypothesis testing) is justified given the aims and the time limitations of this project.

Although I attempted to describe and record vocal behaviour, I did not analyze most of those data. The indoor air circulation system created a white-noise effect around the mandrill enclosure which effectively inhibited the reliable recording of vocal behaviour. Because of their penetrating loudness, screams (usually occurring during agonistic encounters) were the only vocal behaviours that could be recorded reliably and used in further analysis.

Duration of Study

During the first month of study, before formal behavioural recording began, I watched the mandrill group to obtain an idea of the range of behaviour displayed by group members. To avoid premature interpretation, behaviour was described as patterns of physical movement rather than in terms of consequences (Hinde 1970, 1973). In other words, an activity was described as "Willy bobbed his head vertically toward Bertha", rather than as "Willy threatened Bertha". Approximately 75 behaviours were described initially in this manner and numerically coded. When previously unseen or unrecognized behaviours became apparent, these were described, numberically coded, and added to the list of values for BEHAVIOUR UNIT. In all, 80 BEHAVIOUR UNITS were recorded. The 31 for which frequency, duration and direction information were used for correlation analysis (see Data Analysis, below) are defined in the Appendix.

I conducted formal behaviour recording sessions from May 7, 1978, to August 30, 1978. In 44 days of observation, I accumulated a total of 198 observation hours.[1] Observations took place between 9:30 a.m. and 3:00 p.m. and totalled 4.5 hours per day. Until I was completely familiar with the numerical codes, I tape recorded verbal descriptions of the mandrill behaviour during observation sessions and transcribed them each evening. When I had memorized the numerical codes, I wrote them directly onto prepared recording sheets (see Figure 2) during the actual behaviour recording sessions. Recording sheets had plenty of room for longhand written comments. Therefore, not only could specific behaviours be recorded with great reliability by means of numerical entries, but additional interpretive comments could accompany the quantitative data as well.

Data Analysis

The organization and coding of the data made it relatively easy to transfer behavioural information from field records to magnetic tape for computer analysis. The first step in data analysis was completion of a series of data quality control checks to eliminate detectable errors (Denham 1978:75-77).[2] Every behavioural entry was checked to insure that only valid values appeared in each variable column. When an illegal code was detected, that particular behavioural entry was printed out and compared

to the original field records. In some cases mistakes were due to typographical errors in the transfer of data from field records to magnetic tape. Comparisons with original records enabled the correction of such errors. In other cases, mistakes were due to observer error in field recording. The context provided by original field entries and accompanying longhand notes made possible the reliable correction of most of these errors. Where correction was uncertain or impossible, the whole entry containing the invalid value was eliminated. This course of action was necessary in less than a dozen of the 36,040 behavioural entries that I made during the entire period.

One source of error that was not detectable by such data quality control checks was the incorrect use of valid codes during behavioural recording. For example, if I accidentally recorded "Willy (1) grooms (312) Mandy (2)," when what I meant to record was, "Willy (1) stands together with (213) Mandy (2)" there would be no way to detect this error. Both 312 (groom) and 213 (stand together with) were valid values for the BEHAVIOUR UNIT variable. The fact that I became very familiar with the numerical codes before using them during formal field recording sessions minimized, but could not entirely eradicate, this possible source of error.

Following data quality control checks, the next step in data analysis was to obtain various sorts of

frequency information. Individual BEVRECS data were used to determine grooming and proximity duration. Group and Individual BEVRECS data were combined to determine all other frequency information. First, two-way frequency distributions of BEHAVIOUR UNIT by ACTOR and BEHAVIOUR UNIT by ORIENTATION were generated. This process answered questions on how often each individual performed or received any particular behaviour (Denham 1975:177-178).

Crosstabulating ACTOR by ORIENTATION while controling for specific behaviours produced information on how often a particular individual performed a specific behaviour toward any other individual. The square matrices produced by these crosstabulations made possible the detection of quantitative patterns in the dyadic interactions within the group. For example, crosstabulations revealed "who aggressed on whom and how often." Obtaining this directional information was critical in light of the controversy that direction of aggressive behaviour, rather than frequency of aggressive behaviour, is correlated with other measures of dominance (Tokuda and Jensen 1969; Varley and Symmes 1966; Alexander and Bowers 1969; Bernstein and Sharpe 1966; Bernstein 1969, 1970; Richards 1974). That is, the animal who ranks highest on frequency of aggressive behaviour may not necessarily rank highest on the basis of other criteria of dominance. The top ranking animal, according to other measures of dominance, may have little need to be frequently aggressive. Rather, what is more

important than frequency of aggressive behaviour, is toward whom one performs and from whom one receives (i.e., direction of) aggressive behaviour.

A customized FORTRAN program was used to compute durations of activities. Thus, it was possible to calculate how much time one individual spent grooming, spent grooming another particular individual, was groomed, or was groomed by another particular individual.

Converting frequency, direction and duration information to rank orders was the next step in data analysis. Rank ordering was a straightforward process for the two-way frequency distributions of BEHAVIOUR UNIT by ACTOR, BEHAVIOUR UNIT by ORIENTATION, duration by ACTOR, and duration by ORIENTATION. Figure 3, for example, shows how the frequency information on "lunging" was used to establish rank orders.

However, serious problems were encountered in trying to derive rank orders from direction data. Depending on how one addressed the direction data, it was possible to derive at least four different rank orders from the same set of data. Unfortunately, in the work of those researchers who had done direction analysis of aggressive behaviour, it was not possible to find a clear statement of how rank order had been derived from direction data (Allee 1942; Richards 1974). This is a serious methodological problem. While investigators are attempting to relate direction-based rank orders to dominance, different researchers may be using

FIGURE 3. Conversion of frequency information to rank order. With regard to aggressive behaviour: the ACTOR having the highest frequency of the specified behaviour and the ORIENTATION having the lowest frequency would rank highest; the ACTOR with the next highest frequency and the ORIENTATION with the next lowest frequency would rank second, and so on. Thus, individual 6 ranks first for frequency of lunging, while individual 1 ranks first for frequency of receiving lunges. With regard to submissive behaviour: the ACTOR having the lowest frequency of the specified behaviour and the ORIENTATION having the highest frequency would rank highest; the ACTOR with the next lowest frequency and the ORIENTATION with the next highest frequency would rank second, and so on.[3]

ACTOR	FREQUENCY OF LUNGING	RANK
1	4	4
2	7	2
3	6	3
5	0	6
6	23	1
8	2	5

ORIENTATION	FREQUENCY OF RECEIVING LUNGES	RANK
1	0	1
2	2	3
3	4	4
5	9	5
6	1	2
8	26	6

different criteria to derive rank orders from direction data. Thus, results claiming a relationship between direction-based rank orders and other measures of dominance should not be considered comparable until the criteria for establishing direction-based rank orders are made explicit.

The fact that different rank orders can be derived from the same set of direction data, depending on how the data are addressed, is best illustrated by example. The following represent four different approaches to deriving rank orders from directional data:

I. Whoever receives behaviour X from the fewest individuals ranks highest.

II. Whoever performs behaviour X towards the greatest number of individuals ranks highest.

III. (a) Whoever performs behaviour X toward the greatest number of individuals ranks highest (or, in the case of submissive behaviour, this animal would rank lowest).

(b) If two or more animals tie on the basis of criterion (a), next determine which of the tied animals in addition receives behaviour X from the fewest individuals. This animal would then rank higher than the one it tied with according to criterion (a) (or, in the case of submissive behaviour, this animal would rank lower).

(c) If two or more animals tie on the basis of criterion (b), next determine which of the tied animals in addition receives behaviour X from the other tieé with the lowest frequency. This animal would then rank higher

than the one it tied with according to criterion (b) (or, in the case of submissive behaviour, this animal would rank lower).

IV. (a) Whoever receives behaviour X from the greatest number of individuals ranks highest (or, in the case of aggressive behaviour, this animal would rank lowest).

(b) If two or more animals tie on the basis of criterion (a), next determine which of the tied animals in addition performs behaviour X toward the fewest individuals. This animal would then rank higher than the one it tied with according to criterion (a) (or, in the case of aggressive behaviour, this animal would rank lower).

(c) If two or more animals tie on the basis of criterion (b), next determine which of the tied animals in addition performs behaviour X toward the other tieé with the lowest frequency. This animal would then rank higher than the one it tied with according to criterion (b) (or, in the case of aggressive behaviour, this animal would rank lower).

By applying each of these four methods to the same directional data in Figure 4, it is possible to obtain the four different rank orders seen in Figure 5.

In the present study, I used Method IV to derive rank orders from directional data. Methods III and IV

FIGURE 4. Directional data on lunging behaviour. This square matrix, produced by crosstabulating ACTOR by ORIENTATION while controlling for BEHAVIOUR UNIT = lunge, allows the ready assessment of how often any mandrill performed a specific behaviour toward, or received a specific behaviour from, any other mandrill.

