BEHAVIOUR, BIOLOGY AND THE SOCIAL CONDITION OF *CERCOPITHECUS AETHIOPS* : THE VERVET MONKEY.

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ABSTRACT

Biotelemetry has been coupled with an ethological approach to investigate a postulate that the physiological, behavioural, and social functioning of individuals coact in order to maintain homeostasis in an everchanging environment. Attention was focussed upon body temperature, behaviour, and the social situation, as they occurred together in each of five 'undisturbed' adult vervet monkeys. One male and one female were housed alone in single cages, and the other three, all females, were part of a natural troop that live together in captivity in a 6.5 metre radius geodesic dome.

Intensive studies, including in-depth and multiple repeated measures at each level of functioning permitted comparisons between and within subjects, so that the connections between body temperature, and individual and social behaviour, could be scrutinised. Techniques for observation, data processing, and factor analysis have been considered, and procedures to facilitate the organisation and interpretation of information are suggested.

The results pointed to individual variations superimposed upon a rhythmic underpinning of all the functions monitored. A synthesis of the data of body temperature with individual and social behaviour supports the contention that the individual responds to the vagaries of the environment as an integrated system within which the different levels of functioning are linked. It was found that the oscillation in body temperature was greater in the vervets that lived alone than in the vervets that lived in a troop. These results were supported behaviourally since the isolated subjects could only complement autonomic thermoregulatory responses with individually based behavioural strategies, whereas their troop-living conspecifics could utilise both individual and socially directed behavioural mechanisms. Within the troop an inverse relationship between body temperature variation and social status was revealed – that is, the lower the status of the subject, the more the body temperature fluctuated around the mean. Behaviourally, it was found that the lower the status of the subject, the more difficult it became to gain access to resources, and to manipulate interpersonal space. In addition, harassment by troop

conspecifics increased and, consequently, the efficiency with which behavioural patterns could be executed, was decreased.

An analysis of the data also led to the proposal that social grooming has evolved as a thermoregulatory mechanism; to the identification of three different facets of individual behaviour and of social behaviour; and to the idea that the rhythmic changes in the troop's spatial conformation reflected cyclical patterns in behavioural and social activity.

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CHAPTER   ONE

INTRODUCTION

The world's a scene of changes, and to be constant,
in Nature were inconstancy.

A. Cowley.

Cercopithecus aethiops pygerythrus, or the vervet monkey, is part
of Durban's indigenous fauna.   The animal is particularly interesting to
man.   Being a primate, it belongs to the same biological group as we do.
Furthermore, it is believed that vervet behaviour, as presently understood,
parallels a critical phase in the story of our past.   Like early man, this
monkey has left the forest, and typically inhabits a forest edge
environment.   Viewed within an evolutionary framework the vervet's
progression from forest to forest edge has been most successful.
"*Cercopithecus* is the most widely ranging primate genus in Africa ...
Because it is able to tolerate more arid environments, *Cercopithecus
aethiops* has the widest distribution of all *Cercopithecus* species"
(Napier, 1981: 88).   The adaptability of the vervet has been accounted
for in terms of anatomical generalisation, relative lack of sexual
dimorphism, behavioural flexibility and the versatility of the social
organisation (e.g. Gartlan and Brain, 1968; Chance and Jolly, 1970;
Rosen, 1974; Tollman, 1981).

The vervet monkey, in common with all the higher primates, including
man, is committed to living in social groups (Lancaster, 1975).   Life in
social groups, according to Kummer (1971b), represents the strong point
of primate adaptation, as it enables its members to meet the demands of
the environment.   Rowell (1979) reinforced this point by declaring that
it is obvious to anyone watching monkeys that it is subjectively very
important to the individual to be part of a group.   Crook drew attention
to the importance of understanding "the social processes operating in
groups which constitute the social environment of the individuals.   Thus,
individual behaviour evolves not only within a physical but also within a

social environment ... The addition of this social dimension to the ethological analysis of behaviour is relatively recent and its full implications need working out" (1978: 59).

No matter whether the gene, the individual or the group is the unit of selection, the behaviour and the physiological functioning of the primate must have evolved within a social context and, it is suggested, these factors are linked. This means that an understanding of the behaviour of an individual is contingent upon the knowledge not only of the physiological status, but also of the social status of that individual. Rubenstein focussed upon individual differences: "a principle so central to evolution – that individuals are different – has largely been omitted from evolutionary theory" (1982: 88). But – how do physiological, behavioural and social functioning interact in one individual? – and what are the idiosyncratic features that would lead to individual differences?

This dissertation commences by describing the background to the study which attempts to examine the relationships between a physiological variable, body temperature, behaviour and the social condition of *Cercopithecus aethiops pygerythrus.* It spans a period of five years during which vervet observations and theorising led to the formulation of the thesis – that physiological, behavioural and social functioning are interrelated. The research setting, the vervets and their suitability as models for studying the variables under scrutiny are considered in Chapter Three. Evidence is presented which points to the vervet monkey as a promising target for study, and to Durban as an ideal locale for pursuing such research. The research objectives are formally presented in Chapter Four. Five monkeys were studied intensively, social conditions were contrasted by monitoring two animals living alone in single cages, and three as part of a troop, and Chapters Five, Six and Seven probe in detail body temperature, behaviour and social functioning respectively. In Chapter Eight, these three levels of functioning are synthesised and, it is argued, the individual differences in behaviour, and in the social condition, supported the direction of the individual variations that were exhibited in body temperature. Chapters Nine and Ten review the thesis by evaluating the research, pointing to its pioneering nature, and summarising the project.

CHAPTER TWO

THE BACKGROUND TO THE STUDY

An understanding of the behaviour of an individual is contingent
upon the knowledge not only of the biological status, but also of
the social status of that individual.

Tollman, 1983: 2

2.1 INTRODUCTION.

Ten years of vervet observation and theorising led the author to
formulate the assertion quoted above, and to the theme of this thesis:
the contention that behavioural, physiological and social functioning are
interrelated.   The following studies provided the background to the
development of this proposition, and to the execution of the research
project which is the subject of this thesis;   that is, an in-depth analysis
of body temperature and thermoregulation, with the accompanying
behavioural and social functioning in five adult vervet monkeys.   The
full text of the studies that have been published, in addition to a
videotape illustrating these studies and including the body temperature
analyses is available, upon request, from the Department of Psychology,
University of Natal, Durban.

2.2 STUDY OF STRATEGIES FOR ADAPTATION.

The research began with an interest in the process of adaptation.
In 1975, two questions were asked:

1.   What are the strategies employed by vervet monkeys when
they deal with an unfamiliar situation?

2.   How does the process of adaptation take place?

In order to answer these questions a free-ranging troop of vervets was
intensively studied for three months and then captured and caged in a

6,5 metre radius geodesic dome situated in the territory of another wild troop (see Tollman and Lucas, 1979, and Chapter Three). Behaviour was monitored continuously day and night from the moment of capture, until adaptation to the novel environment appeared to have been effected – three months later.

The data from this study was selected for publication in the **Proceedings of the International Primatological Conference** in 1981. The following are extracts from the conclusions:

> The success of the vervet may, in part, be due to the versatility of the troop's social organisation where the social structure varies with the environmental characteristics – adverse conditions promoting cohesiveness and favourable circumstances producing diversity of behavioural activities. (p. 51.)
>
> The behavioural mechanisms elicited upon caging were significant increases in proximity by reduction of interpersonal distances (p <.002: sign test); increased physical contact (p <.002: sign test) and social facilitation (p <.02: sign test) as well as a significant decrease in intratroop agonism (p <.002: sign test). The troop seemed initially to function as one organism. (p. 46.)
>
> Thus unity within the troop in order to meet any contingency seemed maximised and disruptive factors were decreased. (p. 49.)

Upon caging, the troop members huddled together.

> During this huddling phase movement was minimal – faeces were liquid and smelly, and the vervets went to sleep far later than in the field. It seemed that the vervets were clustered together in a state of heightened vigilance, and physical preparedness. (p. 47.)

Clearly the change in circumstance elicited behavioural, social and physiological changes. However, in the same way that the behavioural changes seemed to increase individual power by promoting social co-operation and thereby enhancing the chances of collective action if necessary, it is suggested that the social behaviour elicited (e.g. huddling) also served to promote physiological homeostasis which had been disturbed.

During adaptation

Several differentiated activity profiles related to sex, age and
status variables were exhibited. (p. 165.)

Each caste within the caged troop's social organisation contributed
a link toward the process of adaptation. (p. 176.)

The hypothesised roles are described in an unpublished M.Sc.
Thesis (1977).

A point of particular interest which was subsequently scrutinised was
the unexpected disintegration of the adult male when placed in an
unpredictable situation.   It was hypothesised that:

The capacity and flexibility of the female to fulfill a wide spectrum
of roles may free the adult male to act as the "sensor" of environmental
conditions and, by being a focus for the troop, to direct the unit's
responses in relation to the prevailing environmental conditions.   The
transition of the male from outgoing leader to withdrawn submissiveness
served as a signal for all troop members to huddle together, to enhance
their attention toward one another, and to increase their level of
awareness, so that the troop became consolidated as a single, united
entity to deal with an unpredictable situation. (p. 51.)

Behaviour therefore varied according to biological status (e.g. age
and sex), and it became increasingly apparent that this appears to have
social advantages.   Each individual within a troop is able to benefit from
a collective behavioural repertoire – a more extensive and varied set of
behavioural responses than that of any single animal.

2.3   STUDY OF FEEDING BEHAVIOUR: A BIOLOGICAL NECESSITY.

Vervet feeding behaviour is described as 'solitary', 'messy', and
'wasteful'.   The author has reasoned that this feeding pattern is, in
fact, a socially adaptive mechanism, because

1. Despite the apparent existence of a linear hierarchy for access
   to food, the animals of lower status within the troop are given
   an opportunity to feed because their superior conspecifics
   distribute food throughout the territory as they 'spit', 'break'
   and 'drop' the food.

2. Food distribution facilitates the simultaneous feeding of the
   majority of troop members from an initially localised source.
   This can be seen as efficient in relation to factors such as the
   time taken to exploit that source, optimal foraging and predation.
3. The breaking of portions of food into progressively smaller
   pieces enables infants to obtain food of a size which they can
   manipulate and carry.

Together with Simpson, a study comparing the caged troop's feeding
behaviour with that of a free-ranging troop was conducted.   Statistical
support confirmed the hypotheses, which are further elaborated in a
published article entitled "An examination of the apparently 'wasteful'
feeding behaviour in *Cercopithecus aethiops:* a new perspective?"
(Tollman and Simpson, 1975).

Thus feeding behaviour also involves biological, psychological and
social factors.

2.4   INFORMAL STUDY OF ECOLOGY AND BEHAVIOUR.

The troop of vervets in captivity have been developing specific
behavioural modifications in response to the particular ecology of the cage.
As a consequence of the continual presence of two shallow pools of water,
the vervets now moisten their bread before eating it – a phenomenon
not seen when they lived in the field.   This behaviour was introduced
shortly after caging when a subadult retrieved a slice of bread that had
accidentally fallen into the water.   This incident illustrates the dynamism
of vervet behaviour, which adapts to the specific environmental circumstances,
and therefore varies according to the ecology.

2.5 PRELIMINARY STUDY OF PSYCHOLOGY, PHYSIOLOGY AND THE SOCIAL GROUP.

> My scheme simply suggests that a monkey is selected and conditioned to
> see his fitness-related goals in a social landscape of conspecifics
> which to him are resources as well as impediments.

> Kummer, 1979: 42.

At this point, the present researcher shifted her attention from the group to the individual and the relationship between deep body temperature (T_b) fluctuations, behaviour and the social group.

The adult female vervet was the subject chosen for study.   She seemed to display "a capacity for behavioural flexibility which is not present in the male" (Tollman, 1981: 50).   In addition:

> individual female activity profiles varied considerably and a subtle
> distinction between females with infants and those without appeared
> detectable (Tollman, 1977: 168).

Furthermore it seemed (but the author has not verified this) that ongoing female behaviour, because of this change in state, was less predictable than that of the male.   The questions that arose were:

1. To what extent are these behavioural changes biologically influenced?

2. Are they related to different stages in the menstrual cycle?

These two questions were the original aims of the study.

Biotelemetry and the advantages of longlived temperature sensitive transmitters were exploited, as the author and her then supervisor, Mr John Lucas, argued that internal temperature changes during ovulation would occur in vervets, as with humans.   The caged troop were well established (Tollman and Lucas, 1979), so body functioning could be studied in parallel with ongoing behaviour in a social group.   The presence of single cages nearby meant that the internal body temperature of monkeys living alone could also be monitored.

Temperature sensitive transmitters were implanted in the peritoneal cavity of the experimental animals.   During the pilot run (two vervets caged singly), it was discovered that the temperature fluctuations over the

day were larger and more complicated than expected. It also seemed that the temperature changes brought about by the unrestrained daily activity mask any subtle changes that may occur during ovulation. Upon enquiry, Dr Clough, the Head of the Department of Environmental Physiology at the Medical Research Council in England in 1979, wrote that he had not been able to find any references concerning the deep body temperature fluctuations of vervet monkeys. It was clear that this was to be an original investigation, and it was necessary to begin at the beginning.

2.6 CONCLUDING COMMENT.

In order to survive, the individual must adapt to the surroundings – that is, homeostasis must be achieved. Since the individual functions as a whole being, incorporating a physiological, a psychological and a social level, it is contended that these levels are interrelated, and therefore the environment influences a dynamic and complex system. The vervet studies that have been described seem to support the notion of an interplay between an everchanging environment and the responses of the individual. It seems important, therefore, to probe the total situation, and to study the ongoing behavioural and physiological functioning of individuals as they occur together within a social context.

CHAPTER   THREE

THE   SUBJECTS   AND   THE RESEARCH   ENVIRONMENT

3.1   INTRODUCTION.

The vervet monkey, *Cercopithecus aethiops pygerythrus*, is the model used for this research enquiry.   The observations were conducted over a period of eight years at the University of Natal in Durban where a 'natural' troop was captured by the author and caged in a carefully designed 6.5 metre radius geodesic dome which allowed for all the activities seen in the field, except movements over long distances but including hiding places and intertroop encounters.   Since these primates are indigenous to Natal and enjoy protection in several areas, it was possible to watch free-ranging troops, and capture and cage single monkeys or groups of monkeys if necessary.

In this chapter, *Cercopithecus aethiops pygerythrus* is put into context, its appropriateness for the study of *Homo sapiens* is discussed, and then the research subjects and their environment is described.

3.2   *CERCOPITHECUS   AETHIOPS   PYGERYTHRUS.*

3.2.1 Classification.

> While the primates comprise only one of the several orders into which
> the class of mammals is divided, the group is of surpassing significance
> because man himself is classified with this order.
>
> J.H. Crook, 1980: 60.

In 1981, Prudence Napier modified the well-known classification documented by Professor J.H. Napier and herself in 1967, and described the following for *Cercopithecus aethiops*.

ORDER	Primates	Linnaeus	1758
SUBORDER	Anthropoidea	Mivart	1864
SUPERFAMILY	Cercopithecoidea	Gray	1821
FAMILY	Cercopithecidae	Gray	1821
SUBFAMILY	Cercopithecinae	Gray	1825
TRIBE	Cercopithecini	Gray	1821
GENUS	Cercopithecus	Linnaeus	1759

(Guenons: The use of the name Cercopithecus for guenons was validated in 1954 by the International Commission on Zoological Nomenclature)

SPECIES GROUP   Cercopithecus aethiops   Linnaeus   1758

(8 groups are identified)

Napier now recognised a single species and she cited Schwarz (1926), G.M. Allen (1939) and Thorrington and Groves (1970) as providing her model. She divided the numerous subspecies into four groups following Dandelot (1971). These were:

Northern:

C. aethiops sabaeus group	Green monkey	1 subspecies
C. aethiops tantalus group	Tantalus monkey	3 subspecies
C. aethiops aethiops group	Grivet	4 subspecies

Southern:

C. aethiops pygerythrus group	Vervet	14 subspecies

(Napier, 1981: 149).

Thus the vervet in our study belongs to the *Cercopithecus aethiops pygerythrus* subspecies group.

Napier asserted that the taxonomic list of 1981 must not be regarded as a revision or formal reclassification of the 'classic' systematic list of Napier and Napier (1967), but rather as a "worthy arrangement, the result of five years of data input, which not unexpectedly shows some inconsistencies" (p. IX). Schrier and Stollnitz no doubt concur because they complained in 1971 that problems had arisen since Napier and Napier split groups of similar animals into different species rather than leaving

them as subspecies. "This was especially true with the *aethiops* group of guenons *(Cercopithecus sp.)*. Evidently what most field and laboratory researchers have called interchangeably 'green monkeys' or 'vervets' and have designated as *Cercopithecus aethiops* may be subdivided into *C. aethiops, C. pygerythrus* and *C. sabaeus*" (Napier and Napier, 1967: XI). *C. aethiops tantalus* was not mentioned. Gartlan and Brain, in 1968, defended the use of the concept 'subspecies' in order to impose "what must be regarded as essentially an arbitrary boundary on what is in effect a cline" (p. 254). Following Dandelot (1959), they wrote that *C. aethiops* contains five subspecies, *C.a. aethiops Linnaeus, C.a. tantalus Ogilby, C.a. sabaeus Scopoli, C.a. pygerythrus Cuvier,* and *C.a. cynosurus Scopoli.* Napier points to the difficulties in classification of *C.a. cynosurus Scopoli.* She wrote: "another form which is difficult to classify satisfactorily. Dandelot formerly considered it a separate species (1959) but Hill (1966) and latterly Dandelot (1971) relegated it to subspecific rank in the species *C. aethiops pygerythrus*" (p. 150). She explained that within the *C. aethiops pygerythrus* group it is extremely difficult to decide how many races should be recognised since the characters involved are mainly those of colour, and one race blends imperceptibly with another. Schwartz, Tattersall and Eldredge (1978) asserted that not enough attention has been given to the systematic significance of details of the morphology of the anthropoids. They stated that "currently available information is inadequate to the task of reconstructing evolutionary relationships within this group of mammals" (p. 128). Napier (1981) acknowledged Dandelot's (1959) suggestion that the confusion was mainly due to a failure of the taxonomists to study living animals. Museum specimens are often lacking just those portions of their anatomy (head, face, foot and tailtip) that are necessary to make a proper identification. Furthermore, written descriptions involving colour are a difficulty – the green monkey is not in fact green at all, even though it may look green in the wild.

Clearly, the categorisation of *Cercopithecus aethiops* and its subspecies needs further clarification.

3.2.2 Habitat, and the adaptability of the vervet monkey.

> Cercopithecus is the most widely ranging primate genus in Africa ...
> Because it is able to tolerate more arid environments, Cercopithecus
> aethiops has the widest distribution of all Cercopithecus species.
>
> Napier, 1981: 88.