ACTOR \ ORIENTATION	Willy	Mandy	Bertha	A032	Bitch	Chigan
Willy		2			1	1
Mandy			4	1	3	4
Bertha				4	6	1
A032					34	9
Bitch						4
Chigan						

FIGURE 5. Rank orders obtained by applying four different methods to the directional data in Figure 4.

	Willy	Mandy	Bertha	A032	Bitch	Chigan
Lunge I	1	2.5	2.5	4	5	6
Lunge II	2.5	1	2.5	4	5	6
Lunge III	2	1	3	4	5	6
Lunge IV	1	2	3	4	5	6

eliminated more ties and provided finer directional distinctions than Methods I and II, but the selection of Method IV over Method III was arbitrary. That is, although Methods III and IV sometimes produced different rank orders when empty cells were present above or below the diagonal, there was no logical justification for considering one of these rank orders "better than" the other. More time and funding would have permitted analyses using both Methods III and IV, but lack of these necessitated a choice between the two methods.

After converting frequency, direction and duration information to rank orders, the next step in data analysis was to test for significant correlations between the behaviours represented by these rank orders. Correlation coefficients were computed using Spearman's rho, and one-tailed tests of significance were performed on all coefficients. Higher level behaviour categories such as aggressive and submissive behaviour were traditionally used to measure dominance (Richards 1974; Koford 1963). Before testing for correlations between such higher level categories, tests for correlations were first performed on the individual patterns of physical movement comprising these categories. In other words, if significant correlations existed between such behaviours as "lunge", "chase", "hit", "grab", "glare", "vertical head bob", and "raise crest", this relationship provided the justification for lumping these individual

patterns of physical movement into the higher level category of aggressive behaviour.

Tests of correlation were performed between the BEHAVIOUR UNITS for which frequency, direction and/or duration information were obtained. These behaviours are listed and defined in Appendix I. Each BEHAVIOUR UNIT could appear up to three times in correlation analysis. For example, the BEHAVIOUR UNIT "lunge" was tested for correlations with other behaviours in the following three contexts: (1) frequency of performing lunges; (2) frequency of receiving lunges; and, (3) direction of lunging. The purpose of correlation analysis was to establish whether or not significant correlations existed between behaviours that traditionally had been used to measure dominance. Certain behaviours which had not been used previously to measure dominance were also tested for correlations with traditional dominance indicators.

As was stated above, before testing for correlations between such higher level categories as "aggressive", "submissive", or "friendly" behaviour, correlation analysis was first performed on the individual patterns of physical movement comprising these categories. Aggression may be defined as that behaviour shown by an animal who attacks, attempts to attack, or threatens to attack another animal of the same species. Chasing, for example, is often classified as an aggressive behaviour.[4] The behaviours appearing in Table 2 were lumped together and treated as a higher level

"aggressive behaviour" category based on their intercorrelation with "chase". The inter-correlation of the behaviours in Table 2 was established through direction analysis, which yielded a higher number of inter-correlations than analysis based on: (a) frequency of performing the behaviour; or (b) frequency of receiving the behaviour (see Figure 6). Behaviours lacking adequate data for direction analysis were included in the "aggressive behaviour" category if the limited instances of such behaviours occurred in the same direction as the inter-correlated aggressive behaviours.

Submissive behaviours, such as "run away from", are regarded as being the opposite of those most commonly used to signal attack. The behaviours listed in Table 3 were lumped together and treated as a higher level "submissive behaviour" category based on their inter-correlation with "run away from". Again, direction analysis produced the highest number of correlations between the individual behaviours comprising the "submissive behaviour" category. Table 3 includes those behaviours whose low frequency of occurrence prevented direction analysis, yet took place in the same direction as the inter-correlated "submissive behaviours".

One variation on the higher level "submissive behaviour" category was also used in subsequent correlation analysis. This variation was called "submissive behaviour except presenting". By separating presenting behaviour from any

TABLE 2. Behaviours included in "aggressive behaviour" category. See Appendix for behavioural definitions.

BEHAVIOUR	NUMBER OF CASES
bite	2
chase	314
grab	22
grab (attempted)	1
hit	4
lunge	74
push	1
raise crest	96
stare	28
vertical head bob	222
total aggressive behaviours	784

FIGURE 6. Correlations between individual aggressive behaviours using three different contexts: (1) frequency of performing the behaviour; (2) frequency of receiving the behaviour; and, (3) direction of the behaviour. Context 1 (Fig. 6a) gave the fewest correlations; context 2 (Fig. 6b) gave three times as many correlations as context 1; and context 3 (Fig. 6c) produced five times as many correlations as context 1. A correlation significant at the .05 level or better is indicated by an X in the appropriate cell. Only those behaviours having enough data for direction analysis appear in these figures.

6a. Frequency of performing the behaviour.

	lunge	chase	grab	stare	vertical head bob
chase					
grab	X				
stare	X				
vertical head bob					
raise crest		X			

Figure 6b. Frequency of receiving the behaviour (see legend p. 40).

	lunge	chase	grab	stare	vertical head bob
chase	X				
grab	X	X			
stare	X	X	X		
vertical head bob				X	
raise crest	X	X		X	

Figure 6c. Direction of the behaviour (see legend p. 40).

	lunge	chase	grab	stare	vertical head bob
chase	X				
grab	X	X			
stare	X	X	X		
vertical head bob	X	X	X	X	
raise crest	X	X	X	X	X

TABLE 3. Behaviours included in the "submissive behaviour" category. See Appendix for behavioural definitions.

BEHAVIOUR	NUMBER OF CASES
avoidance	126
defecate	1
fear grin	2
present (agonistic)	10
run away from	406
squeal	2
total submissive behaviours	547

higher level behaviour category, this study could test its specific correlation with other behaviours for purposes of comparison with studies that have used presenting to measure dominance.

Display behaviour, such as the BEHAVIOUR UNIT "display jump", consists of stereotyped branch shaking, wire rattling, or bouncing. "Glass jump" correlated with "display jump", and these two behaviours were included in the higher level "display behaviour" category based on frequency of performance.

Correlation analysis was performed on the behaviour units remaining after identification of those belonging to the higher level "aggressive", "submissive", and "display" behaviour categories. Two contexts were used in testing for correlations between these remaining behaviour units: (1) frequency of performing the behaviour; and (2) frequency of receiving the behaviour. Context 1 produced twice as many correlations at the .05 level of significance or better (see Figure 7). The behaviours in Table 4 were lumped into a higher level category and discussed as "friendly behaviour" on the basis of inter-correlations between frequency of performance of these behaviours. Although none of the individual behaviours in this category correlated with every one of the others, each correlated with at least two others (the only exception being the infrequent "relax open mouth" which did not correlate with any other friendly behaviour).

FIGURE 7. Correlations between individual friendly behaviours using two different contexts: (a) frequency of performing the behaviour; and, (b) frequency of receiving the behaviour. A correlation significant at the .05 level or better is indicated by an X in the appropriate cell.

7a. Frequency of performing the behaviour.

	groom time	groom	handle genitals	embrace	touch	nose to perineum	nose to face	figure-eight mouth	relax open mouth
groom	X								
handle genitals		X							
embrace		X	X						
touch	X								
nose to perineum			X						
nose to face					X	X			
figure-eight mouth			X	X					
relax open mouth									
horizontal head shake	X							X	

7b. Frequency of receiving the behaviour. (See legend p. 49)

	groom time	groom	handle genitals	embrace	touch	nose to perineum	nose to face	figure-eight mouth	relax open mouth
groom	X								
handle genitals									
embrace	X	X							
touch									
nose to perineum			X						
nose to face									
figure-eight mouth						X			
relax open mouth									
horizontal head shake								X	

TABLE 4. Behaviours included in the "friendly behaviour" category. See Appendix for behavioural definitions.

BEHAVIOUR	NUMBER OF CASES
embrace	4
figure-eight mouth	258
groom	190
groom time	154.25 min.
handle genitals	62
horizontal head shake	121
nose to face	145
nose to perineum	64
relax open mouth	1
touch	91
total friendly behaviours (except groom time)	936

Two variations on the higher level "friendly behaviour" category were also used in subsequent correlation analysis. These variations were: (1) frequency of friendly behaviour except "grooming"; and (2) frequency of friendly behaviour except "grooming", "figure-eight mouth", and "horizontal head shake". The reasons for including these variations were as follows. Grooming behaviour had been used to measure dominance in previous studies (Sparks 1969; Washburn and DeVore 1961). By separating grooming behaviour from any higher level behaviour category, this study could test its specific correlation with other behaviours for purposes of comparison. With regard to the second variation listed above, "figure-eight mouth" and "horizontal head shake" were sufficiently unique behaviours to warrant the precaution of treating them separately from the higher level "friendly behaviour" category. These two unique behaviour patterns are discussed further in the last chapter.

In addition to the higher level behaviour categories just discussed, several individual behaviour patterns were included in final correlation analysis. Some of these individual behaviours were mentioned previously: "grooming", "horizontal head shake", "figure-eight mouth", and "presenting". BEHAVIOUR UNITS denoting "proximity", "non-agonistic avoidance", "frequency of initiated interactions", "frequency of received interactions", and "frequency of involvement in interactions as both initiator and receiver" were also

included in final correlation analysis to compare results with earlier research which used these behaviours to measure dominance. Table 5 presents a list of all higher level behaviour categories and individual behaviour patterns that underwent final correlation analysis in an attempt to determine whether these different potential measures of dominance agreed with each other.

The behaviours listed in Table 5 were tested for correlations in two different time periods due to the following incident. Between the 13th and 14th days of observation, a fight took place between Mandy and Bertha. I did not see the fight, but two keepers who witnessed it described it to me. Although the keepers did not see who or what initiated the fight, they saw both animals repeatedly threaten each other and engage in aggressive bodily contact including "hitting", "grabbing", and "biting". The fight ended when Mandy repeatedly squealed, disengaged herself from Bertha, and ran away squealing. Earlier, I witnessed a similar fight between Mandy and Bertha which concluded with Bertha's running away from Mandy while squealing repeatedly. Squealing in response to aggression is an indication of fear and/or submission, and the second fight was the first time I was ever aware of Mandy behaving in an overtly fearful or submissive manner toward Bertha.

In the mandrill group, "non-agonistic avoidance" was the single most frequently occurring BEHAVIOUR UNIT that

TABLE 5. Higher level behaviour categories and individual behaviour patterns that underwent final correlation analysis.

CONTEXT OF CORRELATION ANALYSIS	N	BEHAVIOUR
A,O,D	764	aggressive behaviour
A,O,D	547	submissive behaviour
A,O,D	537	submissive behaviour except presenting
A,O	936	friendly behaviour
A,O	746	friendly behaviour except grooming
A,O	367	friendly behaviour except grooming, figure-eight mouth, and horizontal head shake
A	82	display behaviour
A,O,D	479	present (non-agonistic)
A,O	190	groom
A,O	154.25 min.	groom time
A,O,D	258	figure-eight mouth
A,O,D	121	horizontal head shake
A,O,D	379	horizontal head shake and figure-eight mouth
A,O	1232	proximity
A,O	362.1 min.	proximity time
A	3569	frequency of initiated interactions
A + O	7138	frequency of involvement in interactions as both initiator and receptor
O	3569	frequency of received interactions
A,O,D	3352	avoid (non-agonistic)

A = actor, or frequency of performing behaviour
O = orientation, or freqeuncy of receiving the behaviour
D = direction of the behaviour
N = number of cases

(173.25 observation hours represented by this table.)

had been used to measure dominance in other studies of non-human primate behaviour (Richards 1974; Rowell 1966). Prior to the second fight, I would have placed Mandy higher than Bertha in a dominance hierarchy established on direction of "non-agonistic avoidance", whereas after the second fight, I would have ranked Bertha higher than Mandy on the same criterion. Because of its high frequency of occurrence, I was able to rank order the mandrills subjectively on direction of "non-agonistic avoidance". Computer analysis later provided a quantitative confirmation of my subjective rank ordering and verified the switch in rank between Mandy and Bertha after the second fight. Table 6 shows the rank order of all mandrills both before and after the fight based on direction analysis of "non-agonistic avoidance".

The switch in rank between Mandy and Bertha on this one readily visible behavioural criterion indicated the appropriateness of testing for behavioural correlations in two distinct pre- and post-fight time periods. If these time periods were not distinguished, and if all instances of "non-agonistic avoidance" during the whole study period were lumped together, the change in rank between Mandy and Bertha would have been hidden (see Table 6, Days 1-44). Thus, to perform correlation analysis with rank orders that reflect a more accurate picture of behavioural interactions, rank orders for all behaviours had to be constructed for both pre- and post-fight time periods.

TABLE 6. Rank order of mandrills based on direction analysis of non-agonistic avoidance.

ANIMAL	RANK		
	DAYS 1-44	DAYS 1-13	DAYS 14-44
Willy	1	1	1
Mandy	2	2	3
Bertha	3	3	2
A032	4	4	4
Bitch	5	5	5
Chigan	6	6	6

CHAPTER III

RESULTS AND DISCUSSION

Introduction

Correlation analysis is first performed to identify clusters of individual behaviours belonging to higher level behaviour categories. Final correlation analysis is performed on these higher level behaviour categories as well as on specified individual behaviours (all of which are listed in Table 5) in order to identify a cluster of inter-related behaviours which are herein defined as indicating dominance. (Again, for purposes of this thesis, dominance is defined as an inter-correlated cluster of behaviours, one of which is the ability to aggress on an individual without that individual responding with aggression.) This second level of correlation analysis is the subject of the present chapter. Some of the behaviours employed in final correlation analysis have been used by other researchers to measure dominance, while others have not been tested previously as dominance indicators. The purpose of final correlation analysis is to determine whether any of these behaviours are significantly inter-correlated. As stated under Methodology, significant inter-correlation provides the only legitimate rationale for considering different behaviour patterns to be measures of

the same phenomenon: dominance.

Of the behaviours listed in Table 5, the following showed significant correlations with each other both in days 1-13 and in days 14-44 (see Figure 8; separation of observations into two time periods is explained in Chapter II, pp. 48-52): direction of aggression, frequency of performing submissive behaviour, frequency of performing submissive behaviour except presenting, direction of submissive behaviour, direction of submissive behaviour except presenting, frequency of receiving non-agonistic presents, direction of non-agonistic presents, and direction of non-agonistic avoidance. Identification of this inter-correlated cluster of behaviours indicated that dominance relationships did operate in this captive group of mandrills. The rank orders from these eight measures of dominance were used to calculate an overall dominance rank for each group member (Figure 9). The rank order of the mandrills from most to least dominant in days 1-13 was: Willy, Mandy, Bertha, A032, Bitch, Chigan. The only change in the rank order for days 14-44 was a tie between Mandy and Bertha for second position.

The inter-correlated behaviours which were used to measure dominance and construct a dominance hierarchy in this group are discussed in the following sections. Behaviours which were not useful indicators of dominance are also discussed, and the utility of the dominance concept is evaluated in light of these research results.

FIGURE 8. Behaviours showing significant inter-correlations both in days 1-13 (Fig. 8a) and in days 14-44 (Fig. 8b). Levels of significance are indicated in parentheses at the bottom of each cell, and correlation coefficients are indicated at the top of each cell.

8a. Days 1-13

	performing submissive behaviour	performing submissive behaviour except presenting	receiving presents (non-agonistic)	direction of aggressive behaviour	direction of submissive behaviour	direction of submissive behaviour except presenting	direction of presents (non-agonistic)
performing submissive behaviour except presenting	1.0000 (.001)						
receiving presents (non-agonistic)	0.7741 (0.37)	0.7714 (0.37)					
direction of aggressive behaviour	0.8857 (.010)	0.8857 (.010)	0.9429 (.001)				
direction of submissive behaviour	0.8857 (.010)	0.8857 (.010)	0.9429 (.003)	1.0000 (.001)			
direction of submissive behaviour except presenting	0.8857 (.010)	0.8857 (.010)	0.9429 (.003)	1.0000 (.001)	1.0000 (.001)		
direction of presents (non-agonistic)	0.8857 (.010)	0.8857 (.010)	0.9429 (.003)	1.0000 (.001)	1.0000 (.001)	1.0000 (.001)	
direction of avoidance (non-agonistic)	0.8857 (.010)	0.8857 (.010)	0.9429 (.003)	1.0000 (.001)	0.9429 (.003)	1.0000 (.001)	1.0000 (.001)

8b. Days 14-44 (see legend p. 53).

	performing submissive behaviour	performing submissive behaviour except presenting	receiving presents (non-agonistic)	direction of aggressive behaviour	direction of submissive behaviour	direction of submissive behaviour except presenting	direction of presents (non-agonistic)
performing submissive behaviour except presenting	1.0000 (.001)						
receiving presents (non-agonistic)	0.9429 (.003)	0.9429 (.003)					
direction of aggressive behaviour	0.8857 (.010)	0.8857 (.010)	0.9429 (.003)				
direction of submissive behaviour	0.8857 (.010)	0.8857 (.010)	0.9429 (.003)	1.0000 (.001)			
direction of submissive behaviour except presenting	0.8857 (.010)	0.8857 (.010)	0.9429 (.003)	1.0000 (.001)	1.0000 (.001)		
direction of presents (non-agonistic)	0.8857 (.010)	0.8857 (.010)	0.9429 (.003)	1.0000 (.001)	1.0000 (.001)	1.0000 (.001)	
direction of avoidance (non-agonistic)	0.9429 (.003)	0.9429 (.003)	1.0000 (.001)	0.9429 (.003)	0.9429 (.003)	0.9429 (.003)	0.9429 (.003)

FIGURE 9. Calculation of overall dominance rank for each group member based on rank orders from the inter-correlated measures of dominance. Numbers in cells represent each mandrill's rank order for the corresponding behaviour on the left. Overall dominance rank is calculated by summing each animal's separate rank orders for individual activities. The individual with the lowest sum receives a rank of 1 while the individual with the highest sum receives a rank of 6.