Cercopithecus monkeys have only been found in Africa, and have been
described as the most abundant monkeys on the continent (Tappen, 1960;
Struhsaker, 1967b; Napier, 1981).   The *C. aethiops pygerythrus* group
extends from Ethiopia to the Cape of Good Hope, and exhibits a wide
environmental tolerance as they have successfully exploited environments of
all types between the extremes of forest and grassland, and between high
rainfall and semi-arid regions (Washburn and Hamburg, 1965; Chance and
Jolly, 1970; Poirier, 1972; Rosen, 1974; Lancaster, 1975; Kavanagh,
1980; Barnett, 1981; etc.).   Only a few primates live in the extensive
savanna biome of Africa which supports a great diversity of vegetation
types.   These include two species of *Galago,* baboons *(Papio)*, the vervet
monkey *Cercopithecus aethiops,* and the patas monkey *C. (Erythrocebus)
patas,* all species that forage to a greater or lesser extent on the ground
(Bigalke, 1978).   The vervet tends to use the fringes of the forest,
especially where these adjoin grassland, and the adaptive significance of
exploiting this ecological niche along the Orange River in South Africa was
pointed out by Gartlan and Brain in 1968.   The lower 200 miles of this
river flows through arid countryside so impoverished that no monkey could
exist.   By remaining in the narrow strip of riverine vegetation *C. aethiops*
extend to the sea.   Despite the diversity of vervet habitats, Cheney and
Seyfarth (1981) noted that they are generally more open than primary
forest, affording greater visibility, but exposing the monkeys to increased
predation.

Each ecological condition brings its own set of problems and it seems
that there is a link between primate social organisations and habitat.   In
1966 Crook and Gartlan, on the basis of the available field data, classified
the primates into five grades of socioecological adaptation, on the basis
that "as insectivorous primates radiated within the forest, they took to
fruit-eating and became diurnal" (Crook, 1980: 63).   Two main selective

pressures operated during the evolution of terrestrial open-country monkeys, according to Crook: predation and food. These researchers categorised *Cercopithecus aethiops* in Group IV: "Forest fringe, tree savannah". Group V, at the terrestrial extreme, consists of the patas monkey and hamadryas and gelada baboons and their habitat is described as "grassland or arid savannah" (Crook, 1980: 62). Krebs and Davies (1981) criticised this scheme. They maintained that variation in features such as home range, size, and group size, is continuous and so division into discrete groups becomes arbitrary. In addition they pointed out that different aspects of social organisation such as breeding system and group size do not vary together in the same way. According to Krebs and Davies (1981), the most recent attempt to unravel the complex relationship between social organisation and habitat has been by Clutton-Brock and Harvey (1979). These researchers, like Gartlan and Brain, considered group size as a variable, and sought for correlations with ecology. Richard Wrangham (1980) suggested, however, that simply considering group size is naive because there are many different kinds of primate groups. He pointed to the fact that males and females have different investments within a group. He has proposed that strong female bonds occur in groups where the species is exploiting food supplies distributed in discrete defensible patterns and cooperation for defence is necessary, and looser female relationships exist in species that feed on food supplies such as leaves or stems which tend to be more evenly distributed throughout the territory. This hypothesis suggests that ecological variables not only influence group size but also the kind of relationships within a group.

Anatomical data attempting to explain the adaptability of the vervet was presented by Jolly in 1963. He compared the length of the vervet's limbs with those of other guenons. He found that the vervet's upper arm length is different from that of the more arboreal species *Cercopithecus mitis*, but similar to the patas monkey of the dry savanna country, *Erythrocebus patas*. The lower arm length, however, is different from the patas monkey, but similar to *Cercopithecus mitis*. Further research by Gartlan and Brain (1968) revealed that the vervet is anatomically intermediate between these two more specialised species, that is, the forest species *Cercopithecus mitis* and the terrestrial species *Erythrocebus patas*, and it is this generalised structure which enables the vervet to deal

with a variety of environments. Gartlan and Brain (1968) theorised that the vervet is physically adapted for a wide and variable environment because of its "anatomical generality and relative lack of sexual dimorphism" (p. 259). These researchers also pointed to "a flexible social system, the origin of which is presumed to have been the need for efficient exploitation of the proliferating savannas during the Pleistocene" (p. 290).

Further evidence for the versatility of the social organisation of *Cercopithecus aethiops* was described by the author in 1981. She found that the social structure varied according to environmental characteristics – adverse conditions promoted cohesiveness and favourable circumstances produced diversity of behavioural activities. Barash (1979) explained that "fitness is relative to the environment and the environment is always changing" (p. 24). The flexibility of the vervet thus enhances its survival in varying environments.

3.2.3 The appropriateness of *Cercopithecus aethiops* for the study of *Homo sapiens*.

> ... when we study nonhuman primates we are but one step removed
> from the study of ourselves.
>
> Rasmussen, 1981: 96.

The importance of studying animals to understand ourselves seems irrefutable since the publication on November 24, 1859, of **On the origin of species.** Charles Darwin's convincing demonstration that all living things are as they are because they have become what they are, and that change and not immutability is the rule of living things is one of the most important contributions ever made to knowledge (de Beer, 1964). Because man is now considered to be biologically and behaviourally continuous with other animals, differing from them only as one species differs from another, it seems that much is to be gained from understanding both the evolutionary background and the ecological setting.

The primates are currently being studied at almost every level of

enquiry. Held (1981) stated: "These animals are especially valued because of their evolutionary kinship to man, both in gross anatomical resemblance and behavior as well as in specific biochemical similarities. Because of this close relationship, biomedical and behavioral studies of nonhuman primates offer particular insight into parallel situations in man" (p. 27). Further support is to be found in many articles and books (e.g. Washburn and Harding, 1970; Lancaster, 1975; Zaneveld, Bhattacharya, Kim, Schumacher and Beluhan, 1977; Bernstein, 1978; Crook, 1978; Essock and Dumbaugh, 1978; Jayaraman, Hurkadli and Gopalakrishnan, 1978). Wilson (1978) commented on the use of primates to study the effects of applied environmental influences such as drugs and other chemicals on intrauterine development. He reflected the concern, particularly since the Thalidomide debate, of the inability of the conventional laboratory animals to predict "with any degree of certainty potential embryotoxic hazards" (p. 255).

King (1980) pointed to a controversy that exists over the reconstruction of early hominoid behaviour. Some researchers strongly emphasise carnivores, others the exclusive use of nonhuman primates, for providing the clues. King has concluded that this argument should "give way to discussions of how best to coordinate the data from these two valuable sources of inference" (p. 99). *Cercopithecus aethiops*, the vervet monkey, is particularly interesting to man. Being a primate, it belongs to the same biological group as we do - and like the majority of the primates it is committed to life in social groups. Furthermore, this monkey, like early man, has left the forest and typically inhabits a forest edge environment. The vervet as presently understood, therefore, parallels a critical phase in the story of our past. Physiologically, the vervet monkey may be the model of choice for studying steroid excretion during the reproductive cycle and in pregnancy. Setchell, Bull and Adlercreutz (1980) have concluded that "initial studies of steroid excretion by the vervet monkey *(Cercopithecus aethiops pygerythrus)* indicate much closer similarities to humans than any other species of Old World monkeys previously studied" (p. 375). Their paper includes specific comparisons with rats; marmosets; squirrel, aotus and rhesus monkeys; and the baboon. Since steroid excretion is rhythmic this finding is encouraging for investigations such as body temperature, which also display a rhythmic pattern.

One of the most serious questions to arise when comparing animal behaviours and when generalising from the animals to humans is whether the behaviour in question is homologous or analogous; that is, can the behaviour be traced back to a common ancestor, or is the behaviour which appears similar not derived from a common evolutionary background and, therefore, unlikely to be based on the same mechanisms in the different species? Convergence, according to Atz (1967), is prevalent because of intense selection pressures as well as limited possible responses by the animals. He actually enquired whether the process of homologising behaviour is legitimate. Homologous structures can be shown to be similar, and similarity in structure may carry over to the functional level. On the other hand, the connection between behaviour and a specific part of the nervous system is not only extremely tenuous because of lack of knowledge, but behaviour is habitually treated as an abstraction without any reference to structure. Atz concluded by stating that to deny that homologous behaviour exists would seem to deny that behaviour is subject to evolutionary change – the concept of homology is continuity in phylogeny, and this must hold for behaviour as well as for structure. Clearly caution must be exercised to avoid naive extrapolations.

3.3   THE RESEARCH SUBJECTS.

On June 10, 1975, eleven vervet monkeys were successfully removed from a free-ranging troop living at Beachwood Golf Course, tagged and caged in an enriched 6.5 metre radius geodesic dome organised by the author. The entire removal and reinstatement process was executed within one hour (see Tollman and Lucas, 1979).

These monkeys, classified as *Cercopithecus aethiops pygerythrus*, have been the major focus in this research project. The troop still inhabits the dome, which is in the open and allows for all the behaviours seen in the field, including hiding places and intertroop encounters, and excludes only troop movements. Although familial bonds among the captured animals remained intact, the composition upon capture was changed as follows:-

TABLE 3.1

CHANGE IN TROOP COMPOSITION UPON CAGING

CATEGORY	FREE-RANGING TROOP	CAGED TROOP
Adult male	2	1
Adult female	9	5
Immature vervets	25	3
Infants	4	2
TOTAL	40	11

All the animals captured were healthy specimens. A detailed description of the procedure used for trapping and tagging, the capturing sequence, and their physical description have been recorded in the author's unpublished M.Sc. Thesis (1977). Both the Beachwood Golf Course and the University of Natal Gardens fall within the Durban Metropolitan Area, and are separated by a distance of 17 km. All the subjects studied were captured from the Durban area and medically examined by the Natal Institute of Immunology. The behaviour of the caged monkeys was compared to that of free-ranging troops dwelling at Burman Bush, a 45,43 hectare protected park (refer to Figure 3.1, a locality map).

3.4   THE RESEARCH AREA : DURBAN, NATAL.

Position: Latitude   29° 57   South
                Longitude   30° 59   East

The climate is subtropical. Summers are warm, humid and rainy, and winters are mild and dry.

Annual temperature (mean °C) : 20,3
Humidity   (mean %) : 78
Rainfall   (total mm) : 1010

STUDY AREA
Free ranging
(Beachwood)

STUDY AREA
Free ranging
(Burman Bush)

INDIAN OCEAN

UMCENI RIVER

DURBAN

THE CAGES

FIGURE 3.1
LOCALITY MAP

scale 1:50000
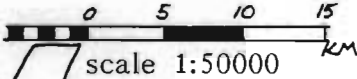
Main roads
Main railways

The location of the comparative study areas

The following table describes the climatic conditions during the periods of intensive observations. The mean daily atmospheric temperature was recorded at this time and, in addition, every time a body temperature reading was taken, the atmospheric temperature was noted.

TABLE 3.2

CLIMATIC CONDITIONS DURING INTENSIVE OBSERVATIONS

Month	Rainfall	Humidity	Temperature (°C)			Sunlight (mean hours per day)
			Minimum	Maximum	Mean	
1975						
February	206.9	83	21.5	37.0	23.7	4.4
March	41.4	77	18.9	26.5	22.4	5.7
April	108.1	78	16.3	26.4	21.1	8.8
May	60.3	80	13.5	24.4	18.8	7.2
June	7.1	75	10.6	23.5	16.8	7.5
July	31.4	71	9.3	23.0	16.1	7.7
August	21.2	71	11.5	23.6	17.5	7.0
1978						
October	163.2	81	16.8	23.4	19.7	4.8
November	243.9	97	18.5	25.0	21.8	5.5
December	48.8	81	20.0	27.0	23.3	6.6
1979						
April	32.4	80	19.3	26.9	22.9	6.6
May	24.0	73	15.4	24.9	20.1	6.8
June	3.2	67	11.6	23.6	17.4	7.8
July	131.9	69	11.6	21.7	16.5	6.8

3.4.1   The study area.

The article "The design and establishment of a primate troop enclosure" written by the author and her supervisor, John Lucas, was published in the South African Journal of Psychology in 1979, and is available upon request. Since no such facility had previously existed, the author was responsible for the initiation, the planning, organising and establishment of the caged vervet troop.   This article provides a detailed description and evaluation of the success of the 6.5 metre radius geodesic dome, by examining the behaviour and wounding incidence and comparing it to the free-ranging troops.   It was concluded that the cage overcame many of the difficulties customarily involved in cage studies, for the following reasons:

- "Building a geodesic dome, instead of the customary cube.   This maximises the utilisation of space - and eliminates corners.
- Designing apparatus for the interior which will provide for as many activities as possible seen in the field, including sleeping places, hiding places, aunting circles and shelter from the weather.
- Providing simultaneous provisioning at several different foci by remote control.
- Trapping a 'natural' troop to preserve genealogical links.   This will improve the credibility of studies into social behaviour."

(Tollman and Lucas, 1979: 143).

Please refer to Figures 3.2, 3.3 and 3.4, which display a topo-cadastral transparency over an aerial photograph of the geodesic domed troop enclosure, its construction details, and the interior, respectively. Monitoring was carried out in an observation hut, so that ongoing activity was not disrupted.

Three conventional 1.75 metre cube cages have been built only 9 metres distant from the cage, for the observation of individual animals living alone (see Figure 3.5).   Surrounded by bush, these cages cannot be seen by the troop.   Internally, half of the single cages are enclosed on three sides for protection against the weather, and half is exposed.   A ladder, a bucket, logs and rope were provided.

Beachwood Golf Course, the original home of the caged troop, is a lush, well-tended 45.6 hectare tract of subtropical land, and has been
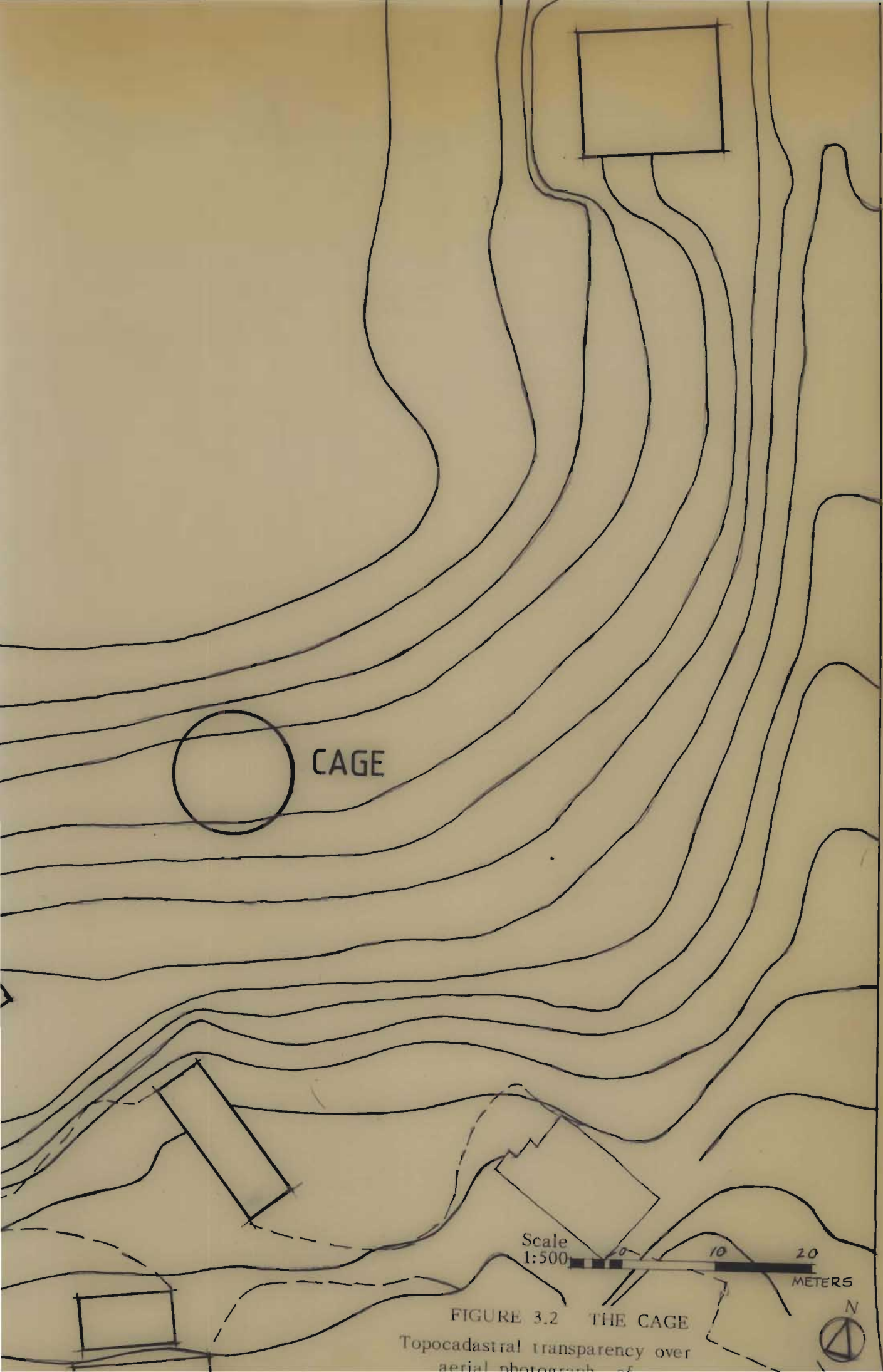
21