9a. DAYS 1-13

	Willy	Mandy	Bertha	AO32	Bitch	Chigan
performing submissive behaviour	1	2	4	3	6	5
performing submissive behaviour except presenting	1	2	4	3	6	5
receiving presents (non-agonistic)	1	3	2	4	6	5
direction of aggressive behaviour	1	2	3	4	5	6
direction of submissive behaviour	1	2	3	4	5	6
direction of submissive behaviour except presenting	1	2	3	4	5	6
direction of presents (non-agonistic)	1	2	3	4	5	6
direction of avoidance (non-agonistic)	1	2	3	4	5	6
sum of each animal's separate rank orders =	8	17	25	30	43	45
overall dominance rank of each animal =	1	2	3	4	5	6

9b. DAYS 14-44

	Willy	Mandy	Bertha	AO32	Bitch	Chigan
performing submissive behaviour	1	3	2	4	6	5
performing submissive behaviour except presenting	1	3	2	4	6	5
receiving presents (non-agonistic)	1	3	2	4	5	6
direction of aggressive behaviour	1	2	3	4	5	6
direction of submissive behaviour	1	2	3	4	5	6
direction of submissive behaviour except presenting	1	2	3	4	5	6
direction of presents (non-agonistic)	1	2	3	4	5	6
direction of avoidance (non-agonistic)	1	3	2	4	5	6
sum of each animal's separate rank orders =	8	20	20	32	42	46
overall dominance rank of each animal =	1	2.5	2.5	4	5	6

Aggressive Behaviour

Some investigators have used direction of aggression to measure dominance (Richards 1974, in rhesus macaques; Bernstein and Sharp 1966, in rhesus macaques; Bernstein 1969, in pigtail macaques; Baldwin 1968, in squirrel monkeys; Varley and Symmes 1966, in macaque species), while others have tried to correlate frequency of aggression with traditional dominance measures (Reynolds and Luscombe 1969, in chimps; Kaufman 1967, in rhesus macaques). My study indicated that direction rather than frequency of aggression was the more appropriate measure. Direction of aggression was significantly correlated with seven other inter-correlated measures of dominance. Neither frequency of receiving nor frequency of performing aggressive behaviour was correlated with each of the eight inter-correlated dominance indicators.

The precipitating factors in aggressive encounters were often difficult or impossible to identify. Nonetheless, aggressive behaviour was repeatedly observed in the following contexts:

1. Intervention. In response to disturbances from within the group (e.g., an infant screaming or an agonistic encounter) an individual initially removed from the scene would run to the site of commotion and threaten, chase, or attack the animals involved in the disturbance. Similar behaviour categorized under a variety of names, such as "policing" and "punishing", had been described by other observers

(Saayman 1971:42 for Papio ursinus; Bernstein and Sharpe 1966:97 for Macaca mulatta; Rowell 1966:435 for Papio anubis). Such intervention terminated the original disturbance and was only performed by Willy, Mandy and Bertha. Although the intervening animal was always higher ranking than those creating the disturbance, this did not imply that intervention measured dominance. Since only half of the individuals in the group performed intervention behaviour, I could not test intervention as a dominance indicator.

2. Unsolicited Support. In an agonistic encounter between two individuals, a third animal of intermediate rank might, without being solicited, support the higher ranking individual. This situation differed from intervention in that: (a) the animal involved in intervention was higher ranking than either of those creating the disturbance, whereas the animal giving unsolicited support was only higher ranking than one of those involved in the disturbance; (b) the animal involved in intervention might threaten any one or all of the animals involved in a disturbance, regardless of their rank, whereas the animal giving unsolicited support only aggressed on the lower ranking animal; and (c) agonistic encounters appeared to be shortened by intervention action since all participants generally dispersed in the presence of the higher ranking individual, whereas agonistic encounters were often

prolonged by animals giving unsolicited support since the lowest ranking participant had two, rather than the original one, animals to avoid.

3. Protected Threat (Kummer and Kurt 1965; Richards 1974) was a behaviour used to enlist the aid or support of another individual. It consisted of one individual threatening another while simultaneously either presenting to a third individual (the potential supporter), or repeatedly glancing back and forth between the third individual and the individual being threatened. This behaviour often prompted an aggressive response from the enlistee toward the third animal.
4. Redirected Aggression. Sometimes after being aggressed upon by a higher ranking animal, a mandrill would immediately turn around and, with no other apparent provocation, behave aggressively toward a lower ranking individual.
5. Competition Over Mates. Discussions on the relationship between mating success and dominance have a peculiar tendency to focus almost exclusively on male competition over estrous females. Because there was only one adult male in this mandrill group, I could say nothing with regard to male competition over females. However, several apparent instances of female competition over the single adult male were recorded when Mandy threatened and/or chased other females away from Willy. Such agonistic competition on Mandy's part was elicited when

other females presented to, were mounted by, or engaged in grooming with Willy.

6. Competition Over Food. Fresh vegetable snacks were thrown into the mandrill enclosure once or twice a day. Aggressive encounters over food were sometimes observed at such times.

While direction of aggression measures dominance, and while aggressive behaviour occurs in the contexts of competition over mates and food, this study is unable to clarify whether or not priority of access to food and/or mates are useful measures of dominance in the captive situation. Other investigators have used priority of access to water (Boelkins 1967; Castell and Heinrich 1971), priority of access to food (Dumond 1969; Mason 1961), and priority of access to mates (Conoway and Koford 1965; Altman 1962; Hall 1962) to measure dominance. I am unable to rank order the mandrills on priority of access to food, water, or mates (a prerequisite to correlation analysis with other potential measures of dominance) for the following reasons:

1. Frequency of copulations is used to rank order animals on priority of access to mates; however, the only observed copulations have been between Mandy and Willy. Such limited occurrence of this behaviour precludes an attempt to rank order the female mandrills with respect to priority of access to mates. The presence of two lactating females in the group is undoubtedly a factor in

the low frequency of copulations.

2. In group situations, the orders in which animals feed at a food pile (Richards 1974) or drink at a water bottle (Boelkins 1967) have been used to rank order animals on priority of access to food and water. I had no control over feeding or watering facilities for the mandrills and was thus unable to provide the controlled access situations necessary for ranking animals on priority of access to food and/or water. Furthermore, approaches to obtaining rank orders for feeding and drinking require closer examination.

The apparent necessity for creating controlled or limited access situations in order to elicit feeding and drinking hierarchies indicates that the postulated relationship between priority of access and dominance may be the result of very specific circumstances. Under natural conditions where food is relatively scattered and individuals forage alone, it is difficult to imagine how one would measure priority of access to food. A quick, clever, but low ranking animal with a good nose may be most successful in finding food. Priority of access in such a situation has nothing to do with traditional, agonistic-related dominance indicators. This fact highlights the implicit, but usually unstated assumption that priority of access involves direct competition. Situations of direct competition over food occur much less frequently in the wild than in

captivity. Where direct competition over food occurs infrequently, a long period of fieldwork is necessary in order to collect enough data to rank order animals on priority of access to food. Even in the captive mandrill group, direct competition over food occurs infrequently enough that a much longer period of fieldwork is necessary in order to try to construct a feeding hierarchy and test its correlation with other measures of dominance.

While I did not test for correlations between priority of access to incentives and other measures of dominance, my observations indicate that many factors besides aggression (which is one of the measures of dominance) confer priority of access. For example, individual preference plays a role in who mates with whom. In a study on the relationship between dominance and reproductive success in baboons (Papio cynocephalus), Hausfater (1975) documents selectivity in an individual's choice of consort partners. First ranking males do not form consort relations with certain estrous females, even when no other estrous females are available. Whether this pattern of selectivity is the result of male or female choice remains to be determined.

Factors other than aggression which may confer priority of access to food include non-agonistic avoidance, friendship, kinship, and age/sex relations. In addition, aggression at a food source does not necessarily confer priority of access as is illustrated by my observations of

animals being threatened over food and responding by carrying the food away with them. In view of the fact that a variety of factors contribute to priority of access to incentives, it must not be assumed that priority of access is correlated with direction of aggression or any of the other measures of dominance. Such a correlation, if it does exist, must be demonstrated by quantitative analysis.

In summary, situations of limited food distribution may produce a correlation between feeding priority and other measures of dominance. On the other hand, this correlation may not exist if factors other than dominance (e.g., kinship, friendship, age/sex relations, etc.) play a significant role in conferring priority of access. Careful quantitative analysis is necessary for clarifying the relationship between dominance and priority of access. In the next section, submissive behaviours are discussed as dominance indicators.

Submissive Behaviour

Submissive or appeasement behaviour consists of certain postures or gestures which are regarded as being the opposite of those most commonly used to signal attack (Marler and Hamilton 1966). Certain submissive behaviours occur in direct response to aggression, including "defecate", "fear grin", "run away from", and "squeal". Other patterns of behaviour which have been classified as submissive, such as presenting and avoidance, do not typically occur in

direct response to aggression. When viewed in this manner, presenting and avoidance appear to be complementary to, rather than opposites of, those postures or gestures most commonly used to signal attack.[5] For purposes of discussion, submissive behaviour is divided into three subcategories: (1) submissive behaviour, i.e., those behaviours that occur in direct response to aggression (see Table 3); (2) presenting; and (3) non-agonistic avoidance.

Submissive Behaviours. Both direction of submissive behaviour (Richards 1974) and frequency of performing and/or receiving submissive behaviour (Rowell 1966) have been used to measure dominance. Results from my study indicate that direction of submissive behaviour, as well as frequency of performing the submissive behaviours listed in Table 3 (p. 42) are useful measures of dominance. The latter result conflicts with those of Rowell (1966), who finds frequency of receiving, rather than frequency of performing submissive behaviours to be a better dominance indicator. The reasons for this discrepancy are probably related to Rowell's method of correlation analysis. Rather than testing for inter-correlations between various behaviour patterns that may measure dominance, Rowell tests for correlations between individual behaviour patterns and what she calls "apparent ranking". "Apparent ranking...is the straight line hierarchy into which the author was prepared to order the older baboons at the completion of observations and before the data were analyzed"

(Rowell 1966:430). Thus, Rowell is testing for correlations between individual behaviours and a subjectively defined standard. This approach is weak because of the undefined, subjective element in determining "apparent ranking", against which individual dominance indicators are compared, and because no attempt is made to correlate the individual behaviours that are claimed to indicate dominance. Both deficiencies prevent reliable comparison of other research results. Thus, while Rowell's results indicate that frequency of receiving submissive behaviours may be used to measure dominance and my results do not, this is probably due to different approaches to measuring dominance.

Further clarification of this discrepancy in results may be possible by asking how Rowell determines "apparent ranking" in her group of baboons. Although Rowell herself does not clarify this point, my own experience suggests a possible explanation. As stated earlier, I am able to rank order the mandrills subjectively on direction of "non-agonistic avoidance" prior to quantitative analysis because of the high frequency of occurrence of this behaviour pattern. Computer analysis later provides a quantitative conformation of my subjective rank ordering and verifies the correlation of this behaviour pattern with an inter-correlated group of behaviours thought to measure dominance. Rowell comments on the relatively high frequeny of "non-agonistic approach/ retreat" interactions in her baboon group (Rowell 1966:437),

so it is entirely possible that this behaviour pattern (the same as my non-agonistic avoidance) forms the basis for her subjective "apparent ranking". If this assumption is correct, Rowell's "apparent ranking", or dominance hierarchy, is synonymous with "direction of non-aggression-response avoidance". Thus, Rowell's assertion that frequency of receiving submissive behaviour indicates dominance may be more appropriately interpreted as: frequency of receiving submissive behaviour correlates with direction of non-agonistic avoidance. I, too, find that frequency of receiving submissive behaviour correlates with direction of non-agonistic avoidance. However, I do not find that frequency of receiving submissive behaviour correlates with all of the other inter-correlated behaviours measuring dominance. Since dominance indicators may be identified as a cluster of inter-correlated behaviours by my definition of the phenomenon, and since frequency of receiving submissive behaviour does not belong to such a cluster, I cannot say that frequency of receiving submissive behaviour indicates dominance.

The preceeding discussion is significant because it illustrates a specific example of two widespread methodological problems in dominance related research. The first involves subjective determination of dominance hierarchies. On the one hand, there may be species and situations in which a subjectively determined hierarchy is shown to be correct by objective assessments. Given the limitations on time and/or visibility in observations made in the wild, there often exists a strong temptation to avoid quantitative

behaviour recording procedures that then require analysis, when subjectively derived hierarchies may be correct. However, these considerations must be contrasted with the need to allow valid and reliable comparison with other research results for the same species, let alone across species. The need for comparison demands that behaviour patterns used to determine dominance be specified explicitly.

The second methodological problem involves the following sequence of events:

1. Determining a "dominance hierarchy" (either subjectively or objectively) on the basis of <u>one</u> behaviour pattern, such as direction of non-agonistic avoidance.
2. Correlating another behaviour pattern, such as frequency of receiving submissive behaviour, with the "dominance hierarchy" delineated in step 1.
3. Concluding that frequency of receiving submissive behaviour indicates dominance, based on the correlation established in step 2.

This sequence of events is potentially misleading for two reasons. First, rank ordering of animals according to a single behaviour pattern (as in step #1, above) does not constitute a dominance hierarchy. Animals may be ranked on a number of criteria, including frequency of performing different behaviours, age, stature, weight, etc. There is little justification for referring to the rank order of animals based on a single criterion as a "dominance"

hierarchy. Rather, a dominance hierarchy should be delineated on the basis of a cluster of inter-correlated behaviours, and in accordance with the original intention of the concept of social dominance, one of the inter-related behaviours should be the ability to aggress on an individual without receiving an aggressive response.

Second, even if direction of non-agonistic avoidance is one of an inter-correlated cluster of behaviours indicating dominance, and frequency of receiving submissive behaviour correlates with direction of non-agonistic avoidance, it does not automatically follow that frequency of receiving submissive behaviour is correlated with each of the other behaviours in the cluster indicating dominance. As stated above, in my study precisely this finding is made. The inescapable conclusion is that correlation of behaviours must be shown to occur, for what appears to be a logical deduction may in fact be wrong. Unfortunately, this type of error is exceedingly widespread in studies of non-human primates and is perhaps the major reason why so many behaviour patterns have been linked to dominance.

In discussing which measures of submission indicate dominance, it is interesting to note Rowell's (1966:437) suggestion that "the hierarchy is maintained, or expressed, chiefly by subordinate activities, and that it is the lower-ranking animals which do most to perpetuate rank distinctions." However, the change in rank involving Mandy and Bertha is apparently dependent on the outcome of a single fight that Mandy loses. Thus, while the hierarchy may be "expressed

chiefly through subordinate activities" on a dialy basis, the results of the fight suggest that dominance rank is ultimately dependent on winning decisive agonistic encounters.

Presenting. Presenting "has been described as a gesture of submission whose function is to suppress "attack"" (Rowell 1974:147). However, as other researchers have noted (Richards 1974:923; Rowell 1974:147), presenting is seldom observed in overtly agonistic contexts. In fact, only 10 out of 489 instances of presenting occur in direct response to aggressive behaviour in the mandrill group. Furthermore, presenting occurs in a variety of contexts, several of which are not apparently related to overtly agonistic contexts. For example, presenting is used by receptive female mandrills to invite copulation with the adult male. Similarly, Rowell (1967) documents an increased frequency of presenting in sexually receptive female baboons. Presenting is also observed in the context of obtaining access to desired food (fresh vegetables or tree branches). Richards (1974 in rhesus monkeys) and Poirer (1970 in langurs) have recorded presenting behaviour in similar "begging" contexts.

Since presenting occurred in several different contexts and was seldom observed as a direct response to aggression, it was not strictly comparable to the other submissive behaviours in Table 3 (which were most frequently observed

as a direct response to overt aggression). Accordingly, two types of presenting, "agonistic" and "non-agonistic", were distinguished on a contextual basis for purposes of analysis. "Agonistic presents" occurred in direct response to aggression while "non-agonistic presents" were not directly preceded by aggressive behaviour. "Agonistic presents" were included with the other submissive behaviours in Table 3 for correlation analysis. In addition, "submissive behaviour except presenting" was tested for correlation with other dominance indicators to see whether or not the inclusion of "agonistic presents" altered correlation results. Finally, "non-agonistic presents" alone were tested for correlation with other measures of dominance.