CAGE

FRANCOIS ROAD

Scale
1:500

0   10   20

METERS

N

FIGURE 3.2   THE CAGE

Topocadastral transparency over
aerial photograph of

CAGE

Scale
1:500

0   10   20

METERS

N

Entrance
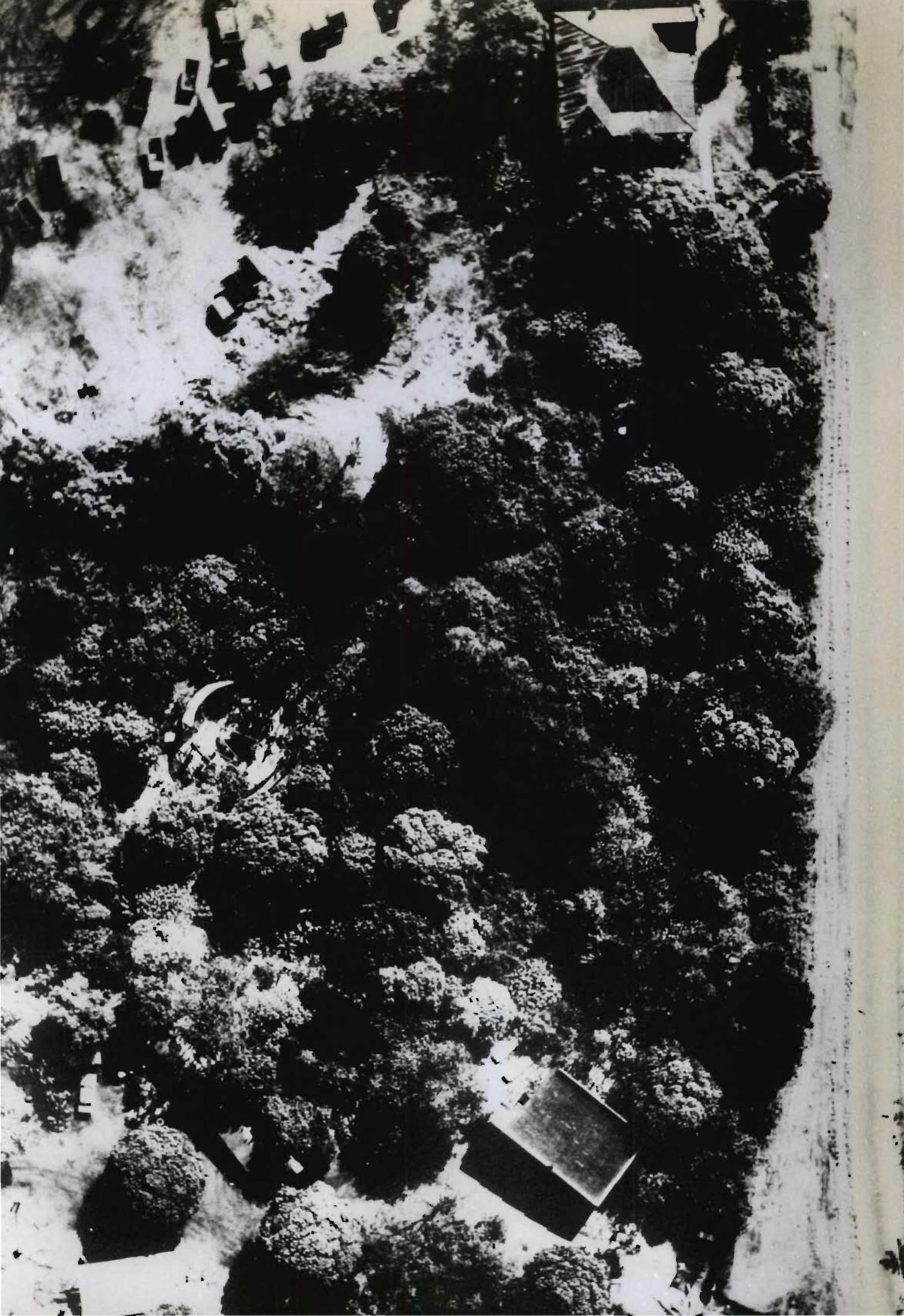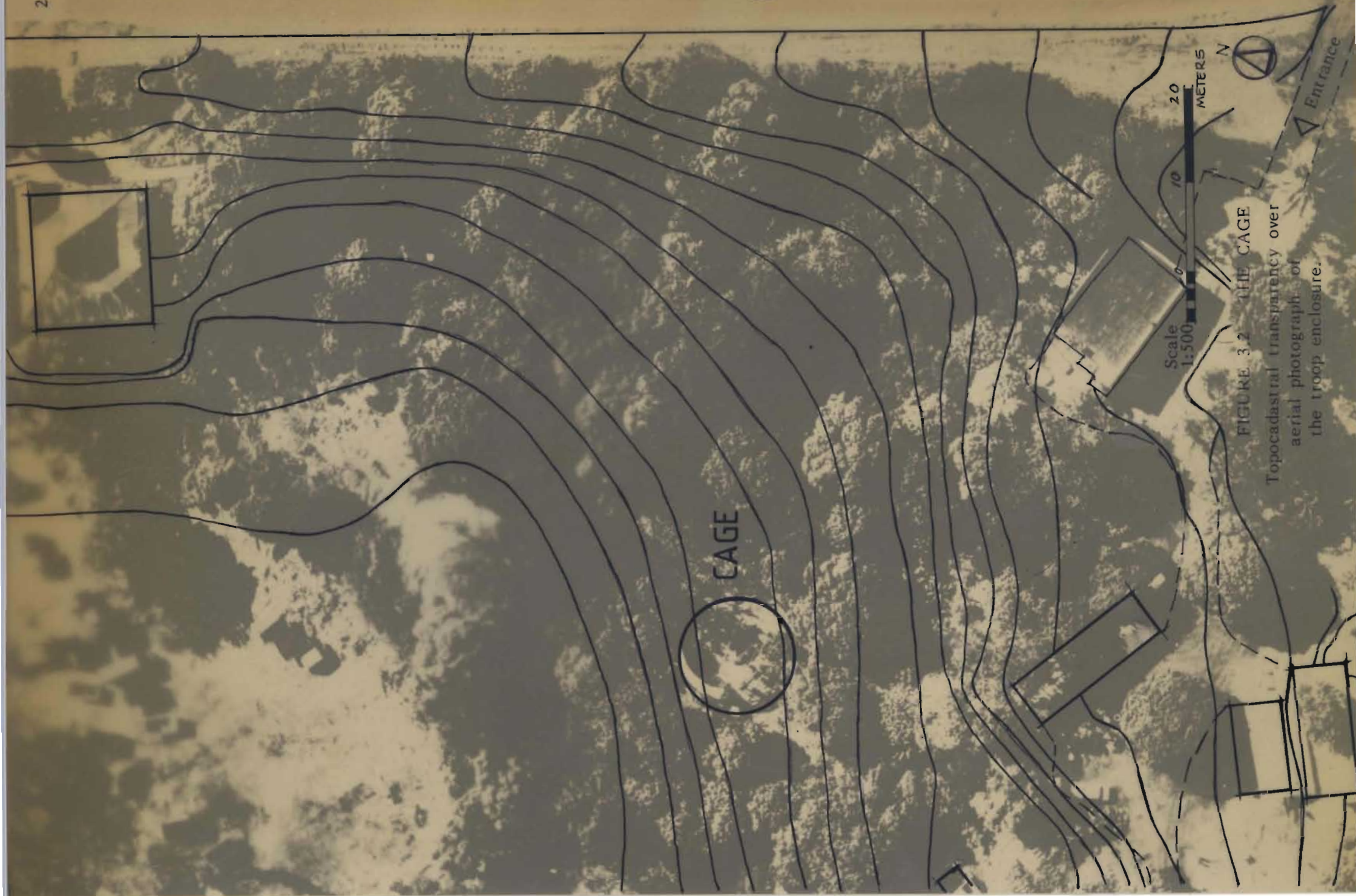
FIGURE 3.2   THE CAGE

Topocadastral transparency over
aerial photograph of
the troop enclosure.

ONE FIFTH DOME
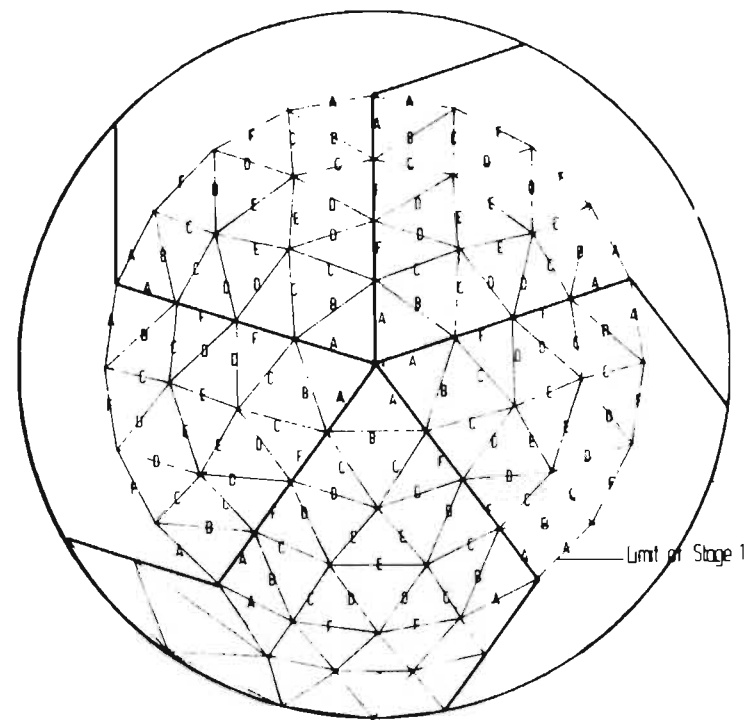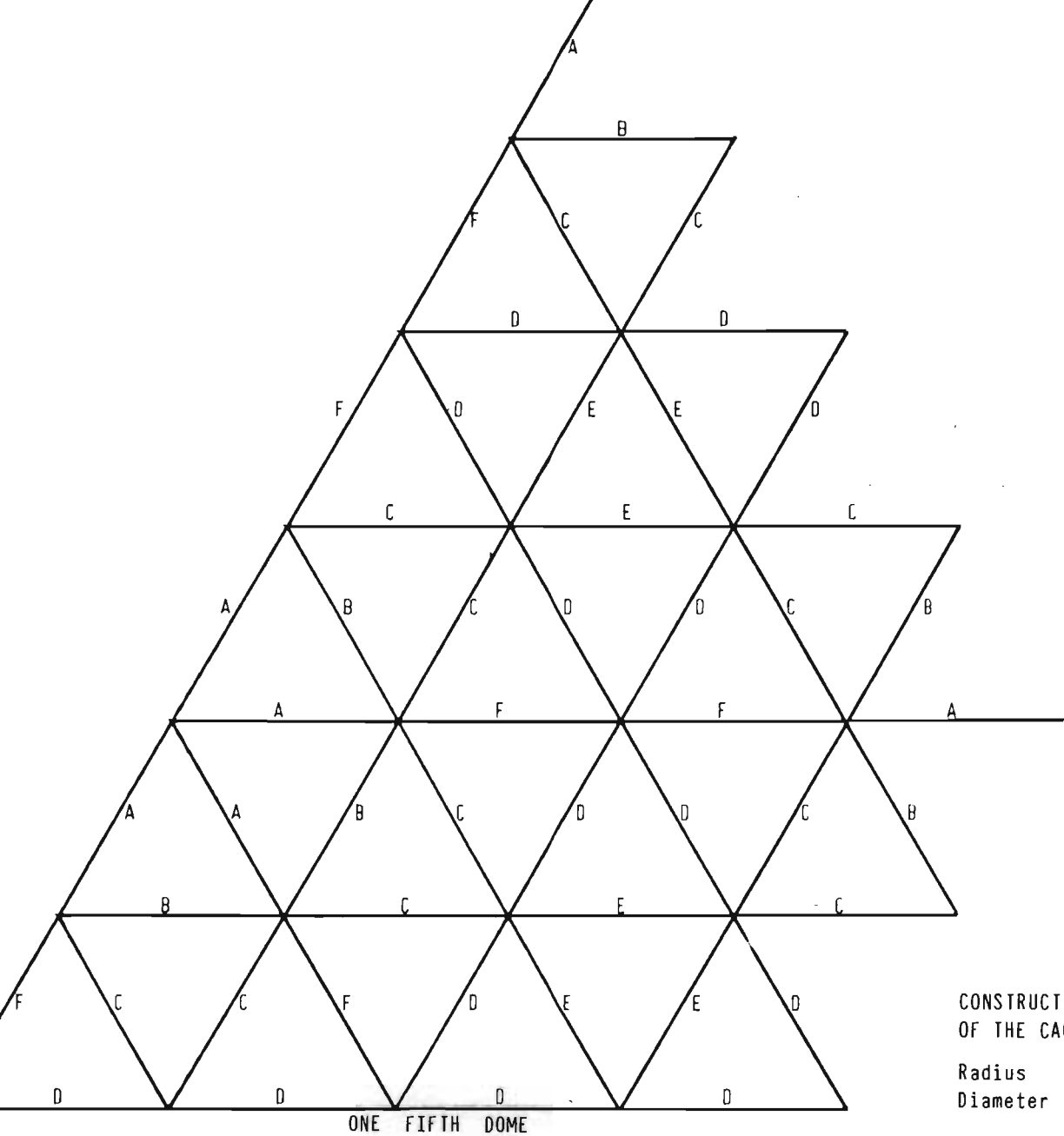
DIAGRAMMATIC PLAN

Limit of Stage 1

CHORD LENGTHS		No. for Dome	No. for Stage 1
A.	1.646	30	20
B.	1.919	30	15
C.	1.914	60	30
D.	2.034	70	30
E.	2.112	30	15
F.	1.914	30	20

Dimensions between bolts.

CONSTRUCTION DETAILS
OF THE CAGE

Radius	6.500 m
Diameter	13.000 m

FIGURE 3.3   CONSTRUCTION DETAILS OF THE CAGE.

N.B. PROTECTED
SHELTER
(ONLY ONE SIDE
NOT ENCLOSED)

POOL

POOL

1

2

3

4

5

13

FOOD

SOURCES

OBSERVATION
ZONE
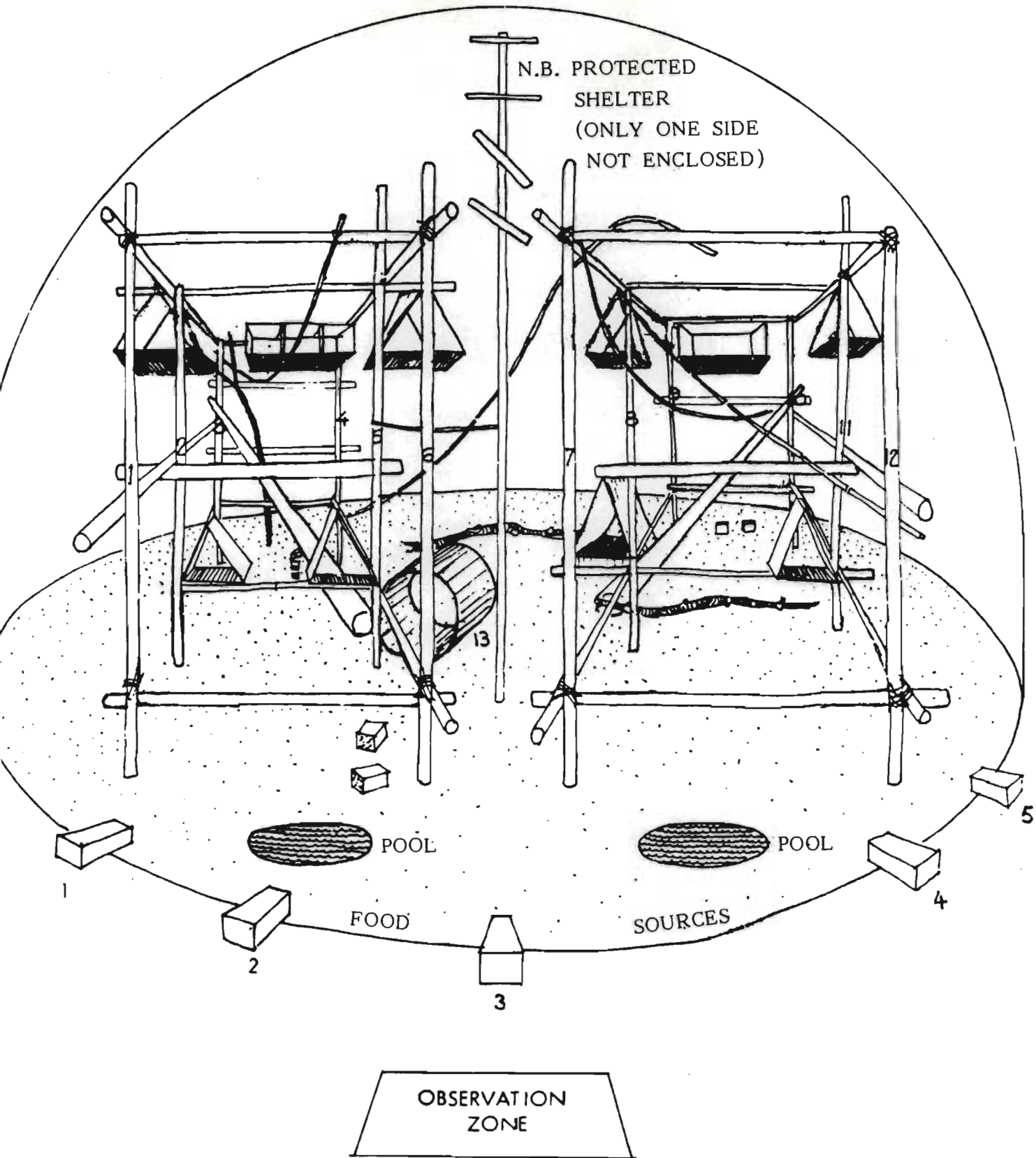
FIGURE   3.4

DIAGRAM OF THE INTERIOR OF THE TROOP CAGE.

Area	=	132.8 m²
Diameter	=	13.0 m
Circumference	=	40.86m
Height (maximum)	=	6.5 m

FIGURE   3.5

DIAGRAM OF THE INTERIOR OF THE SINGLE CAGES.

described in detail by the author (Tollman, 1977). Burman Bush, which houses three free-ranging troops, is a protected park, and has been described by Henzi (1983). A busy road presently cuts through the indigenous subtropical coastal forest, and clearings and paths make access to the entire area relatively easy. The canopy is closed or partially closed, and Bourquin (1968) has identified the vertical stratification as follows:-

i.   Upper canopy of trees and climbers at approximately 8-10m.

ii.   Short tree layer between 3.5-8m.

iii.   *Isoglossa woodii* shrub layer between 1.5-3.5m.

iv.   Sparse ground cover under trees and grass in the open.

3.5 CONCLUDING COMMENT.

The research setting seemed optimal for tackling the complex task of investigating physiological, psychological and social functioning concurrently in order to investigate the links between them. The presence of a caged troop enabled monitoring of an ongoing social situation to be statistically randomised, which was essential if rhythmic activity was to be revealed. Since the cage was in the open and vervets are native to the Durban area, social complications arising from the formation of artificial colonies, or physiological complications stemming from different weather conditions, latitude and time zones, as well as marked dietary alterations, were avoided. Furthermore, the availability of single cages and free-ranging troops allowed the external and internal validity of the caged troop's activity to be examined. The continuation of research studies utilising the cage points to its effectiveness as a research setting.

PLATE   1.0

THE   RESEARCH   ENVIRONMENT

1.1 The study site.

1.2 The troop enclosure.
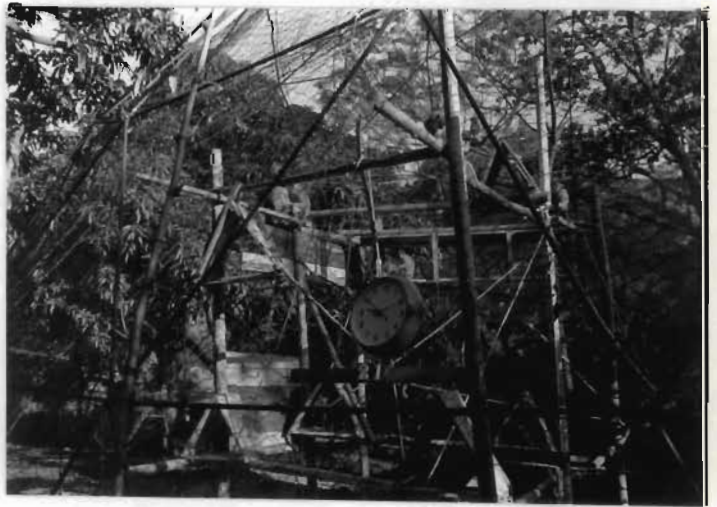
1.3 Cages of vervets living alone.

CHAPTER   FOUR

RESEARCH   OBJECTIVES

4.1   INTRODUCTION.

A doctoral thesis which argues that primates have evolved within a social context, and therefore physiological, psychological and behavioural functioning is linked, must attempt to unravel the complex network of interrelationships that should obtain.   A review of the literature has pointed to a dearth of such studies, even though it would seem that behaviour cannot be fully understood unless the coaction between physiological, and individual and social behavioural responses are clarified.