Both frequency of performing and direction of submissive behaviour were correlated with the other inter-correlated measures of dominance, regardless of whether or not "agonistic presents" were included in these categories (see Figure 8 for probability levels of correlations). Frequency of receiving as well as direction of "non-agonistic presents" were both correlated with the other dominance indicators.

Interesting similarities and differences appear in the results of correlation analysis involving submissive behaviour and non-agonistic presenting. The <u>direction</u> of both of these behaviour patterns is correlated with other inter-correlated measures of dominance. However, whereas

frequency of performing submissive behaviours is correlated with other dominance indicators, it is frequency of receiving non-agonistic presents which measures dominance. In other words, while the direction of both behaviours is correlated with other dominance indicators, in one case it is frequency of performing and in the other case frequency of receiving that measures dominance. This difference may be viewed as support for the decision to separate "non-agonistic presents" from other behaviours in the submissive behaviour category.

Non-agonistic avoidance occurred when one animal walked quietly out of the way of an approaching animal who showed no observable signs of aggression. This behaviour sometimes resulted in the avoider being supplanted at a food source, perch, or digging hole (i.e., a hole in the dirt where the monkeys dug, possibly for food or in search of mice). Interactions involving non-agonistic avoidance accounted for over one half of all observed interactions that underwent final correlation analysis.

Data on non-agonistic avoidance, which is also called displacement, approach-retreat, or yielding ground behaviour, has been used by a number of researchers to indicate dominance (Bernstein and Sharpe 1966; Richards 1974; Rowell 1966; Simonds 1965; Kaufman 1967; Alexander and Bowers 1969; Jay 1965). Direction of "non-agonistic avoidance" in mandrills is correlated with an inter-related

group of behaviours measuring dominance. Thus, results from this study support the conclusion that direction of "non-agonistic avoidance" indicates dominance. If mandrill A moves out of the way of mandrill B, this is a good indicator of the relative dominance status of A and B.

Display Behaviour

Bertrand (1969, in stumptail macaques) and Richards (1974, in rhesus macaques) used frequency of stereotyped branch shaking, wire rattling and bouncing to measure dominance. Similar display behaviour by the mandrills occurred most frequently at sounds of disturbance from outside the group (e.g., loud bird calls, the rattling of chains when windows were opened, a gardener noisily dragging tree branch trimmings across the floor in front of the mandrill enclosure), and might have served to alert the group. In many cases, the eliciting stimulus for display behaviour was not identified, and the function of such displays are unclear.

Frequency of displaying by the mandrills failed to correlate with the inter-correlated dominance indicators. Richard (1974) identified a cluster of inter-correlated dominance indicators in several different groups of rhesus macaques, and frequency of display behaviour was a part of this cluster in 10 out of 12 groups. Since display behaviour was only recorded for three of the six mandrills,

the failure of display behaviour to correlate with other dominance indicators might simply be due to an inadequate sample of this particular behaviour. Longer term observation of the mandrill group is necessary to clarify this point.

Friendly Behaviour

A variety of friendly behaviours have been related to dominance. Accordingly, seven categories of friendly behaviours are tested as dominance indicators in the mandrill group: (1) friendly behaviour (including those behaviours listed in Table 4); (2) friendly behaviour except grooming; (3) friendly behaviour except grooming, figure-eight mouth, and horizontal head shake; (4) grooming frequency; (5) grooming duration; (6) frequency of proximity; and (7) duration of proximity. Not one of these categories of friendly behaviour is correlated with my inter-related dominance indicators, regardless of whether frequency/duration of performing the behaviour or frequency/duration of receiving the behaviour is used as the measuring criterion.

Again, I suggest that the reason so many friendly behaviours have been linked to dominance is due to a widespread methodological error. This error involves delineating a dominance hierarchy on the basis of a single behaviour pattern, discovering a correlation between this behaviour pattern and a friendly behaviour such as grooming, and then

claiming that grooming patterns measure dominance without demonstrating a correlation between grooming patterns and each of the behaviours in an inter-correlated cluster that measures dominance. If "frequency of being groomed" is related to dominance, one expects to see this behaviour distributed throughout a group in a manner that correlates with all other dominance indicators. In fact, this is not the case for the mandrill data.

Statements like, "The most dominant animal is groomed the most," are frequent in the primatological literature and are potentially misleading because of the implied relation between dominance and "frequency of being groomed." Frequency of being groomed, unless it is distributed along a continuum throughout the group in a manner correlating with other measures of dominance, is not related to, nor is it an indicator of, dominance.

Frequency of Involvement in Interactions

Rowell (1966) related different measures of involvement in behavioural interactions to dominance. She also reported that Kummer had a subjective impression that high ranking animals took the initiative in social behaviour but was unable to test this impression with his data (Kummer 1956 quoted in Rowell 1966:439). "Number of initiated interactions", "number of interactions received", and "frequency of involvement in interactions as both initiator and

receptor" were calculated for each mandrill in the group. None of these factors correlated significantly with each of the other measures of dominance, and hence were not considered to be dominance indicators.

Ambiguous Behaviours

"Figure-eight mouth" and "horizontal head shake" were sufficiently peculiar behaviours to warrant the precaution of treating them separately from any higher level behaviour category. In the "figure-eight mouth" display, the lips were pulled apart at the corners exposing the molars, but met in the middle to cover the incisors. This display could occur separately, or in conjunction with horizontal head shaking. The simultaneous occurrence of these behaviours was originally interpreted as a threat gesture (Andrew 1963), probably because of the somewhat "ferocious" (from a human perspective) appearance of the display. However, this display had never been noticed to elicit or lead into attack. The horizontal head shaking, if interpreted as ritualized looking away movements (Radican 1975), supported the idea that this was not a threat display. More recent interpretation categorized this compound display as a type of fear grin (van Hooff 1969). Although I never observed this display as a direct response to aggression, it was frequently performed during avoidance. On the other hand, Willy and Mandy were observed to embrace and play

after Willy approached Mandy performing the "figure-eight mouth"/"horizontal head shake" display. At other times, this display gave rise to the same behaviour as in the performer or simply preceeded an approach that led to sitting together. Van Hooff (1969:33) suggested that "If the advertisement of a non-hostile motivational state in the performer results in a lowering of the tendency to flee in the partner, approach may become possible." Thus, he proposed a "reassuring function" of the "figure-eight mouth"/ "horizontal head shake" display (van Hooff 1962, cited in van Hooff, 1969:33).

During final correlation analysis, "figure-eight mouth" and "horizontal head shake" were treated separately, together, and lumped with the higher level friendly behaviour category. None of these behaviours were significantly correlated with the inter-related dominance indicators, regardless of whether frequency of performing, frequency of receiving, or direction of the behaviour was used as the measuring criterion.

General Discussion

Social dominance theory has been used to explain an almost limitless number of aspects of social organization, including maintenance of group cohesion, who grooms whom, who spends time with whom, who mates with whom, who leads whom, who has priority of access to food, water and sleeping

places, who avoids whom, etc. The following two quotations illustrate the pervasive influence primatologists have attributed to social dominance:

> The main characteristics of baboon social organization, as revealed in the Kenya and southern Africa studies, are derived from a complex dominance pattern among adult males that usually ensures stability and comparative peacefulness within the group, maximum protection for mothers and infants, and the highest probability that offspring will be fathered by the most dominant males (Hall and DeVore 1965:71).
>
> The dominance relations in Macaques as well as Baboons...are, therefore, conspicuous by being constantly present and influencing every aspect of behaviour (Chance 1956).

Since the time these statements were published, there has been a growing recognition that factors other than dominance contribute significantly to non-human primate social structure. In a 1968 review article, Gartlan outlines a number of problems confronting social dominance theory. Nonetheless, the concept of dominance continues to be widely employed, seldom with redefinition. Thus, use of the term dominance continues to imply a characteristic capable of explaining a wide variety of social behaviour.

This research attempts to determine which aspects of the behavioural repertoire are appropriately related to dominance. Of all the behaviours observed and recorded in this study, the following inter-correlated cluster is identified as measuring dominance: direction of aggression, frequency of performing submissive behaviour, direction of

submissive behaviour, frequency of receiving non-agonistic presents, direction of non-agonistic presents, and direction of non-agonistic avoidance. On the basis of these parameters, relative dominance rank is assessed, and the mandrills are arranged in a linear dominance hierarchy.

Applicability of This Research

An inevitable question arising at this point concerns the extent to which these research results apply to non-captive situations. First, to reiterate, the utility of social dominance theory depends on its ability to explain behaviour in more than one particular instance. This implies that several behaviours should indicate dominance, and that all should be correlated in the manner in which individuals are ranked. This study indicates that social dominance in a captive mandrill group explains only a relatively restricted range of behaviours, including agonistic interactions, non-agonistic approach-retreat behaviour, and non-agonistic presenting. Thus, although the mandrill group has a clear-cut dominance hierarchy, this concept only explains limited features of mandrill social organization. The major significance of the mandrill dominance hierarchy is that it provides a high degree of predictability for a limited number of behaviours.

The idea that captivity is responsible for the appearance of dominance hierarchies bears further investi-

gation since it may provide clues concerning the formation of dominance hierarchies. Strictly speaking, lack of a comparative data base due to methodological differences in assessing dominance makes it difficult to determine whether delineation of a dominance hierarchy is dependent on captivity. The major impetus to social dominance theory has come from early detection of dominance hierarchies in captive primate groups. Gartlan (1968) marshalls evidence suggesting that captivity produces severe social stress by increasing the frequency of aggression. On this basis he concludes that, "The behaviour exhibited in captivity and which permitted the construction of the social dominance hypothesis as a descriptive and explanatory concept may therefore be only indirectly related to the structure and behaviour of groups living under adequate environmental conditions in a habitat to which they are adapted" (Gartlan 1968:103). In response to this conclusion, one may legitimately question whether captivity per se is the decisive factor in producing observed behavioural differences. Many of these captive groups consist of individuals who are comparative strangers. This situation contrasts sharply with the normal, long-term relationships established between socially living primates. Southwick (1967) documents significant increases in frequency of aggression when social strangers are introduced in an established group of monkeys. Hence, social factors involving unfamiliarity of group members rather than captivity per se, may have been responsible for the increased

levels of aggression noted in the studies cited by Gartlan.

Other variables, such as distribution of food and overall space reduction, have been correlated with increased levels of aggression in captive primate groups (Southwick 1967). These results suggest that specific aspects of captivity, rather than captivity per se, may play the crucial role in whether or not behavioural differences are observed between captive and wild populations. Clearly, more controlled experimentation is required to elucidate the significance of different variables operating in captive situations. Results from such studies may radically alter our thoughts concerning the validity of captive/wild comparisons.

Since dominance hierarchies result in predictability of outcome of certain behavioural interactions, we should ask under what circumstances such predictability may be useful or at least expected to occur. The most clear-cut examples of dominance hierarchies (as measured by direction of agonistic encounters) come from two sources (see reviews of dominance by Gartlan 1968 and Bernstein 1970):

1. Non-captive observations of species thought to exhibit relatively high rates of aggression (e.g., various macaques and baboons), and
2. Captive situations, which in themselves are thought by some to increase rates of aggression.

The common element in these two sources suggests that relatively high frequencies of aggression are somehow

connected with the appearance of dominance hierarchies. The fact that dominance hierarchies occur in situations characterized by increased levels of aggression or increased social stress has been noted by several people (Gartlan 1968; Rowell 1966). This observation is typically used to devalue or discredit the whole concept of dominance (i.e., if dominance is produced under such unnatural conditions, it may be regarded as an abnormal, pathological response, or as Gartlan (1968:107) calls it, a "social artefact"). Dismissing the concept of social dominance in this fashion may be unwarranted. In the following discussion, I attempt to explore more fully the dominance concept and the possibility that dominance hierarchies may be an adaptive response to any situation, captive or wild, that is characterized by increased levels of aggression.

The criteria for measuring dominance in this study include measures of aggressive, submissive, presenting, and avoidance behaviours. Agonistic and avoidance behaviour appear to be widespread in the primate order. Such behaviours may vary in intensity, frequency and distribution. For example, aggressive behaviour may be of high or low intensity, occur very frequently or relatively rarely, and be distributed in a random or non-random fashion between group members. Theoretically, then, these behaviours can occur without contributing to the formation of a dominance hierarchy (i.e., without being distributed in a non-random fashion from which a hierarchical structure can be derived).

A variety of factors, including phylogenetic, ecological and social variables, may influence the intensity and frequency of agonistic behaviour. Phylogenetic affiliation has been implicated in accounting for similarities and differences in the frequency of agonistic behaviours. Richards (1974:926), for example, states that "Macaques have been reported to show more...fighting and submissive behaviour such as cringing and fear-grinning than other species." On the other hand, studies of ecological variability indicate that primate behaviour may be more habitat than species specific. Differences in frequency of aggression which correlate with habitat differences have been reported for Papio anubis (Peterson 1973), Macaca mulatta (Jay cited in Gartlan 1968; Southwick, Beg and Siddiqui 1965), Presbytis entellus (Compare Sugiyama 1965 and 1967 to Jay 1965), and Cercopithecus aethiops (Gartlan 1966). These results indicate that ecological differences may be correlated significantly with the differential expression of certain behaviours even in the same species.

In spite of the caution issued earlier, it is also possible that certain features of captivity may contribute to an increased frequency of aggression between group members. This assumption does not identify the specific causes of increased aggression (although certain possibilities have been noted), nor does it imply an increase in aggression relative to other types of behaviour. Indeed, Rowell (1967) documents an increased frequency in all types of social

interactions in a captive baboon group as compared to a wild group.

These observations on factors influencing the intensity and frequency of agonistic behaviour and the circumstances under which dominance hierarchies are most frequently detected suggest that increased rates of intra-group agonistic behaviour result in the formation of dominance hierarchies. Increased frequencies of agonistic behaviour provide more opportunities for learning which individuals one can or cannot aggress upon with impunity. This learning process may easily result in the non-random distribution of agonistic behaviour (and other associated behaviours) which constitute a dominance hierarchy.

Low frequencies of agonistic behaviour may: (1) either prevent the formation of a dominance hierarchy (not enough opportunities to learn who one should appease or avoid); or (2) inhibit the detection of dominance hierarchies (much longer period of fieldwork is necessary in order to detect direction of agonistic behaviours where frequency of agonism is low). The suggestion that increased frequency of agonistic behaviour results in the formation of dominance hierarchies is a testable hypothesis requiring quantitative assessment of agonistic behaviour in a variety of settings and a common approach for assessing dominance, such as that outlined in this study.

Rowell, while crediting the role of learning in establishing dominance relationships (Rowell 1974), also suggests an alternative to learning as a mechanism for establishing dominance hierarchies. She proposes that increased levels of stress work directly on all animals, producing greater physiological and behavioural changes in some than in others (Rowell 1966). This idea implies an internal mechanism which regulates physiological and behavioural response to stress, and which varies in sensitivity from individual to individual. Those animals having an extremely sensitive "stress-response mechanism" respond with subordinate behaviour and pathological physical symptoms. The subordinate behaviour, according to Rowell, is then responsible for "giving rise to a hierarchical social organization."

Although it is beyond the scope of this thesis to resolve whether learning or an internal stress response mechanism of Rowell's type explains the rise of dominance hierarchies, some comments are in order. An internal stress response mechanism of the type described by Rowell would be expected to operate on frequency rather than direction of behaviour, since directional response apparently involves individual recognition and a high component of learning. Since dominance indicators include more measures of direction than of frequency (see Figure 9), and since learning accounts for the ability to develop consistent direction-

dependent responses, learning would appear to be the major mechanism through which dominance hierarchies become established.

On the other hand, it is also possible that an internal stress response mechanism and learning operate sequentially in contributing to the formation of a dominance hierarchy. For example, a differential stress-response mechanism may allow the linear ordering of animals in a small group by producing behavioural changes, such as increased submissive behaviour, in stress-intolerant animals. Indeed, frequency of submissive behaviour is found to be a reliable dominance indicator in this study. Such behavioural changes on the part of stress-intolerant individuals may produce yielding behaviour from which stress-tolerant animals learn their own "superiority".

Only future research can ascertain whether an internal stress-response mechanism, learning, or some combination of the two is instrumental in establishing dominance hierarchies. Whether the hierarchies themselves constitute an "adaptive response" is a moot point. If a hierarchy does indeed significantly prolong the lifespan and increase the fertility of higher-ranking animals over lower ranking ones, then the higher ranking animals will have a selective advantage. It is worth emphasizing, however, that what is being selected for is not position in a hierarchy, but stress tolerance. Under selection pressures, the population will have increasingly greater proportions of stress tolerant animals if the trait is truly under some

genetic control. Hence, the ranking based initially on differential stress-response would be expected to disappear.

Another problem with trying to discuss the adaptive significance of dominance hierarchies is that it appears that many animals in a group occupy different positions in the hierarchy through the course of their lifetimes. Until the long term patterns of dominance status are fully explored, it is not possible to tell if the hierarchy would indeed increase the fitness of any individuals over others.