Washburn declared, in 1978, that the analysis of any system of animal behaviour must include an understanding of the biology of the actors in that system.   Chalmers, last year, extended that view when he wrote (Nov. 1983, pers. comm.) that behavioural primatologists must spend more time taking physiological factors into account in their explanation of social behaviour than they have done hitherto.   Snowdon (1983) supported Chalmers' contention by suggesting that evidence for physiological functioning not only to influence but to be influenced by social functions is accumulating.   Since the individual behaves as an integrated unit, a synthesis seems necessary.   It would appear that in-depth studies of the dynamic responses of individuals as integrated systems within which the different levels of functioning interrelate to preserve homeostasis in an everchanging environment, are indicated.

4.2   OBJECTIVES.

The principle aim of this study was to explore the interrelationships between body temperature, and social and individual behavioural responses, in five 'undisturbed' vervet monkeys.

On the basis of the author's previous studies it was hypothesised that:-

1. An underlying rhythm of functioning will be exhibited at the thermoregulatory level, at the individual behavioural level, and at the social level.

2. Despite an overall pattern, individual differences will be exhibited at each level of functioning.

3. Between subject differences at any one level of functioning will be in agreement with the direction of differences at other levels of functioning.

4. Changes at any one level of functioning will be accompanied by changes in other levels of functioning.

5. Since the individual has evolved and adapted within a social context, social mechanisms will be incorporated into the strategies employed for survival.

The execution of this project required the creation of research conditions in which the body temperature, and individual and social behaviour of undisturbed and freely moving vervets could be monitored concurrently, and unknowingly, in an ongoing social environment. The impact of social living had to be assessed by comparing vervets living in a group with vervets living alone. Obfuscation by circadian rhythms demanded a recording schedule that was rigorously randomised over the days and over the weeks. The examination of body temperature, of behavioural and of social functioning are described in each of the three chapters that follow: that is, Chapters Five, Six and Seven respectively. In Chapter Eight, these three levels of functioning are integrated and links between thermoregulation, behaviour, and the social condition are postulated.

C H A P T E R   F I V E

T H E R M O R E G U L A T I O N

5.1   INTRODUCTION.

The physiological variable scrutinised in this research project is internal body temperature.   Petersdorf (1980) described the importance of thermoregulation as an indicator of physical fitness.   He stated that temperature is "such a sensitive and reliable indicator of disease that thermometry is probably the commonest clinical procedure in use" (1980: 345).   During the last decade, hypothermia has been found to be an effective prognostic factor for conditions such as kwashiorkor in children (Brooke, 1972; Popper, 1982, pers. comm.) and vulnerability to flu in the elderly (Goldman, 1978, pers. comm.).   The development of strategies to maintain the integrity of thermoregulatory function, therefore, would seem to contribute to the survival of the individual.

A biotelemetric technique was employed for obtaining body temperature measurements, because the subjects can remain in an ongoing social situation.   Although not previously used in Natal, it seemed that "Only the use of telemetry, therefore, seems suitable to obtain 'basal' values from undisturbed animals" (Müller, 1982: 250).   Readings are made from a receiver distant from the signal source ensuring "disturbance-free measurement of physiological parameters" (Kimmich, 1980: 3).   Reite and Pauley (1976) suggest that "totally implantable biotelemetry systems are uniquely valuable, and may in fact represent the only feasible way to collect artifact-free data" (p. 62).   It was decided that implantation of a temperature sensitive radio transmitter using the then (1978) newly developed 'longlived' lithium batteries ($\pm$ 6 months), rather than procedures involving any form of handling during the study, would help to preserve the spontaneity of the subjects under observation, while permitting repeated measurements on the same subject, so essential for detecting rhythmic activity.

5.2   LITERATURE   REVIEW.

5.2.1   Body   temperature.

> ... normal body function depends upon a relatively constant body
> temperature.
>
> Ganong, 1981: 193.

Primates are homoiotherms.   Guyton (1981) distinguished between
the constancy of the internal or core temperature and the lability of the
surface temperature (the temperature of the skin or tissues immediately
underlying the skin) which rises and falls with the temperature of the
surroundings.   Clough (1982) explained that in most instances the deep
body temperature is higher than that of the surrounding air, resulting in
a temperature gradient from the central parts of the body through the
superficial layers, to the surrounding air (T_a).   Homoiotherms are
therefore considered to consist of a core (T_b) and a shell (T_s).

In 1778, Hunter recognised a diurnal variation in body temperature
and in 1906 Simpson and Galbraith undertook extensive circadian studies in
animals.   It has now been established that most mammals (e.g. bats, rats,
camels, primates, and man) have prominent T_b circadian variations,
although dogs and cats display rhythms that are rather obscure and of
small amplitude, in line with their other rhythmic behaviours (Moore-Ede,
Sulzman and Fuller, 1982).   Meis, Hulcher, Rose, Halberg and Halberg
(1980) worked with juvenile African green vervets, *Cercopithecus aethiops*,
and found "statistically significant circadian rhythms" (p. 66).

The T_b rhythm consists of a maximum and minimum temperature
each day.   The maximum normally occurs during an animal's active
phase, and the minimum during the rest phase.   In nocturnal rodents the
T_b peak has been found at night while in the diurnal squirrel monkey it
peaks during the day (Moore-Ede, Sulzman and Fuller, 1982).   Moore-Ede
and Sulzman (1981) found that T_b exhibits a square wave pattern.   This
is possibly one of the reasons for the discrepancies in time estimates of
peaks and troughs described by various researchers, for example, in humans
the minimum temperature occurs between 2 a.m. and 4 a.m., according to
Petersdorf (1980), at 4 a.m. according to Canon (1932), and at 6 a.m.

according to Ganong (1981).   Neither the latitude, the season, the light-dark regimen nor the lifestyle of the subjects, factors which probably influence those times, were mentioned.   The peak according to Petersdorf is between 6 p.m. and 10 p.m., to Ganong in the evening, and to Brown (1982) in the afternoon.   These researchers all pointed to individual differences in body temperature both between and within species, and within the same subjects at different ages.   On the other hand, Reite, Pauley, Kaufman, Stynes and Marker (1974) found relatively little intersubject variability when working with monkey infants, $M.$ $nemestrina$, aged 24, 26 and 35 weeks respectively.   Perhaps a rigorous measure of what constitutes individual differences needs to be introduced. In young children T_b is more labile than in adults, and transient elevations after relatively slight exertion in warm weather are frequently observed. As age increases in human subjects (41 to 73 years) so, apparently, does the tendency toward the spontaneous occurrence of internal desynchronisation (Petersdorf, 1980;   Ganong, 1981;   Wever, 1982).

The circadian rhythm in body temperature is generated by a thermoregulatory system, and is not a secondary consequence of daily changes in activity or metabolism because when Fuller, Sulzman and Moore-Ede (1979a) examined body temperature, skin temperature and heat production, heat loss displayed a circadian rhythm but not heat production (oxygen consumption).   The T_b rhythm is endogenous – it free-runs in constant conditions and does not entrain to day-night cycles with period lengths outside of a circadian range (Wever, 1979;   Moore-Ede, Sulzman and Fuller, 1982).   This endogenous rhythm, however, is modulated by particular exogenous factors.

Physical modulators include:-
- Ambient temperature: Fuller, Sulzman and Moore-Ede (1980) found that the T_b of primates is sensitive to alterations in ambient temperature, and more to warm than cold temperatures.
- Light: Light during the subjective day has little effect on temperature, but during the subjective night light produces a "large increase in body temperature" (Moore-Ede, Sulzman and Fuller, 1982: 277).   This indicates that in a light-dark cycle half the amplitude of the circadian rhythm is due to the endogenous rhythm, and half is due to the exogenous masking effects of the light-dark cycle.   Meis, Hulcher,

Rose, Halberg and Halberg (1980) found considerable variation in relation to the light-dark cycle.

Behavioural factors also modulate temperature:-

- Food: Food intake triggers an increase in metabolism and heat production, which, in turn, may elevate the body temperature. Fasting human subjects, however, continue to show circadian rhythms in body temperature (Wever, 1979) so the thermodynamic action of food does not play a major role in the normal diurnal temperature variation. Species variability in the immediate effect of food intake has been shown, because in squirrel monkeys only a very small temperature increase was found in response to the once-a-day meal, while in rats the effects were relatively large (Sulzman, Fuller and Moore-Ede (1978a). In vervets, Meis, Hulcher, Rose, Halberg and Halberg (1980) found marked individual variation in the extent to which the acrophase shifts when meal-times are altered.

- Activity: The rest-activity cycle and the sleep-wake cycle have relatively little influence on the temperature rhythm, even though they do affect temperature. Vigorous exercise can elevate body temperature, and more during the night than during the day (Ganong, 1981; Moore-Ede, Sulzman and Fuller, 1982). Sleep also influences thermoregulation selectively. A drop in brain temperature will induce an increase in heat production in awake animals, but this response is reduced in animals during slow-wave sleep, and even more so in REM sleep (Glotzbach and Heffer, 1976). Physiologically, heart rate rhythm and T_b rhythm in rats seem linked and independent of activity (Meinrath and d'Amato, 1979). Endorsement for this observation comes from Reite and Short (1980) who found that in pigtail monkey infants, animals with higher body temperatures tended to have higher heart rates. In addition, more active animals had higher body temperatures and heart rates day and night. Buttner and Wollnik (1982) contend that body temperature and locomotor activity, LA, do not follow independent oscillators. They pointed to a "physiological delay of BT rather than an uncoupling of BT from LA and HR" (p. 324). For them, "significant correlations exist between these three variables". They supported their argument by citing Honma and Hiroshige (1978) who demonstrated that "the correlation of LA with BT follows a circadian rhythm and that the correlation coefficient reaches a maximum

in the dark period" (p. 324). Variations in cerebral bloodflow and thermogenesis and thermolysis correspond to T_b variations, but the strength of the connection is not yet clear apparently (Roussel, Dittmar and Chouvet, 1980).

- Stress and emotion: Body temperature may also be disturbed by events which elicit 'stress' or 'emotion'. Van Holst, working with implanted transmitters in *Tupaia*, the tree shrew, wrote: " 'Core temperature' changed very quickly in physical or emotional stress situations; up to 2°C within 2-3 minutes" (1981, pers. comm.).

Georgiev (1978) worked with rats and demonstrated "the sensitivity of the nuclear temperature to environmental influences however slight they may be" (p. 234). He found temperature changes were elicited by differences in noise level between workdays and non workdays; the presence of unfamiliar persons; daily experimental procedures; and in extreme conditions such as a storm, peaks of up to 1.4°C. Clough (1982) endorsed Georgiev's results. Millan and Emrich (1981) also experimented with rats and mice, and found that "acute stress is also associated with an increase in TC" (p. 48). In monkeys, behavioural agitation corresponding with an elevation of body temperature was discovered by Reite, Short, Kaufman, Stynes and Pauley (1978). They found that when pigtail monkey infants were separated from their mothers, "the behavioural agitation reaction immediately following separation was accompanied by increases in heart rate and body temperature" (p. 91). Bush, Custer, Smeller and Bush (1977) found significant elevations in rectal temperature during excitement in nonhuman primates in the families *Callithricidae, Cebidae, Cercopithecidae* and *Pongidae*. At the human level, Dabbs and Moorer (1975) linked social interaction with an increase in arousal, and discovered that: "Temperature measured at the tympanic membrane increased during social interaction" (p. 517). Guyton (1974) found that when humans "express extreme emotions that cause excessive stimulation of the sympathetic nervous system, the amount of heat production may become great enough to raise the body temperature a degree or so" (p. 403), and Kenshalo (1976) had similar results. According to Keele and Neil (1971): "Emotional stimuli can raise the body temperature by as much as 2°C and may account for some unexplained fevers" (p. 337). The 'emotional stimuli' are not clearly delineated. It seems that more

attention to operational definitions is needed. In the initial stage of fever, shivering may occur, leading to a 'cold' sensation. These authors also described 'hyperhidrosis' or 'mental sweating', which can occur in emotional states and is limited as a rule to the palms, soles and axillae, though it may become generalised. Ganong (1981) described a "slight rise in temperature due to excitement and apprehension at the time of admission to hospital" (p. 193). It seems as though a disturbance of the 'vegetative state' may give rise to an increase in temperature in all homoiotherms.

The influence of social factors on circadian rhythms includes the body temperature cycles. Wever (1982) described synchronisation of rectal temperatures in a group of four subjects collectively isolated in an environment of constant conditions. He recommended that the type of social zeitgebers effecting mutual synchronisation should be investigated because all that is clear is that it must be based somehow on mutual social contacts.

All the factors described contribute to the oscillation around the mean, but the integrity of the underlying circadian rhythm of body temperature remains undisturbed.

Superimposed upon the daily T_b rhythm are the changes in temperature which accompany the rhythms of the mammalian reproductive system. The oestrus cycle of rodents is 4-5 days, while the menstrual cycle of the higher primates and humans is approximately 25 to 35 days, and in many mammals these rhythms are modulated by seasonal patterns of breeding (Moore-Ede, Sulzman and Fuller, 1982). According to Rowell (1972) no relationship has been found between female reproductive state and sexual behaviour of the vervet monkey ... "apart from a few weeks after the birth of an infant, most females appeared to be in permanent oestrus" (p. 129). As early as 1937, Rubenstein investigated the relationship between the human menstrual cycle and body temperature. With his relatively crude instruments he concluded that there is a "constant relation between the lowest body temperatures of the month and the characteristic ovulative smear, and of the highest temperatures with the characteristic premenstrual smear" (p. 640). Recent research indicates that the mean

temperature becomes elevated in the latter half of the human female menstrual cycle after ovulation has occurred (Petersdorf, 1980). The temperature trough increases earlier in the menstrual cycle than the daytime maximum, thus for daily comparisons measurements must be made at the same time each day, preferably in the morning (Zimmerman, 1982, in Moore-Ede, Sulzman and Fuller, 1982). The actual timing of the oestrus cycle has recently been shown to be determined by the circadian system and not the light-dark cycle (Moore-Ede, Sulzman and Fuller, 1982). However, as with the other body rhythms, social factors can affect the menstrual cycle. "Sexual cyclicity of female mammals is well known to be sensitive to social influence" (Rusak, 1981: 198). The importance of social factors should always be considered, it seems, and would exert particular effects upon the body temperature of each individual animal. This may explain, in part, the finding by Bauman (1981) who studied basal body temperature charts from the menstrual cycles of 98 women as evaluated by six physicians. Only 17 (22.1%) of the 77 cycles determined by endocrine profiles to be ovulatory were accurate. She concluded: "mounting evidence presented in this and other studies indicates that BBT patterns are inaccurate in the majority of women" (p. 732). The following observation made by Horvath and Drinkwater (1982) is of particular importance to the present study: "the overall response of women to exercise and heat stress during three phases of the menstrual cycle suggest that minor cyclic alterations in physiological systems apparently at risk are masked by the demands of the activity and the environment" (p. 790).

5.2.2   Circadian   rhythms.

... just as mammalian physiology can be conceptually divided into cardiovascular, respiratory and other systems, so can a circadian timing system be defined.

Moore-Ede, Sulzman and Fuller, 1982: VIII.

The recurrence of any event within a biological system at more or less regular intervals can be considered a biological rhythm (Aschoff, 1981). The circadian system is concerned with events of an approximately 24 hour time scale, and knowledge about the structure and function of the

circadian timing system has been rapidly expanding over the past twenty-five years (Brown, 1982; Moore-Ede, Sulzman and Fuller, 1982).

The reason for the paucity of research into this important biological mechanism and its implications for behaviour seems to be reflected in the reasons for the choice of the term 'circadian' rather than 'endogenous'. In the nineteenth and the first half of the twentieth century claims of 'innate' rhythms were often rejected "as sheer mysticism" (Bunning, 1982: VII).   All organisms were much like a clean slate at birth.   However, the "blossoming of ethology, sociobiology and the new emphasis on cognitive processes are part of a shift in the zeitgest from the restrictive concepts of simplistic S-R notions and 'radical' behaviourism or empiricism" (Webb, 1982: XIII).   It is now possible to consider 'inborn' phenomena, but with caution.   Possibly technological advances and the developments that flow from them also helped to rekindle an interest in body rhythms.   Improved physiological procedures, artificial lighting, and increased funding generated because of the implications of air travel and space programmes (e.g. 'jet-lag' and 'shift-work') - that is, for situations in which environmental cues and behavioural rhythms are manipulated - are examples.   'Chronobiology' is the term denoting this form of enquiry and is defined as a "science that objectively quantifies and investigates mechanisms of biologic time structure, including rhythmic manifestations of life in physiology and behaviour" (Halberg, Carondente, Cornellissen and Katinas, 1977: 50; in Brown and Graeber, 1982: 450).

According to Brown (1982), the pseudoscientific biorhythm theory as well as Canon's (1932) well accepted theory of homeostasis are both hindrances to a valid understanding of the rhythmic aspects of our existence.

The pseudoscience of 'biorhythms' developed in parallel with a growth in interest of the scientific study of biological rhythms also formerly called 'biorhythms', and the dual usage of this term has led to confusion. The pseudoscience of 'biorhythms' claims that what happens to a person physically and psychologically is greatly influenced by the relationships among three allegedly universally invariant rhythms which begin at birth: a 32 day 'physical' rhythm, a 28 day 'emotional' rhythm, and a 33 day

'intellectual' rhythm. A discussion of the spurious assumptions underlying this theory, e.g. the incorrect statistic of a universal 28 day menstrual cycle average in humans (Treloar, 1973), can be found in Brown and Graeber (1982).

The concept of 'homeostasis' referred to so critically by Brown is fundamental for the appreciation of physiological functioning, and an important principle for this thesis. If the cells of the body are to continue living, the composition of the extracellular fluid must be controlled very "exactly from moment to moment and day to day with no single important constituent ever varying more than a few per cent" (Guyton, 1974: 4). This is the task of the physiological systems of the body, and Canon (1932) referred to the maintenance of constant conditions (including body temperature) in these fluids as homeostasis. Primates are homoiotherms, individuals that maintain "body temperature within narrow limits despite changes in environmental temperature" (Groves and Schlesinger, 1982: 920). In contrast, poikilotherms possess no internal temperature control mechanisms to counter the climatic vagaries of the environment. Brown (1982) argued that Canon's definition emphasises a 'steady state' rather than the variability and rhythmic aspect of physiological processes, and he has modified Canon's definition to read: "The coordinated **and systematically rhythmic** physiologic processes which maintain most of the steady states in the organism" (p. 462). Brown also maintained that the concept of homeostasis is as acceptable to psychologists as it is to modern physiologists. The term has been extended to include behaviour and is defined as "the tendency of the organism as a whole to maintain constancy or to attempt to restore equilibrium if constancy is disturbed" (Chaplin, 1975: 237).

There seems to be considerable agreement about the formal properties of the circadian timing system (e.g. compare books by Moore-Ede, Sulzman and Fuller, 1982, with all the articles edited by Aschoff, 1981, and Brown and Graeber, 1982). It seems that the individual generates spontaneous circadian rhythms in many behavioural and physiological responses because if placed in an environment free of periodic environmental inputs, the rhythms continue. These rhythms, however, are no longer synchronised to a precise twenty-four hour period, but free-run instead

with periods which are close to but usually significantly different from twenty-four hours.

Circadian responses are usually synchronised to oscillating inputs from the environment, termed "zeitgebers", the "most prominent example of which is the twenty-four hour light-dark cycle" (Moore-Ede and Sulzman, 1977: 17). In the laboratory artificially simulated day-night cycles also have the capacity to act as "zeitgebers" (Wever, 1982). The synchronisation of a self sustaining rhythm by a zeitgeber is termed entrainment and during entrainment the frequencies of the two oscillations are the same or integral multiples of each other (Pittendrigh, 1981; Moore-Ede, Sulzman and Fuller, 1982).