This study, of course, was not designed to test either theories concerning the cause of dominance hierarchies or their adaptiveness. What was done here was to establish methods and criteria for testing for the existence of dominance in a group of primates. This study found that the major significance of the dominance hierarchy was increased predictability of outcome of certain types of interactions. Any beneficial consequence deriving from a dominance hierarchy should be explained in terms of this increased predictability.

Perhaps, on the most general level, increased predictability of outcome of behavioural interactions enhances group adaptation in the following manner. Groups that experience increased levels of random agonistic interactions have their attention diverted from other, more productive, activities such as food-getting, child-rearing, and predator defense. Increasing the predictability

of outcome of agonistic interactions may mean that less attention is invested in "watching out for" aggressive behaviour on the part of other animals. Consequently, more attention may be invested in activities which increase the chances of that group parenting future generations.

CHAPTER IV

CONCLUSIONS

Dominance has been credited with influencing virtually every aspect of primate social organization, from the determination of troop movement to who associates with whom. The widespread influence attributed to social dominance, and the corresponding variety of behaviour patterns used to measure it, are most probably due to methodological errors in assessing dominance. Clearly, there should be a statistical correlation between different behaviour patterns that measure the same phenomenon, yet this correlation has not been demonstrated to exist between the variety of behaviours used to measure dominance.

One methodological error in assessing dominance lies in the subjective determination of dominance relations without supportive quantitative data. This approach undermines the basis for comparison since one person's assessment of dominance may be based on entirely different subjective criteria than those employed by another. Furthermore, subjective determination provides too much leeway for inconsistent application of the criteria used to assess dominance.

A second source of error in the assessment of dominance arises as follows. First, a researcher uses one behavioural criterion to measure dominance rather than delineating the inter-correlated cluster of behaviours of which the one behavioural criterion is a part. Next, the researcher discovers a correlation between the first behavioural criterion and a second behaviour pattern. On the basis of this correlation, the researcher claims that the second behaviour pattern also measures dominance. This is a clear methodological problem for two reasons. First, a rank order based on a single behavioural criterion should not be confused with a "dominance hierarchy". Rather, dominance hierarchies should be delineated on the basis of a cluster of inter-correlated behaviours, one of which is the ability to aggress on an individual without receiving an aggressive response. Second, even if the first behaviour used by the researcher above is part of a behavioural cluster indicating dominance, proof is provided only for correlation of behaviours 1 and the cluster, and 1 and 2. As shown in this study, although one may expect behaviour 2 and the cluster also to be correlated, this does not necessarily follow. Any claims for behaviours being dominance indicators must, therefore, rest on demonstrated inter-correlations between such behaviours.

A third source of error in the assessment of dominance arises from a misleading type of statement that

appears with great frequency in the primate literature. An example of this type of statement is that "the most dominant animal receives the most grooming." The fact that one animal receives more grooming than another is appropriately related to dominance (as implied in the statement above) only if frequency of being groomed is distributed throughout the group in a manner correlating with the demonstrated cluster of behaviours that measure dominance.

A combination of these different sources of error is undoubtedly responsible for the wide variety of behaviours that are claimed to be related to dominance, and the resulting conception that dominance is a pervasive element in determining social organization. Results from this study indicate that such conclusions are unwarranted, and that the primary significance of social dominance lies in conferring predictability to certain limited types of behavioural interactions, including agonistic encounters, non-agonistic approach-retreat behaviour and non-agonistic presenting.

The present study was undertaken both because of a curiosity about mandrill behaviour and from a desire to resolve some of the confusion surrounding the concept of dominance. The choice of this species was not completely idiosyncratic, for one study had claimed the existence of dominance in a captive mandrill group (Emory 1975). The initial approach to the problem required a formal definition of dominance. In this study, dominance was defined

operationally as the ability to aggress on an individual without that individual responding with aggression. Second, an objective approach for detecting dominance indicators was applied. This approach resulted in the identification of a cluster of behaviours measuring dominance. On the basis of these dominance indicators, a dominance hierarchy was constructed for the mandrill group.

This research succeeds in delineating specific dominance relationships in a captive group of mandrills. The types of behaviour used to predict these relationships are somewhat more restricted than the long list of behaviours that are often thought to indicate dominance. It is possible that, given more adequate research conditions, other behaviours such as priority of access may be added to the list of dominance indicators in captive mandrills. Whether a relationship holds between these research results and conditions of non-captivity remains to be ascertained.

With respect to the role of dominance in the broader primate context, the hypothesis detailed below is advanced. It is based on the observation that dominance hierarchies are most commonly found in situations where aggression is relatively frequent. Increased frequency of intragroup agonistic behaviours, regardless of the source of such behaviour, results in the formation of dominance hierarchies. Two mechanisms through which such dominance hierarchies may become established are identified as: (1) learning; and

(2) an internal stress response mechanism. Whether learning, an internal stress response mechanism, or some combination of the two is responsible for establishing dominance hierarchies is an area for future research. Results from this study suggest that while an internal stress response mechanism may initiate rank differences, learning is probably the major mechanism through which dominance hierarchies are established and maintained.

NOTES

1. Besides the BEVRECS data sets, an Orientation Data Set was compiled during the course of this study. The head and body orientation of individuals toward other group members have been related to dominance (Emory 1975, 1976). The purpose of the Orientation Data Set was to record such orientational information so that its relationship to other measures of dominance could be tested.

   A total of 24.75 hours of observation were spent collecting data on head and body orientation. Due to lack of time, this orientation data is not analyzed or discussed in the present report.

2. Unless otherwise stated, all computer analysis was carried out using SPSS (Nie, et.al., 1975) procedures and programs.

3. An explanatory note is necessary regarding the difference in determining top rank when submissive vs. aggressive behaviours are being analyzed. The concept of dominance implies power and influence. Consequently, the winner in an agonistic interaction is deemed more dominant, or more powerful, and receives a higher rank than the loser, who is regarded as less dominant. When the frequency, rather than direction, of all agonistic interactions are considered, the individual performing the most aggressive behaviours would rank highest (i.e., be the most dominant or powerful) while the individual performing the most submissive behaviour would rank lowest (i.e., be the least dominant).

4. Chasing occurs in playful as well as agonistic contexts. However, play behaviour was rarely observed between adult mandrills, and I never saw chasing as a component of adult play. These facts reduce the amount of potential error in classifying "chasing" as an aggressive behaviour.

5. The idea of viewing "presenting" as complementary to, rather than the opposite of aggression was expressed by Susan Hornshaw in one of our early, pre-data analysis, discussions of this material. I am grateful to Susan for this insight, one which my own data supports.

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APPENDIX: BEHAVIOUR UNIT DEFNITIONS

BEHAVIOUR UNIT	DEFINITION
avoidance (agonistic)	to walk away from an animal in response to receiving an aggressive behaviour from that animal
avoidance (non-agonistic)	to walk quietly out of the way of an approaching animal who shows no observable signs of aggression
bite	sink teeth into the coat or skin of another individual
chase	run after an individual
defecate	in response to receiving aggressive behaviour from another individual
display jump	repeated jumping or bouncing action on ground or branches; head usually tucked into chest
embrace	place arms around and hug another individual
figure-eight mouth	lips are pulled apart at corners exposing teeth but meet in the middle to cover the incisors
glass jump	animal takes flying leap at plexiglass wall and rebounds off of wall producing loud smacking noise
grab	grasp and seize another individual
grab (attempted)	to make a grasping motion toward another individual without making contact with that individual

BEHAVIOUR UNIT	DEFINITION
groom	to tend another individual's coat and skin with characteristic picking, combing and/or brushing movement of the groomer's hands and mouth; this activity had to last for greater than or equal to three seconds to be recorded as grooming
groom time	duration of a grooming bout between two animals
handle genitals	touch another individual's genitals
hit	strike another individual
horizontal head shake	shake head back and forth in a horizontal plane
lunge	sudden forward movement or starting motion toward another animal
nose to face	place nose within three inches of another individual's mouth or face.
nose to perineum	place nose within two inches of another individual's perineum
present (agonistic)	direct hindquarters toward another individual in response to that individual's aggressive behaviour
present (non-agonistic)	direct hindquarters toward another individual while crouching to some degree; this behaviour pattern is not in response to an aggressive behaviour
proximity	to be two feet or less from another individual for at least three seconds with no other activity (e.g., grooming) taking place

BEHAVIOUR UNIT	DEFINITION
proximity time	amount of time two animals spend two feet or less from each other
push	place hand(s) on another individual and press him/her away
raise crest	erection of hair along midline of scalp to form a peak
relax open mouth	relaxed facial features with widely opened mouth; lips usually cover teeth
run away from	rapid fleeing action
squeal	rapidly repeated, high-pitched, shrill cry
stare	look fixedly at someone with tensed facial features
touch	place hand on any part of another individual's body except the genitals
vertical head bob	shake head up and down in a vertical plane