Evidence for the existence of a multi-oscillator timing system is convincing (e.g. see Satinoff, 1978; Pittendrigh, 1981; Wever, 1982). It seems that one or more rhythmic variables will desynchronise in continuous light or dark, or if zeitgebers are manipulated. In the same squirrel monkey in continuous light, Moore-Ede and Sulzman (1977) found that the circadian rhythms of feeding and body temperature demonstrated a free-running period of approximately 25 hours, while the circadian rhythms of urinary potassium and water excretion demonstrated a circadian period of 20-21 hours. Humans in isolation have repeatedly shown the desynchronisation of two groups of rhythmic functions, one group which follows the sleep-wake cycle, and the other group coupled with the circadian rhythm of core body temperature (Aschoff, 1965; Wever, 1979).

The effects of different environmental zeitgebers, and the location of the pacemakers are also of concern. Moore-Ede and Sulzman (1977), working with squirrel monkeys, tested the following time cues in the absence of any other temporal cue: light-dark cycles (LD); temperature cycles (HC); social interaction-isolation cycles (SI); sound cycles (NQ); cycles of water availability (WT); and cycles of food availability (EF). Only LD and EF cycles were effective "zeitgebers", and further work has revealed that the LD cycle conveys information to the temperature rhythm, and the EF cycle to the drinking and urinary system (Sulzman, Fuller, Hiles and Moore-Ede, 1978).

Differential cue sensitivity implies that there is more than one pacemaker in the body, and Menaker and Binkley (1981) theorise that the nervous and endocrine systems contain the circadian system.   Researchers seem to accept the lesion studies that point to the suprachiasmatic nucleus, SCN, of the hypothalamus as playing a role (Webb and Dube, 1981; Poirel, 1982; Moore-Ede, Sulzman and Fuller, 1982).   Work is presently being directed at the pituitary-adrenal axis, and Moore-Ede, Sulzman and Fuller (1982) have suggested that the evidence points to the ventromedial or the lateral hypothalamic area as a second pacemaker because of their sensitivity to stimuli such as food, water and plasma levels of glucose, free fatty acids and insulin.   They envisage multiple pacemakers hierarchically arranged because hormonal mediators appear to control only those rhythms below them in the hierarchy.   Satinoff (1980) concurred with supporting evidence.

Studies of behavioural rhythmicity are in their infancy and mainly equivocal.   Brady (1981) asserted that behaviour has only rarely been put into a circadian perspective or circadian rhythms in a behavioural one. "In 1979 and 1980 less than .6% of the articles in the Psychological Abstracts were classified under Biological Rhythms", Webb confirmed (1982: XII).   Webb suggested that the concept of biological rhythms has been slow to penetrate behavioural research because the research designs focus on time as a behavioural determinant in contrast to the classically conceived behavioural determinants, such as schedules of experience or deprivation or the environmental determinants of stimulation and non repetitive growth factors.

It seems that the difficulties of studying rhythmicity must also be taken into account.   These are so daunting that Brown (1982) declared: "In several ways rhythmic research is heroic" (p. 25).   Enormous amounts of data have to be collected for each individual subject not only conscientiously and precisely, but continuously and with rigorous timing if rhythmic parameters of the variable are to be accurately determined. Moore-Ede, Sulzman and Fuller (1982) described how difficult it is to isolate circadian phenomena from other events, termed 'masking effects' by Wever (1979).   For example, unexpected changes in atmospheric temperature sometimes disturbs a circadian rhythm such as locomotion activity, because

an animal may move around more to keep warm during a cold snap. This activity would mask the expression of the circadian rest-activity cycle, because when conditions return to 'normal' the rest-activity cycle will resume its free-run from a phase determined not by that environmental cycle, but by its own continuously running clock. Further complications arise from the significant plasticity of phase that has been revealed (Moore-Ede and Sulzman, 1980), and the individual differences the rhythms exhibited (Moore-Ede, Sulzman and Fuller, 1982). All these problems had to be addressed in this research project.

The adaptive significance of the circadian timing system seems easy to explain. It allows the individual to predict events which are well correlated with the twenty-four hour period of the earth's rotation. "In particular, it appears to be of survival advantage to predict the day-night patterns of predator activity, food availability and environmental conditions" (Moore-Ede and Sulzman, 1977: 17). That is, "endogenous programming in relation to inevitable exogenous daily change" (Pittendrigh, 1981: 62). Barnett (1981) was not satisfied with such explanations. He found it difficult to speculate on the survival value of any system that will function spontaneously and is not related to a deficit. He illustrated his problem with the irrigation cycle of the lugworm, which includes a burst of activity accompanied by defaecation at intervals of about 40 minutes. Defaecation in this instance does not depend on a full rectum, but on a pacemaker – so carries on regardless of the actual situation.

The extent to which biological rhythms, that is, endogenous factors influence and direct behaviour is controversial. Gould (1982) discusses "clocks and drives" (p. 181). Epstein (1980) compares 'instinct' and 'motivation', while Barnett (1981) rejects these terms as being misleading. Barnett advocates working within an epigenetic framework and then "the extent to which behaviour is labile, either in natural conditions or experimentally has to be found out for each species and each behaviour pattern" (p. 575). To date, the behavioural cycles of eating and fasting, rest and activity, and sleeping and waking have received the most attention. Currently, phase-shifts are being studied because of their implications for night-shift and jet-travel. The constant illumination often provided in intensive-care units is criticised, because absence of cues may be detrimental to the patient's functioning. With a growing concern about

the effects of rhythms on behaviour, investigations probing such wide-ranging phenomena as aggression, cognitive function, vocalisation, sexual behaviour, suicide, drug effects and manic-depression are being conducted. Unfortunately, autorhythmicity reports are suspect (Brown, 1982), so rhythms in human behaviour are difficult to get at, and the majority of studies are confined to animals. Contrary to the "progress in biology and medicine, most psychological variables still lack empirical rhythmic determinations of the times of maximum and minimum values ... and the statistical specifications of normal values relative to some acrophase" (Brown, 1982: 17). Gould (1982) sums up: "How do these timers on which so much of behaviour depends actually work? Alas, we have many intriguing pieces of the puzzle, but no answers" (p. 183).

It seems that all the rhythms are synchronised to the 24-hour zeitgeber period, but the internal phase relationships between the rhythms are different. Moore-Ede and Sulzman (1981) maintain that the light-dark cycle is the predominant zeitgeber for synchronising circadian rhythms in most vertebrate species, although other zeitgebers, e.g. sound, social cues and feeding cycles, have been shown to play some role. In man, according to Aschoff and Wever (1981), all circadian rhythms maintain a distinct phase relationship to the sleep-wake cycle.

Rusak (1981) examined the effectiveness of social stimuli in synchronising mammalian activity rhythms, and quotes studies which demonstrate a tendency for social synchronisation among conspecifics; the susceptibility of the sexual cyclicity of female mammals to social influences; and the rhythmicity of a mammalian mother influencing the rhythmicity of her offspring. He suggested that if social synchronisation does not represent a simple masking effect, it implies susceptibility of a central timekeeper either to social events as zeitgebers or to feedback from activity that is stimulated by social contact. Either of these possibilities suggests a largely unexplored field in the circadian system.

5.2.3   Thermoregulation.

> In general, the thermoregulatory system maintains a relatively
> stable temperature of the body core, but to do this mammals have
> evolved a large repertoire of effective mechanisms for altering
> the heat content of the body.
>
> Moore-Ede, Sulzman and Fuller, 1982: 241.

Heat is continually being produced in the body as a by-product of metabolism, and body heat is also continually being lost to the surroundings through conduction, convection and radiation.   An individual is in heat balance when the rate of heat production is exactly equal to the rate of heat loss, but when the two are out of equilibrium the body heat and therefore the body temperature will either be increasing or decreasing. A control system involving negative feedback enables the thermoregulatory system to coordinate autonomic and behavioural effector mechanisms so as to maintain the body's optimal temperature level.   The body temperatures are sensed by thermoreceptors, apparently compared with reference levels, and modified to bring the temperatures to the appropriate level (Petersdorf, 1980;   Ganong, 1981;   Guyton, 1981;   Moore-Ede, Sulzman and Fuller, 1982). "Because the same signal activates all thermoregulatory responses, the fact that some responses in an animal's repertoire appear earlier than others would depend on the threshold of the particular response" (Satinoff, 1978: 17).

Satinoff postulated that instead of a single integrator there are as many integrators as there are thermoregulatory responses, and these integrators are represented at many levels of the nervous system, with each level facilitated or inhibited by levels above and below.   She supported her argument with many examples.   She described, for example, a series of experiments conducted by Carlisle and Ingram (1973) investigating the effects of thermally stimulating the spinal cord and hypothalamus on two thermoregulatory behaviours in pigs - operant responding for heat and postural changes.   They found that the operant response was controlled more by the temperature of the hypothalamus, but the postural response more by the spinal cord temperature.   A cooled hypothalamus increased the rate of working for heat, yet if the spinal cord was warmed, the pigs lay down but not in a cold-defence position, implying that the pigs did

not feel cold. These results suggest parallel individual circuits, hierarchically controlled. However, "the details of the central synaptic connections concerned with thermoregulation are still unknown" (Ganong, 1981: 196).

According to Moore-Ede, Sulzman and Fuller (1982), temperature regulation appears to be influenced by both of the major pacemakers of the circadian timing system. Control of the circadian rhythm appears to be located outside the SCN* because bilateral lesions of the SCN interfere with the rest-activity cycle, but not with the temperature rhythm. On the other hand, the skin temperature rhythm maintains a consistent relationship with the sleep-wake cycle, suggesting that heat loss rhythmicity is predominantly controlled by the SCN. Eastman, Mistlberger and Rechtschaffen (1984) disagree. On the basis of their experiments of implanting thermistors 1-2mm in rats' cortices, they wrote that there was "no support for the notions that anatomically distinct oscillators control the circadian rhythms of temperature and activity, or that an oscillator outside of the SCN controls the circadian rhythms of temperature" (p. 357). Their experiments need to be replicated because, as they themselves acknowledged, the rats were exposed to continuous dim light which is known to have a disruptive effect on free-running rhythm in rats. There does seem to be agreement, however, that information from all the diverse sites monitoring changes in body temperature is transmitted to the posterior hypothalamus (Moore-Ede, Sulzman and Fuller, 1982). It also seems that the two pacemakers act at different sites, because the autonomic and behavioural components of the thermoregulatory system are separately located (Satinoff, 1980). For example, in rats non-shivering thermogenesis is controlled by neurons in the spinal cord (Fuller, Horowitz and Horwitz, 1977), while behavioural thermoregulatory responses are controlled by the lateral hypothalamus (Satinoff, 1978). The preoptic anterior hypothalamus controls autonomic responses (Lipton, 1968; Carlisle, 1969; Satinoff and Rutstein, 1970; Petersdorf, 1980).

Physiological processes involved in thermoregulation:

The importance of physiological or autonomic responses in maintaining the integrity of body temperature is undisputed. The argument centres around the relative importance of the behavioural strategies, which are examined in the following section. As Satinoff (1980) asserted: "to most psychologists the constancy of internal body temperature is primarily an autonomic achievement ... to many physiologists, autonomic responses are also paramount"

*SCN = suprachiasmatic nuclei of the hypothalamus

(p. 189).   This statement seems to be supported by papers describing human physiology (e.g. see Petersdorf, 1980;   Guyton, 1981;   Ganong, 1981).

Heat production :   According to Guyton (1981), the following factors play a major role in determining the rate of heat production: the basal rate of metabolism of all the cells of the body which is increased by muscle activity;   the effect of thyroxine on cells;   the effect of norepinephrine and sympathetic stimulation on cells;   and increased body temperature. A resting adult mammal of a given species has a 'zone of thermal neutrality' at which metabolic heat production is at a minimum.   For a house mouse it is ± 34°C;   for a naked human ± 26-29°C (Barnett, 1981). Petersdorf (1980) considered the major source of basal heat production to be through thyroid thermogenesis and the action of adenosine triphosphatase (ATPase) on the sodium pump of all membranes, and the muscles most important in promoting increased heat production with exercise through increased shivering.   In most cases this consists of small increases and decreases in the number of nerve impulses to the muscles causing inapparent relaxing and tensing.   Ganong (1981) included food intake as an important contributor to body heat production because of its specific dynamic action.   He also pointed out that heat production can be varied by endocrine mechanisms in the absence of food intake or muscular exertion: epinephrine and norepinephrine produce a rapid but short-lived increase in heat production, and thyroid hormones produce a slowly developing but prolonged increase.

Heat loss :   Heat is lost from the body in several ways.   Small amounts are used in warming food or drink and in the evaporation of moisture from the respiratory tract.   Most heat, however, is lost from the surface of the body by the mechanisms of convection, radiation and evaporation.   The principal method of regulating heat loss is by varying the volume of blood flowing to the surface of the body.   A rich circulation in the skin and subcutaneous tissues carries heat to the surface, where it can escape. When there is a need for conservation of heat, adrenergic autonomic stimuli cause a sharp reduction in the flow of blood to the surface. Horripilation or piloerection will also reduce heat loss (or in a hot climate – heat gain), by manipulating the air trapped in the layer of hair or fur next to the skin.   The erection of the hairs will reduce heat transfer across the trapped air layer and therefore heat loss.   Humans substitute clothes for this layer of hair, although 'goose pimples' are the visible

manifestation of cold-induced contraction of the piloerector muscles attached to "the rather meager hair supply" (Ganong, 1981: 195). Moore-Ede, Sulzman and Fuller (1982) point to the importance of skin temperature for modifying convective and radiative heat loss. Lynch, Adair and Adams (1981) discovered that the vasodilation threshold in squirrel monkeys is "approximately a linear function" of central (preoptic/anterior hypothalamic) and peripheral (mean skin) temperature.

Sweating (under the influence of the sympathetic nerves which in this instance mediate cholinergic stimuli) also causes heat loss by providing water to be vaporised (Petersdorf, 1981). Some mammals lose heat by panting, the rapid shallow breathing greatly increasing the amount of water vaporised in the mouth and respiratory passages and therefore the amount of heat loss. Schwartz and Rosenblum (1983; 1984) pointed to "unusual" acute thermoregulatory behaviours evolved by small, densely furred primates which face acute hypothermia during periods of intense activity or heat stress. These include the "opportunistic" use of urinary (Robinson, 1980) and respiratory fluids (sneezing).

Gordon and Heath (1983) "suggest that fundamental rhythmic properties incorporated into temperature regulation have been ignored. The nervous system must have the capacity to integrate the intrinsically rhythmic characteristics of thermoregulatory effectors (e.g. shivering, bloodflow and sweating)" (p. 486). Perhaps the situation is not as serious as these authors believe, because the complexities of the interaction of oscillatory systems are being investigated. Fuller, Sulzman and Moore-Ede (1979b) have demonstrated the importance of proper temporal synchronisation of the circadian timing systems for effective thermoregulation. In constant light, adrenalectomised squirrel monkeys with 24-hour cortisol replacement became internally desynchronised, since a portion of the circadian system is entrained by cortisol and the rest free-runs. It is interesting that cortisol is also involved in 'stress' reactions. The intimate relationship of brain, behaviour and social factors is further illustrated by Millan and Emrich (1981), who described studies demonstrating that "endogenous opioid peptides are involved in the mediation of the elevations in nociceptive thresholds, core temperature, exploration and grooming behaviour elicited by stress" (p. 43). Vincent, Paré, Prenatt and Glavin (1984) pointed to the importance of behavioural strategies to compensate for the change in core body temperature elicited by stress.

A sustained elevation in temperature produces a fever – perhaps the oldest and most universally known hallmark of disease.   When it occurs "the thermoregulatory mechanisms behave as if they were adjusted to maintain body temperature at a higher than normal level" (Ganong, 1981: 196). It is as if the thermostat has been reset.   The temperature receptors then signal that the actual temperature is below the new set point, and temperature-raising mechanisms are activated.   This usually produces chilly sensations due to cutaneous vasoconstriction and occasionally enough shivering to produce a chill (Ganong, 1981).

Glib extrapolations across species have to be avoided because no animal possesses all the existing thermoregulatory mechanisms, and some animals have developed one form of regulation to a much greater degree than other forms.   Satinoff (1978) cited Heath, who described three examples of endothermic extremes: "The arctic fox, an insulation specialist;   the shrew, a metabolic specialist;   and the elephant, a surface-to-volume specialist" (p. 21).   Kamau, Johansen and Maloiy (1980) found cutaneous evaporation from active sweating more important for heat loss in the slender mongoose *(Herpestes sanguineus)* in contrast to respiratory evaporation in dogs and cats.   Muller (1979) revealed that unlike most higher primates who increase evaporative cooling by sweating, the prosimians mainly rely on panting as a means of heat dissipation.   Further examples are quoted by Le Maho, Goffart, Rochas, Felbabel and Chatonnet (1981); Müller and Jaksche (1980) and Müller, Kamau and Malory (1983).

Species differences exist in the biochemical systems as well.   Myers (1969; 1978) has investigated the neurochemical systems of thermoregulation in the hypothalamus, but Ganong (1981) cautioned, and pointed to marked species variations in the temperature responses to the biochemical actions of serotonin and norepinephrine.   The former is suggested to be a synaptic mediator in the centres controlling the mechanisms activated by cold, and the latter in those activated by heat.

With technological advances encompassing increased use of microwaves, Adair (1979; 1981a; 1981b; 1983) and Adair and Adams (1980a; 1980b) are probing the changes that they apparently exert.   Sweating, peripheral vasodilation, and changes in basal metabolic rate and behaviour are elicited

to "ensure precise regulation of the internal body temperature at the normal level" (Adair, 1981a: 421).   Adair's results highlight that behaviour is an integral aspect of the spectrum of thermoregulatory responses.

Behavioural mechanisms involved in thermoregulation:

Opinions regarding the importance of behavioural strategies for the maintenance of thermoregulation in homoiotherms vary.   Hardy, Stolwijk and Gagge (1971, cited in Satinoff, 1980) believe that there is no real need to study behaviour as opposed to autonomic thermoregulation because the systems are the same except for the effector actions which close the regulatory loop.   In contrast, Satinoff (1980) demonstrated by selective lesioning that the control of behavioural and autonomic thermoregulatory responses are neuroanatomically separate from one another.   Moreover, behavioural thermoregulatory responses are the only responses available to more primitive poikilotherms and are therefore phylogenetically older than autonomic responses.   Furthermore, in mammalian ontogeny, behavioural responses are not only more effective than autonomic responses but may also be crucial for maintaining a constant body temperature.   Behavioural thermoregulatory responses seem to be elicited when either the skin temperature or the deep body temperature is altered.   Bligh (1973) wrote: "In man, the conscious awareness of heat and cold, and of thermal comfort and discomfort when skin temperature is varied has been shown to be dependent on the prevailing level of core temperature" (p. 212).   Thus it seems that the steepness of the gradient between skin temperature and core temperature determines thermal comfort or discomfort.

The relationship between autonomic and behavioural mechanisms was investigated by Adair and Wright (1976), who found that if they allowed squirrel monkeys in a test chamber to select from two air temperatures, 10°C and 50°C, by pulling a chain, their behavioural responses thermoregulated efficiently.   When the force required to pull the chain was increased in steps, the interresponse interval increased, resulting in wider temperature swings within the chamber.   Nevertheless, internal body temperature (unlike skin temperature) remained nearly the same due to a compensatory increase in metabolic heat production.   She suggested that her result confirms

Corbif's (1970) generalisation that behavioural regulation will give way to autonomic regulation when behavioural efficiency is low. Authors generally appear to acknowledge the importance of behavioural thermoregulation for homoiotherms, but neglect to examine the mechanisms involved (e.g. Myers, 1969; Petersdorf, 1980; Ganong, 1981; Guyton, 1981; Groves and Schlesinger, 1982). Possibly without the newly developed techniques such as biotelemetry it was difficult to study. 'Ongoing' behaviour needs a disturbance-free situation.

Heat loss : Behaviourally, heat loss can be controlled in various ways. The individual may select his 'microenvironment' – sun or shade; exposure or protection; wind or shelter. Postural changes such as curling up in a ball reduce the surface area and are a common reaction to cold in animals, with a counterpart in the position some people assume when climbing into a cold bed (Ganong, 1981). Conversely, in heat an animal may adopt a splayed out position. Further mechanisms include social huddling, or wetting the fur during grooming (Moore-Ede, Sulzman and Fuller, 1982). Pauls (1979) has demonstrated the efficiency of nest use for thermoregulation in red squirrels. 'Anorexia' and 'apathy and intertia' will also decrease heat production (Ganong, 1981).

Heat production : Heat production can be augmented through increased voluntary activity (Finger, 1976) or eating. Barnett (1981) described investigations to illustrate that the sparing effect of huddling on food consumption is very marked. "Even quite large mammals benefit: the oxygen consumption of piglets can be reduced by 30% (p. 98). He also cited evidence for mammals learning novel habits to control temperature: rats will press a lever to turn on heat when they are in a cold environment, or to have a cool shower when they are in a hot environment. Adair, 1980; 1981) and Adair and Adams (1980b) have been investigating the effects of microwaves on thermoregulatory behaviour in the squirrel monkey and found it highly efficient.

The effectors that the animals use for thermoregulation are a function of the ambient temperature. When an animal is in a cold environment heat loss mechanisms operate at a minimal level and body temperature is regulated solely by changing the level of heat production. Conversely, if

the animal is in a warm or thermally neutral environment, the metabolic level is maintained at a minimum and heat loss mechanisms (first dry, then evaporative) maintain body temperature. The coordination between behaviour, social and environmental conditions seems to be a feature of animal life. Heinrich (1981a; 1981b) found that bees on the mantle of a honeybee swarm will cluster tightly to elevate the temperature of the core if T_a drops. These bees will also shiver and push inwards.

Bishop (1979) compared four field studies of the langur monkey *Presbytis entellus* living in the Himalayas. She found that "shared social characteristics include behavioural buffers against cold and inclement weather" (p. 251). Huddling was engaged in by all age-sex classes and appeared throughout the year (more frequently in winter than in summer). It correlated most strongly with inclement weather, rest periods, and with being at the sleeping trees both in the early morning and evening. Behavioural buffers also included adjustments to the daily activity cycle, seeking out sleeping sites with best exposure to the sun and lengthy bouts of morning sunning in the sleeping trees, deliberately moving to the terminal ends of the branches facing the sun. Postures varied according to the weather. In winter, the langurs left their trees one to two hours later than in the spring. Social interaction frequencies between all group members were lower in winter, which was characterised by affiliative behaviours between adult males (grooming, play and embraces). Migration and dietary adjustments, such as only eating oak leaves when nothing else was available, were further adjustments noted. These behavioural adjustments are supported by other primate studies (e.g. Suzuki, 1979; Stelzner and Hausfater, 1980; Paterson, 1981).

It is important for newborn mammals to maintain a relatively high body temperature, and the major responses to achieve this are social (Satinoff, 1980). Litters of rat pups tend to huddle. Alberts (1978) has shown that huddling by rat pups is an active process whereby the body temperature of individual members of the huddle are regulated. When nest temperatures are low, rat pups move downwards into the warm centre of the pile and when nest temperatures are reversed, the direction of pup flow is reversed to the top of the pile. Similarly, a very good behavioural system has been shown for mice, puppies and rabbits. The search for

contact comfort in very young animals is postulated to have a thermoregulatory component. Rabbits orientate toward a furred artificial mother in a cold environment but not in a warm one. Infant macaques during the first twenty days of life, given a choice between warm wire surrogate mothers and cool cloth surrogates, showed a preference for the warm surrogate (Satinoff and Hendersen, 1977).

In any community the resources, such as sun and shade, may be insufficient to go around. Saint-Girons (1977) studied social dominance and interrelationships in captive populations of *Lacerta viridis*, the green lizard, for four years. He found that all the lizards spent much time basking in the sun to increase their internal temperature, especially during prolonged cool weather. The dominant females, however, had first access to the sunny spots and tended to sunbathe for a longer time and produce more eggs than submissive females.

Thermoregulatory responses are not necessarily exclusive to the thermoregulatory system; the same response can serve apparently totally different functions. "Shivering and piloerection are also emotional responses. Vasomotor tone is of primary importance for cardiovascular regulation" (Satinoff, 1978: 21). Satinoff has proposed that "most, if not all the thermoregulatory reflexes evolved out of systems that were originally used for other purposes" (1978: 21). As one example, she cited Cowles' (1958) explanation of the evolutionary development of the peripheral vasomotor system. This basic mechanism for changing bloodflow at the surface, he argued, first served as a supplemental respiratory organ in amphibia, then became a heat collector and disperser in reptiles (regulating the flow of heat from outside the body to inside), and finally an essential temperature regulatory mechanism for endotherms (regulating heat flow from inside the body to outside). According to Satinoff, this development illustrates "the principle of evolutionary coadaptation: a mechanism evolved for one purpose has as a side benefit an adaptive value in an entirely different system" (p. 21). Such an evolutionary theory of endothermy would also explain how the brain came to be organised in such an apparently complicated way - that is, with many independent integrators arranged in parallel at every level of the nervous system, each level facilitated or inhibited by the levels above and below, controlling every conceivable

thermoregulatory response.

In this thesis, it is postulated that social mechanisms such as social huddling and social grooming have become additional thermoregulatory strategies.

5.3   PROCEDURE.

5.3.1   Apparatus.

Please refer to Plate 2.0 which illustrates the arrangement, and to Appendix I for a complete list of the apparatus and materials used in this experiment.

The biotelemetric system used in this project was purchased from The Minimitter Company Inc., P.O. Box 3386, Sunriver, Oregon, 97702, U.S.A.   The principal components are an 'L-M minimitter' (fitted with a 1000 MAH Lithium battery waterproof-coated with 'Parafin/Elvax'), and a model CH Receiver which has three channels available for use when fitted with 'Receive Crystals'.

The minimitter was implanted in the peritoneal cavity and relays temperature information in the form of a noise signal.   The receiver registers this information at a site remote from the source.   The frequency of the signal emitted by the receiver indicates the internal temperature of the vervet - the faster the signal, the higher the temperature.   The L-M minimitter, according to the manufacturers, has a transmission range of "60-150 metres"; "allows detection of temperature changes as small as 1/10th of 1°C"; and the "battery life is 4-5 months".

The centre pole of the troop cage and the rear end of the single cages were fitted with aerials to enhance signal-reception.

The monitoring apparatus was mounted in the observation hut (see Plate 2.1).   A Receiver was connected to a Philips 4 track Reel-to-Reel Recorder (Model 3534) which recorded the temperature signals.   This permitted replay to check the signal frequency.

PLATE 2.0

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DATA COLLECTION.

2.1 The observation hut.

2.2 Recording facilities for
behavioural observations,
body temperature and
atmospheric temperature.

2.3 Biotelemetric T_b apparatus:
(clockwise) Receiver;
transmitter and battery;
receive crystals;
mesenteric skin coating;
paraffin-elvax coated
transmitter.

According to Mackay (1970), counting clicks is the most accurate procedure for estimating temperature, even without special training. Computerised technology might have outdated such a statement, but since the latter procedure would be expensive, and this project depended upon the relative changes in signal frequency rather than estimates of absolute temperature, counting clicks appeared to be the most appropriate technique for recording temperature. An automatic recording of body temperature was organised. Unfortunately, the apparatus allowed for only one channel to be recorded at a time.

5.3.2   Subjects.

Cercopithecus aethiops pygerythrus are the subjects of this research project. Please turn to Chapter Three for a discussion of this species and their ecological niche, together with an outline of the particular situation at the University of Natal.

Eight adult female vervets were used for the present investigation. Three monkeys were part of the caged troop, and five had been captured in the Durban area, and housed in single cages at the Natal Institute of Immunology for a minimum of one month prior to the operation.

In a pilot study, three vervets were used to perfect the implant procedure, as recommended by Mr T. Klomfass and Professor G. Downing. The postoperative behaviour was also noted in two of these monkeys, while the location of the minimitter was repeatedly recorded on X-ray in the third monkey (see Plate 3.2).

The remaining five vervets, numbered from 1 to 5 respectively, were each given minimitter implants, and subjected to intensive, highly structured and simultaneous investigation of thermal, behavioural and social functioning. Vervets 1 and 2, obtained from the Immunological Institute, were housed in the single cages while the troop-living vervets 3, 4 and 5 were returned to their troop after the implant operations. Although there were five adult females living in the cage, the receiver only has three channels, and so the youngest and the oldest female were left alone.

Biographical notes of the three troop-living subjects can be found in an unpublished M.SC. Thesis (1977) – known then as **L** , OB and J respectively. These females each gave birth to apparently healthy infants in the year prior to their operation, and in the year subsequent to the operation. Births occurred as follows:

Subject 3 : 16.10.1978 and 13.10.1979

Subject 4 : 1.11.1978 and 14.11.1979

Subject 5 : 11.12.1978 and 31.10.1979

All the subjects seemed to be healthy throughout the study. The three caged females are still living in the cage (September, 1984).

5.3.3 The recording schedule.

Monitoring was conducted according to a Latin Square Design, rather than a Fixed-Time Schedule, so that an overall picture of ongoing behaviour would be revealed. The situation was unique, and hypotheses needed to be formulated. Furthermore, the Latin Square Design which takes account of all periods (levels) of the day, will allow for detection of rhythmic fluctuations of activity. As illustrated in Table 5.1, each observation (between 07h30-17h30) was divided into five levels of two hours each, and each level was further subdivided into three or four segments to ensure that observations were evenly spread throughout the day. The blocks of twenty-five day recordings were spread over five days per week for four or five weeks, and seventy-five measurements were noted during each block. Thus over each five week period, T_b was registered a total of fifteen times per week, that is, three times at each period of the day, and within that period, once in each time segment. This plan for seventy-five randomised temperature readings was modified in the four week block as indicated on Table 5.1. A total of 930 temperature recordings were taken for each subject. Although only the recordings collected as specified in the randomised blocks are included in the statistical analyses, body temperatures were noted every day of the week. The single-caged observations were conducted for nine weeks between October 23, 1978 and December 22, 1978, and the troop observations for eighteen weeks between April 2nd, 1979 and August 10, 1979. Unfortunately one of the females escaped in the tenth week and, although she was recaptured and returned

TABLE 5.1
RECORDING REGIMEN : BEHAVIOURAL AND TEMPERATURE
(after a Latin Square Design)

BLOCK 1: N = 75

Week	Segment	\\ D A Y — 1	2	3	4	5	Total Days — 25
1	1	T1	T2	T3	T4	T5	
	2	T5	T1	T2	T3	T4	Week 1
	3	T4	T5	T1	T2	T3	
2	1	T3	T4	T5	T1	T2	
	2	T2	T3	T4	T5	T1	Week 2
	3	T1	T2	T3	T4	T5	
3	1	T5	T1	T2	T3	T4	
	2	T4	T5	T1	T2	T3	Week 3
	3	T3	T4	T5	T1	T2	
4	1	T2	T3	T4	T5	T1	
	2	T1	T2	T3	T4	T5	Week 4
	3	T5	T1	T2	T3	T4	
5	1	T4	T5	T1	T2	T3	
	2	T3	T4	T5	T1	T2	Week 5
	3	T2	T3	T4	T5	T1	

BLOCK 2: N = 75

Week	Segment		Day 1	2	3	4	5	Total Days 25	20
1	1	1	T5	T3	T1	T4	T2		
	2	2	T2	T5	T3	T1	T4	Week 1	Week 1
	3	3	T4	T2	T5	T3	T1		
2	1	1	T1	T4	T2	T5	T3		
	2	2	T3	T1	T4	T2	T5	Week 2	Week 2
	3	3	T5	T3	T1	T4	T2		
	4	1	T2	T5	T3	T1	T4		
3	1	2	T4	T2	T5	T3	T1	Week 3	
	2	3	T1	T4	T2	T5	T3		Week 3
	3	1	T3	T1	T4	T2	T5		
	4	2	T5	T3	T1	T4	T2	Week 4	
4	1	3	T2	T5	T3	T1	T4		
	2	1	T4	T2	T5	T3	T1		Week 4
	3	2	T1	T4	T2	T5	T3		
	4	3	T3	T1	T4	T2	T5	Week 5	

NOTE: Each day level was subdivided into segments to provide for all the different times of the day.

DAY LEVELS

T1	07h30–09h30
T2	09h30–11h30
T3	11h30–13h30
T4	13h30–15h30
T5	15h30–17h30

TIME SEGMENTS

120 mins

1   2   3
40 mins

1   2   3   4
30 mins
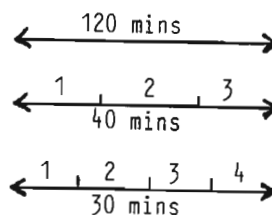
Segments were randomly assigned over the week.

Recording frequency: Subdivision:

after five days, calculations have been based upon five and nine weeks of recordings when all the animals remained undisturbed.

All these recordings have been bound, and are lodged in the Department of Psychology, University of Natal, Durban.

5.3.4 Data collection.

The signal frequencies were measured with a digital stop watch. A procedure which is "convenient, simple, rugged, reliable and relatively insensitive to temperature changes" (Mackay, 1970: 260). In counting the clicks, the procedure as outlined by Mackay was followed "for maximum accuracy and minimum time" (p. 263). The time taken for 50 clicks was measured since "it is preferable to count cycles in a given interval if time increments occur less often than information cycles" (p. 265). Temperature recording was blind, because the observer was unaware of the connections between waveband and subject. Atmospheric temperature was always recorded in conjunction with body temperature.

5.3.5 The implant operation.

Please refer to Appendix 1 for a comprehensive list of drugs and instruments used. Plate 3.0 illustrates the procedure.

The author performed all the operations in the operating theatre at the Natal Institute of Immunology – and the guidance, support and help of the technical assistants is gratefully acknowledged. The author, with the help of Pat Daniel, made a videotape of the operation, which is lodged in the Department of Psychology, University of Natal, Durban.

5.3.5.1 Capturing the subjects.

The troop subjects were captured and the operation commenced and completed on March 26, 1979 – in the order Subject 4, 5, 3 respectively. The singly caged subjects were both operated on on October 18, 1978, in the order Subject 2, 1.

To preserve anonymity, the activated minimitters were randomised by Ms. Daniel before being given to the author for implantation.

Troop members : The geodesic dome is connected to an extension by a trap-door, which is opened and baited with food for trapping troop members when required. When the desired animal comes to feed, the trap-door is closed. If removal or treatment is indicated, a sliding wire grid which has been fitted to the extension of the dome, and is also built into the single cages at the Institute of Immunology, is pulled toward the animal restricting its movement. The animal crouches in fear, and an injection can be administered.

Solitary subjects : Vervets from the Natal Institute of Immunology had been captured with crush cages while free-ranging. The procedure is outlined in detail in an unpublished M.Sc. Thesis (Tollman, 1977).

5.3.5.2 The anaesthetic.

The anaesthetic consisted of an intramuscular injection of 0,65 mgm of Ketalar (Ketamine HCl), used in conjunction with a customary adult dosage of 10 mgm of Valium (Diazepam), a muscle relaxant. The anaesthetised animal was gently removed from the trap, inspected, retagged as per Tollman (1977) if necessary, and transported to the theatre. The ketamine dosage was calculated on the basis of 13 mgm per kg of body weight, with an adult female average weight of 5 kg. This anaesthetic lasts for approximately one and a half hours, after which another ketalar injection of half the original dose can be administered. The operation took about one and a half hours to complete.

5.3.5.3 Surgery.

Please turn to Appendix 1 for a complete list of instruments. They were all steam sterilised at 15 lbs pressure for 40 minutes.

The anaesthetised animal was laid on the preparation trolley, and the fur on its abdomen removed with an electric shaver to prevent infection and to facilitate the operation. The exposed skin was swabbed with an

antiseptic mixture of equal parts Germotol and 70% Alcohol, as a further precaution against infection. The monkey was then taken to the theatre, and positioned spread-eagled on the operating table with weights on the limbs to prevent movement and to ensure maximum accessibility to the abdomen. Next, a sterile cloth was draped over the monkey, and secured by taping so that only the area for incision was exposed and swabbed with physiological saline. The monkey was now ready for surgery.

A site of entry at the mid-point of the abdomen was established, and using tooth scissors a superficial small cut made on the surface of the skin. This incision was then deepened to penetrate the epidermal layer. Forceps were next inserted into the cavity and opened in an anterior-posterior direction to enlarge the incision. This procedure, in contrast to cutting for enlarging the opening, minimises the bleeding. With forceps and fingers, the skin layer was gently separated, and a retractor used to expose the abdominal wall, where a cut parallel but one centimetre distant from the epidermal incision was made.

The muscle wall was opened by lifting each muscle layer in turn, nicking with a pair of scissors, and increasing the size of the aperture by stretching the muscle with a pair of forceps. When the peritoneal cavity was exposed, the minimitter was implanted. The minimitter was removed from a 5% Hibitane solution, in which it had been immersed for at least 24 hours, washed with physiological saline, and inserted into the peritoneal cavity. Each minimitter was handed to the author by Klomfass and Daniel, so that she was unaware of the frequency range – thus all recordings and analyses were done 'blind'. The abdominal wall was closed by blanket stitching with plain 00:90 cm sterile surgical gut and a 3/8 circle reverse cutting atraumatic needle for soluble stitches which became absorbed. Each stitch was tied and knotted separately, and smoothed to avoid buckling. Care was taken to avoid tissue damage, by not tying knots too tightly. The outer skin layer was stitched in the same way, with a half circle reverse cutting atraumatic needle and 00:45 cm braided silk. The closed wound was next washed with physiological saline, and then surgispray, an antiseptic. These stitches fell out after a few days. Finally, an antibiotic (Streptopen 1 ml) was administered as a precaution against infection.

This operation was successful in all eight cases, and no complications were apparent.

5.3.5.4   Recovery.

Each vervet was placed in a recovery cage where it was closely watched by the Immunology staff for 48 hours, after which it was returned to its predetermined environmental condition.   No ill-effects were noted.

When the investigation was completed, the minimitters were removed from the peritoneal cavity in four out of the five single caged animals. In each of these cases, it had become encapsulated with mesenteric tissue. In the fifth case, the minimitter disappeared – a mystery that has not been solved.   Since in this case a considerable delay had occurred between implant and attempted explant, it is suggested that the minimitter was absorbed into the gut and eliminated.   Minimitters were not recovered from the females in the troop, for fear they were pregnant.   They have each given birth to infants subsequent to their operation.   These subjects appeared to be in such good health that subjecting them to the trauma of undergoing another operation seemed unnecessary.

5.3.6   The minimitters.

Two weeks prior to each operation the minimitter batteries were activated.   As pointed out by the manufacturers, the batteries tend to drift at first, and this procedure allowed them to stabilise.

The minimitters were also encapsulated in Parafin-Elvax, a material which renders them physiologically neutral, flexible and waterproof.

At the time of the experiment, the only facilities for constructing a conversion scale of frequency of clicks to absolute temperature were some old waterbaths.   This was not considered a serious problem as this enquiry depends upon comparative changes in temperature within the same subject over time, and not upon the absolute temperature.   Temperature measurements were recorded and analysed as signal frequencies and not

°C. The temperature signals were picked up at the following frequencies:

TABLE 5.2

SUBJECTS' T_b TRANSMITTING FREQUENCIES.

Social Condition	Vervet No.	Frequency Hz
Solitary	1	27.575
	2	27.565
Troop	3	27.555
	4	27.585
	5	27.615

The Department of Electronic Engineering at the University of Natal kindly investigated the output and fall-off characteristics of the cell, by performing tests over the period 20.11.1979 to 21.12.1979. The following salient points are taken from the report by Mr T. Watts:

> In conclusion the writer feels it is reasonable to assume that after switch on the battery requires a period of about 24 hours to stabilise. It then remains stable to within $\pm$ 0,01 volt for all load currents up to 1mA. Finally the battery exhibits a fast decay as the lifetime expires and collapses over a period of 48 hours.
>
> Taking into account variations which may exist from battery to battery, one could safely assume that these batteries have an initial setting time of a week and thereafter the battery voltage remains constant. The last week of the battery's operation is also suspect as the voltage collapses suddenly as the lifetime expires.
>
> It must be borne in mind that only one battery has been tested. One would however expect the characteristics of these lithium cells to be similar although the absolute scales may differ.

All temperature recordings in this study were carried out a minimum of two weeks after activation, and one week prior to fall-off.

PLATE   3.0

BODY   TEMPERATURE   TRANSMITTER   IMPLANTATION.

3.1 Peritoneal cavity exposed
     for implantation.

3.2 X-ray (day 21) to reveal
     body location of
     implanted transmitter.

3.3 Post-experimental surgery
     for removal of minimitter.

5.4   RESULTS.

The Raw Temperature data (secs. per 50 clicks) with accompanying Atmospheric Temperature readings have been bound and lodged with the Department of Psychology, University of Natal, Durban.

The internal temperature data was subjected to:-

1.   Estimates of temperature means and standard deviations.

2.   Graphical representation.

3.   A two-way subject by levels of the day analysis of variance.

4.   A multiple regression analysis of temperature and behavioural factors.

T_b recordings were blind.   A minimum of 135 T_b readings per subject were recorded (i.e. 75 repeated measures per subject per block of 4-5 weeks;   see Table 5.4).   The raw data had to be standardised for between subject comparisons because, in order to monitor >1 subject per block, the T_b signals had to be received on different wavebands.   This was done by adjusting the slopes of linear regression, as illustrated in Table 5.3.   Calculations were carried out on a Hewlett-Packard 11C Calculator.

TABLE 5.3

STANDARDISATION OF TEMPERATURE RECORDINGS.

Statistic	SUBJECTS				
	SINGLE CAGES		TROOP		
	1	2	3	4	5
r	-0,995	-1	-0,999	-0,997	-0,996
r²	+0,99	+1	+0,99	+0,99	+0,99
a	-0,793	-0,830	-0,710	-0,789	-0,841
Conversion Factor	x 1.061	x 1.013	x 1.185	x 1.066	1

KEY:

r = correlation coefficient
r^2 = coefficient of determination
a = slope of the line of linear regression

AXES:

x = temperature °C
y = minimitter frequency (secs.)

CONVERSION FACTOR:

-0.841 - a

NOTE:

(i) Slope of line of linear regression is negative because as the temperature increases the time measurement decreases (i.e. number of clicks per second increase).

(ii) Strength of the coefficient of determination.

(iii) a = subject 5 as standard.

(iv) Standardisation has rendered slopes parallel.

5.4.1 Body temperature:means and standard deviations.

The following table reveals between subject differences in the standard deviations in body temperature.

TABLE 5.4

BIOTELEMETRIC DATA :

COMPARISON BETWEEN THE STANDARD DEVIATIONS

IN T_b OF SUBJECTS.

Table 5.4.1 : After five weeks of randomised recordings

SOCIAL CONDITION	Subject No.	STANDARD DEVIATION s	NUMBER OF RECORDINGS N
Caged Solitary	1	0.321	75
Caged Solitary	2	0.370	75
Caged Troop	3	0.211	75
Caged Troop	4	0.223	75
Caged Troop	5	0.263	75

Table 5.4.2 : After nine weeks of randomised recordings

SOCIAL CONDITION	Subject No.	STANDARD DEVIATION s	NUMBER OF RECORDINGS N
Caged Solitary	1	0.326	150
Caged Solitary	2	0.408	150
Caged Troop	3	0.212	135
Caged Troop	4	0.218	139
Caged Troop	5	0.285	135

NOTE:

(i) T_b standard deviation, that is, the extent to which the internal temperature fluctuates around the mean, is greater in vervets living alone than in vervets living in the troop.

(ii)   Individual differences in standard deviation, even when subjects are living in the same social conditions.

(iii)   These rankings are consistent over time.

(iv) T_b standard deviations have to be low as we are dealing with a physiological fluctuation in healthy animals.

These results begin to take meaning when Cochran's C statistic for homogeneity of variance is applied. The hypothesis tested is that the subject variances are consistent with the assumption that they are sample estimates of a common population variance in temperature variability. In other words, the observed differences in variability are due to sampling error alone.

1.   This null hypothesis is rejected at the 1% level from the five sample estimates.

C_{obs} = 0.339 $C_{5,36}$ = 0.3351
                             $C_{5,144}$ = 0.2644

2.   The null hypothesis is accepted for the variances of the solitary caged subjects.

C_{obs} = 0.571 $C_{2,36}$ = 0.6602
                             $C_{2,144}$ = 0.5813

3.   Similarly the null hypothesis is accepted for the variances of the troop caged subjects.

C_{obs} = 0.423 $C_{3,36}$ = 0.4748
                             $C_{3,144}$ = 0.4031
                             $C_{3,74}$ = 0.4476 (determined by
                                               linear interpolation)

Thus it seems the five subjects can be divided into two different populations: those that live in single cages, and those that live within a group. The data from Table 5.4.1 is analysed (N equivalent for all variances; Troop T_b readings in Table 5.4.2 not recorded simultaneously).

Atmospheric temperature : Even though every behavioural measurement has an accompanying atmospheric temperature observation (in bound volume in the Department of Psychology, University of Natal, Durban), an in-depth study of the relationship between T_a and T_b is beyond the scope of this thesis. Comparative analyses of T_b within and between subjects is the focus of the study, and environmental conditions for the two vervets living alone and then for the troop-living vervets were equivalent, being monitored over the same period of time. The connection between T_a and T_b appears

consistent with the literature review which points to ambient temperature as a physical modulator of T_b, leaving the endogenous rhythm intact (Groves and Schlesinger, 1982). It was found that in the months in which the troop-living vervets were studied T_a monthly means decreased (22.9°C; 20.1°C; 17.4°C and 16.5°C) while as in all homoiotherms, the body temperature fluctuated within very narrow limits (see Table 5.4). Fuller, Sulzman and Moore-Ede (1980) have hypothesised that T_a modulates the T_b, and this idea is supported by the results of this study, because the rhythmic rise and fall of T_a and T_b correspond with one another as both peaks occur in the afternoon, and both troughs occur at night. Further experiments would need to be done to confirm whether T_a influences T_b.

It is interesting to speculate why homoiotherms who have apparently 'freed' themselves from environmental constraints, still appear to function in harmony with predictable environmental rhythms such as light and dark. As Gould (1982) pointed out, it is not known how these timers work. Are environmental cues still important agents in the unmasking and masking of DNA activity or is this phenomenon a vestige of our evolutionary past as poikilotherms, or is it adaptive in terms of utilising environmental resources such as sunlight to maintain homeostasis?

Recordings at 4 a.m. : As pointed out in the procedure, the analysis of body temperature in Table 5.5 refers to the daytime rhythm (between 07h30 and 17h30). The body temperatures contained in Table 5.6 were automatically recorded at 04h00 (limited facilities allowed for only one reading per subject per night).

TABLE   5.5

COMPARISON BETWEEN MEANS AND STANDARD DEVIATIONS
OF BODY TEMPERATURES AND CONCURRENT ATMOSPHERIC
TEMPERATURE RECORDINGS.

Vervet	Body Temperature				Atmospheric Temperature			
	$\bar{\bar{X}}$		s		$\bar{X}$		s	
	after 5 weeks secs/ 50 cks	after 9 weeks secs/ 50 cks	after 5 weeks	after 9 weeks	5 weeks	9 weeks	after 5 weeks	after 9 weeks
1	18.146	18.034	0.321	0.306	23.64	24.98	3.53	5.30
2	21.51	21.380	0.370	0.408				
3	16.848	16.825	0.211	0.212	24.182	22.742	2.572	3.359
4	19.433	19.42	0.223	0.218				
5	21.369	21.239	0.263	0.285				

Block 1: N = 75;   Block 2: N = 150.

NOTE:

1.   Relative constancy of T_b means, but change in mean of
atmospheric temperature over time.

2.   Low standard deviation of T_b mean, higher standard deviation
from atmospheric mean, which increases over larger time intervals.

INFERENCE: Body temperature is a physiological system and must
operate within narrow limits.   Atmospheric temperature
varies with the months and with the seasons.

TABLE 5.6

COMPARISON BETWEEN THE WAKING AND THE SLEEPING
BODY TEMPERATURES OF THE TROOP-LIVING VERVETS.

Vervets	Waking			Sleeping		
No.	N	X (secs/50 clicks)	s	N	X (secs/50 clicks)	s
3	75	16.848	0.211	6	17.97	0.23
4	75	19.433	0.223	24	20.92	0.39
5	75	21.369	0.263	6	22.117	1.391

NOTE:

1. Waking temperature based on mean of randomised recordings between 07h30 and 17h30. Sleeping temperature based on mean of recordings at 04h00.

2. Temperatures recorded as time (secs) for 50 clicks – this means that the greater the recording, the slower the signal frequency and, therefore, the lower the body temperature.

3. Means in different animals differ, because different instruments were used.   (Slopes were standardised – Table 5.3.)

4. Sleeping data is not based on equal or necessarily large numbers of recordings so must (particularly with S5) be regarded with caution.

SUGGESTED INFERENCES:

1. Body temperature drops at night.   (The lowest recorded daytime temperature is higher than the highest recorded nighttime temperature.)

2. The direction of the standard deviations at night correspond to the direction of the standard deviations during the day: least for S3 and greatest for S5.   This suggests that the oscillation of temperature around the mean may be greater at night than during the day, and is least for S3 and greatest for S5.

5.4.2 Body temperature: graphical representation of data.

Graphs 5.1, 5.2 and 5.3 illustrate the T_b fluctuations within and between subjects. These graphs are based on the first five-week block of recordings described in Section 5.3.3, that is, N per subject = 75, and only the daytime period between 07h30 and 17h30 is analysed. The mean temperature at each day-level is reflected.

In order to make the temperature recordings comparable between subjects, and to aid visualisation in terms of body temperature as measured in °C, the body temperature variations are expressed as inverted deviations from the mean.

Graph 5.1 displays T_b differences in individuals living in different social conditions (that is, in a troop, and alone)*. Variations between individuals living in the same social condition are also apparent, for example, note the regularity of T_b in vervet 3 as compared to vervets 4 and 5. The relationship with social status will be discussed in Chapter Eight.

Graph 5.2 illustrates the mean daily temperature cycle for each vervet subject, obtained by subtracting the subject's daily T_b mean from that subject's T_b mean at different levels (periods) over the day.

Graph 5.3 compares the daily T_b rhythm of the vervet subjects with a human temperature cycle. (T_b data of all five subjects were pooled, therefore N per day level = 375.)

5.4.3 Body temperature: analysis of variance.

All computerised data sheets have been bound and lodged in the Department of Psychology, University of Natal, Durban.

The temperature recordings of the troop-living vervets were subjected

* Please refer to Appendix 2 for straight line graphs illustrating the individual body temperature variation.
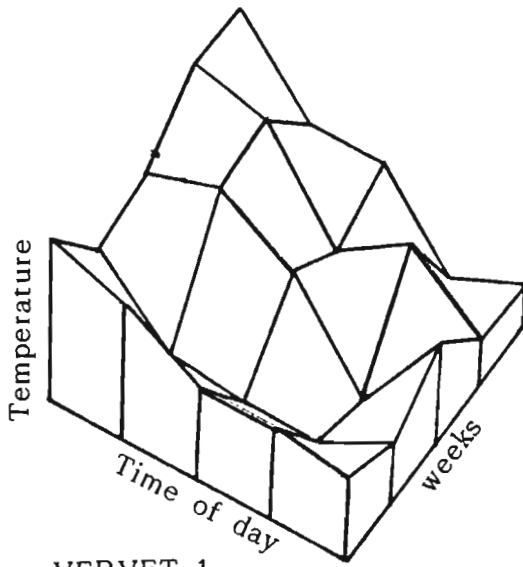
VERVET 1
Single Cage
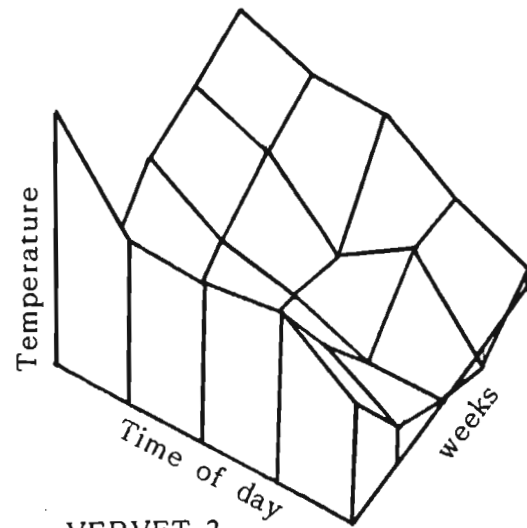
VERVET 2
Single Cage
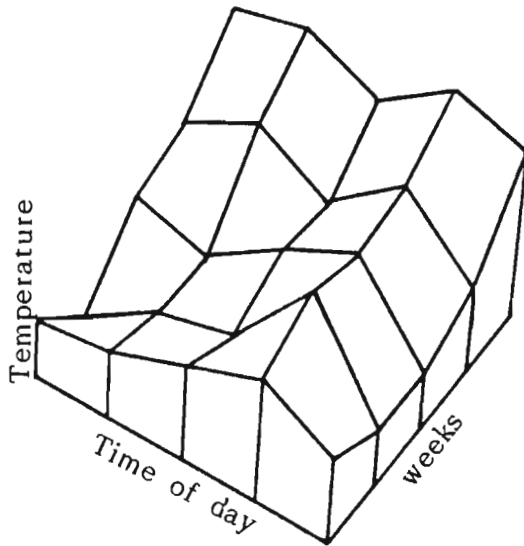
VERVET 3
Troop member Female high-status
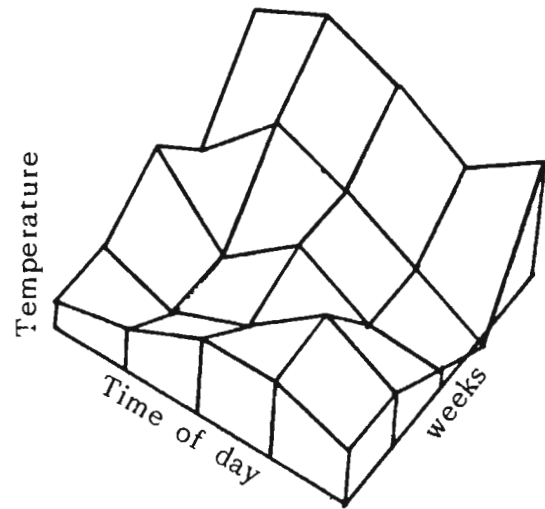
VERVET 4
Troop member Female mid-status
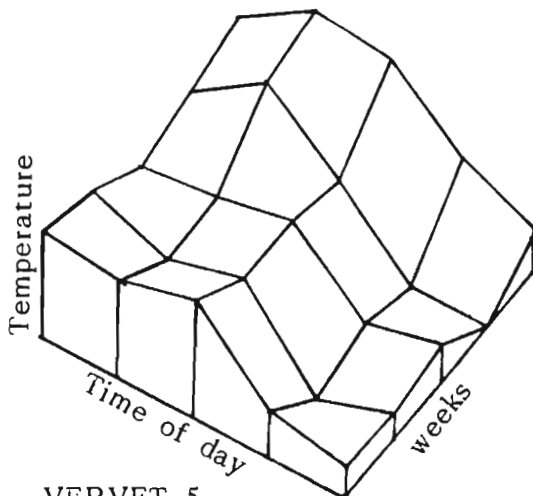
VERVET 5
Troop member Female low-status

GRAPH 5.1

BODY TEMPERATURE : THREE DIMENSIONAL PLOTS OF
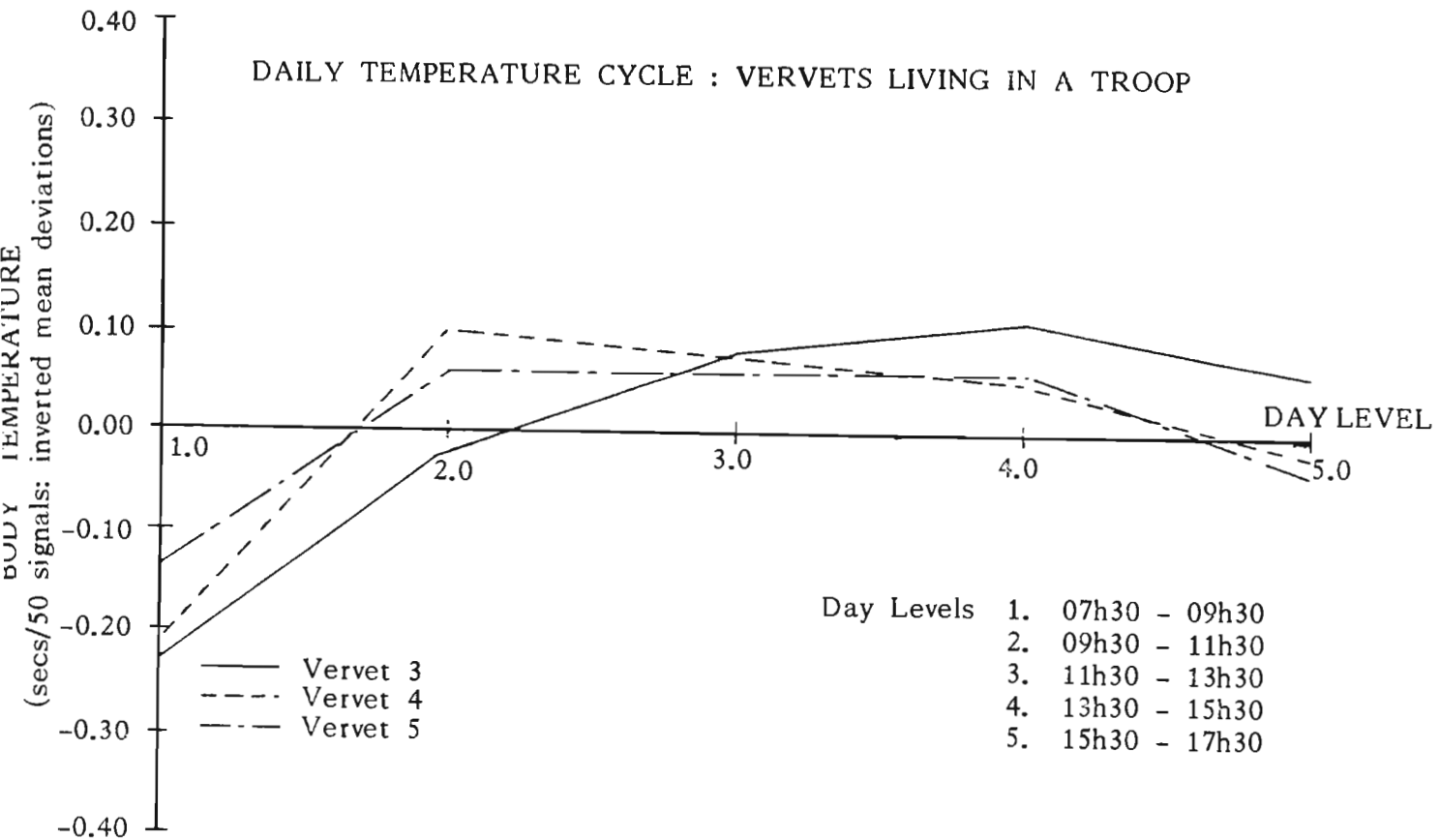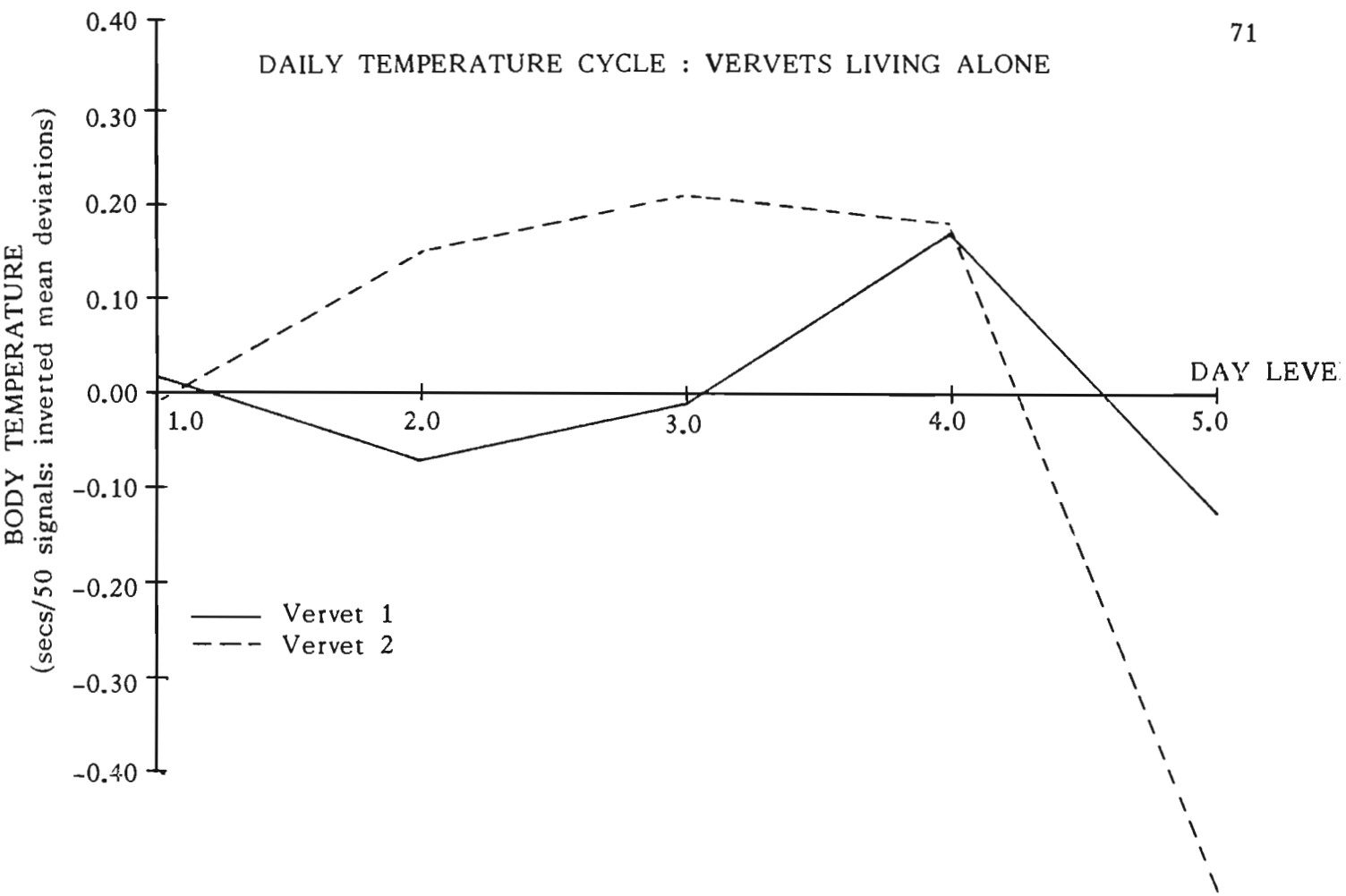
GRAPH 5.2

BODY TEMPERATURE : COMPARISON BETWEEN SUBJECTS'

MEAN DAY-LEVEL VARIATIONS.

HUMAN TEMPERATURE VARIATION

(after Ganong, 1981: 193)

VERVET TEMPERATURE VARIATION

Day Levels 1. 07h30 – 09h30
            2. 09h30 – 11h30
            3. 11h30 – 13h30
            4. 13h30 – 15h30
            5. 15h30 – 17h30
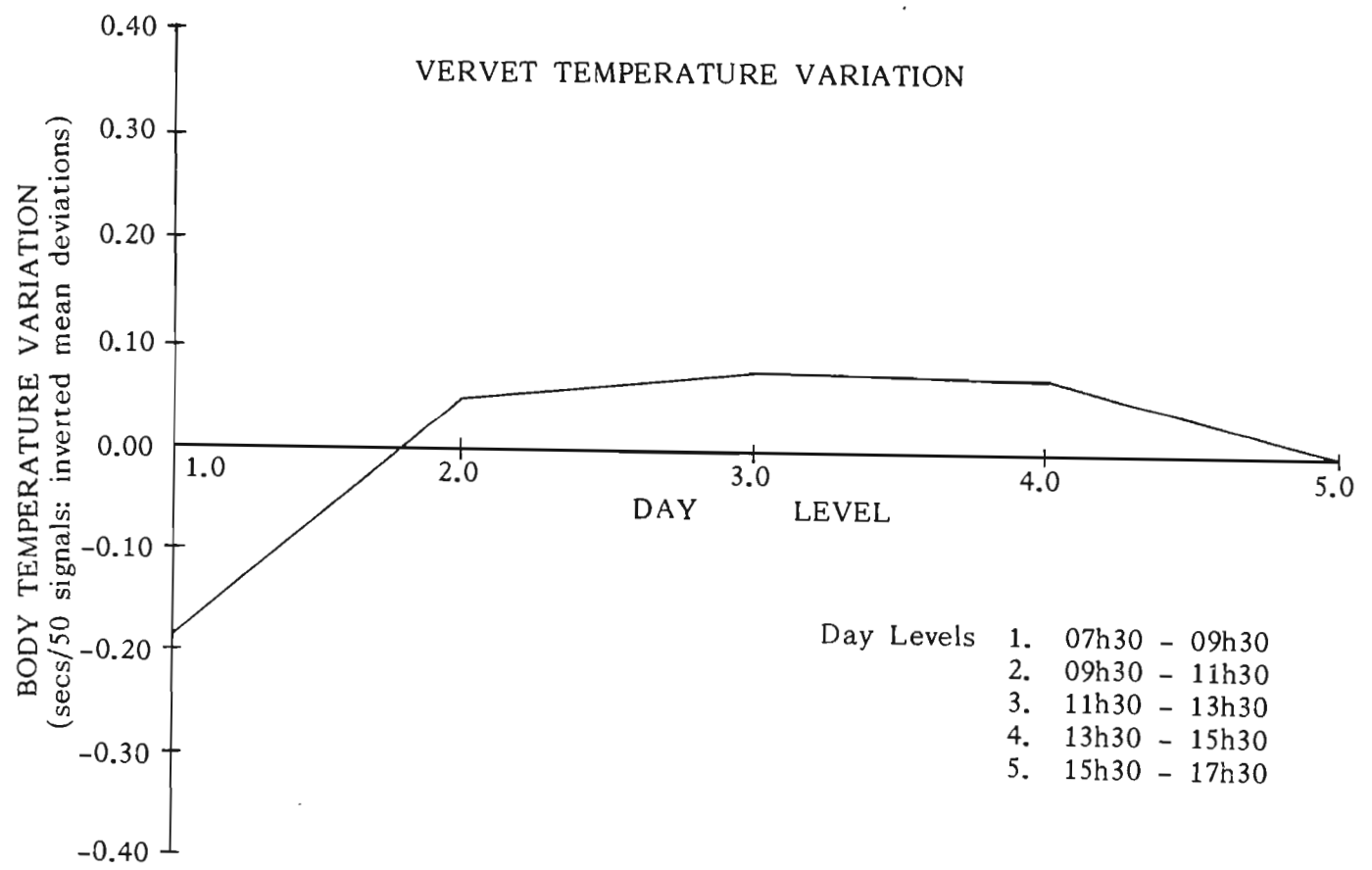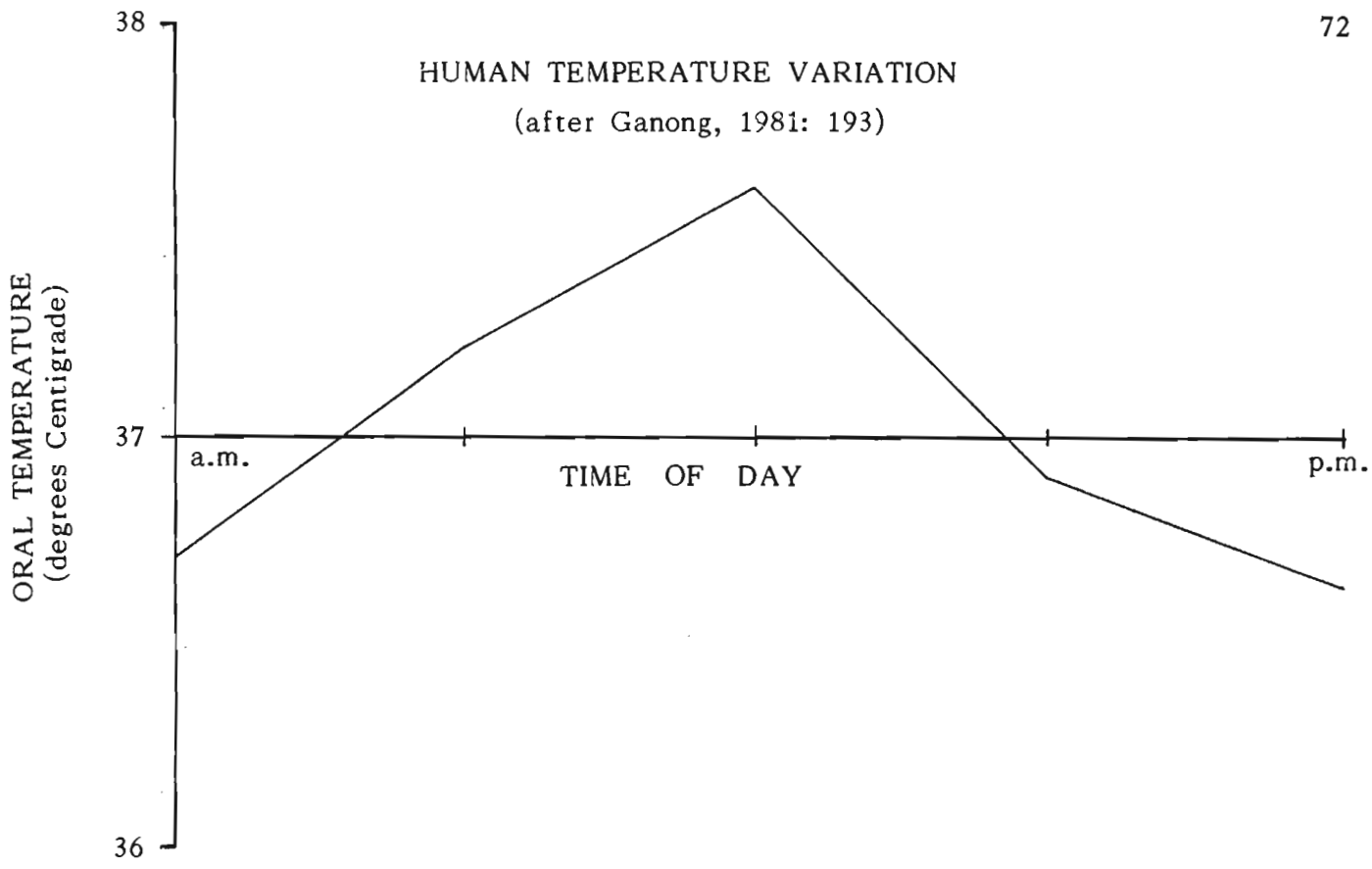
GRAPH 5.3

BODY TEMPERATURE RHYTHMS : HUMAN AND VERVET.

to a two-way analysis of variance.   The main effects examined were those due to subject differences, and those of different levels (periods) during the day.   The results of the analysis are given in the following table.

TABLE   5.7

ANALYSIS OF VARIANCE OF INTERNAL
TEMPERATURE IN SUBJECTS AND IN LEVELS
OF THE DAY.

ANOVA

	F	P
Subject x level	.829	<.5777
Subject	8564.787	<.0005
Level	13.792	<.0005

NOTE:

1.   There is no subject x level interaction, therefore all the subjects show the same temperature trend over the different levels (periods) of the day.

2.   Highly significant differences exist between subjects but this result has to be ignored, because it is due to different instruments operating on different wavebands.

3.   The level differences are highly significant, therefore T_b changes at different periods of the day.

5.4.4   Body temperature: multiple regression on behavioural factors.

This will be discussed in Chapter Eight, when the information gathered about body temperature is synthesised with behavioural and social factors.

5.5   DISCUSSION.

A literature search failed to reveal a study dealing with the body temperature T_b of *Cercopithecus aethiops pygerythrus*, the subjects in this research project.   The present data points to an endogenous T_b rhythm.   Individual differences occur in the extent to which the temperature oscillates around the mean, but in accordance with the characteristics of most physiological systems, and of homoiotherms, the variations occur within narrow limits.

The discovery that body temperature manifests a circadian rhythm is not surprising.   Meis, Hulcher, Rose, Halberg and Halberg (1980) found a statistically significant circadian rhythm in juveniles of the closely related green monkey species, *Cercopithecus aethiops sabaeus*, while Barnett (1981) declares that most mammals display a prominent circadian rhythm. It is suggested that the body temperature of the subjects alters according to an endogenous rhythm because, as described in Table 5.7, an ANOVA reveals the same T_b trend for all subjects, but significantly different temperatures at different times (levels) of the day, p $<.0005$.   (Each subject is treated as a separate variance within treatment class, because of the extent of repeated measures: N per subject per time block = 75; see Table 5.1.)

When graphs 5.2 and 5.3 are inspected, the daytime T_b rhythm of the subjects appears to approximate the human rhythm.   It is tempting to speculate that the similarity between vervet and human daytime (light) T_b function extends to the dark T_b phase, particularly in view of the recordings 'at 04h00, which in all cases studied is less than the lowest temperature recorded during the day (see Table 5.6).   Further study is needed here, with all-night recording facilities.   That the vervet T_b seems analogous to the human T_b is encouraging for researchers that consider the vervet monkey a suitable model for generating hypotheses about human functioning (see Chapter Two, Section 2.2.3).   The idea is reinforced by Setchell, Bull and Aldercreutz's contention (1980) that *Cercopithecus aethiops pygerythrus* is the model of choice for studying steroid excretion, and steroids, it has been postulated, have connections with body temperature.

Even if these researchers have overstated their case, it seems noteworthy that the steroid cortisol is integrally linked with body temperature because it entrains a portion of the T_b rhythm (Fuller, Sulzman and Moore-Ede, 1979b).

The existence of individual differences in body temperature are acknowledged by many authors (e.g. Brown, 1982; Moore-Ede, Sulzman and Fuller, 1982; Ganong, 1981; Petersdorf, 1980), yet it is surprising that an investigation which looks to social conditions to explain this individual variability does not appear to be reported in the literature. It seems that deviations from an endogenous rhythm (with a specific mean per subject) occur as a consequence of modulators. These modulators, according to the literature review, may be physical, such as ambient temperature and light, as well as behavioural (individual or social): (food, activity, stress and emotion). In addition, Wever (1982) actually calls for investigations into the type of social zeitgebers that effect mutual T_b synchronisation, because all that's clear is that it must somehow be based on mutual social contacts.

In a study in which physical modulators are held constant by keeping and monitoring subjects in similar or the same environmental circumstances, it is argued that the individual differences in T_b would to some extent be socially induced. In this study, the social condition appears to exert an important effect because despite the fact that the variances for all five subjects are significantly different $p < .01$, there is homogeneity of variance between those subjects living alone, and those living in a troop, indicating that they belong to two different populations (Cochran's analysis of homogeneity of variance; see section 5.4.1). Examining these results, it is further argued that thermoregulation is more efficient in the troop-living subjects because the standard deviations, that is, the extent to which T_b oscillates around the mean, is greater in those subjects living alone than in the troop-living subjects.

5.6 CONCLUDING COMMENT.

The discovery of a rhythmic T_b cycle of daily peaks is consistent with the literature; so, too, is the finding that individual differences exist. Since this thesis postulates that physiological, behavioural and social functioning are interconnected, the question that now needs to be asked is: How does the behaviour, the social activity and the social condition of each subject help to explain the T_b differences?

Answers are postulated in the chapters that follow.

CHAPTER SIX

BEHAVIOUR

6.1   INTRODUCTION.

Turning from a physiological level to a behavioural level of functioning, an ethological approach was employed for an in-depth examination of the behaviour of each subject.   The aim of this enquiry was to explore those components of behaviour which characterised the subjects living within a troop and the subjects living in isolation, and which distinguished each of the troop-living subjects.

The ethological approach, in keeping with this project, attempts to preserve an "holistic" view of the situation.   Data was collected through direct observation of all the animal's activities during predetermined time samples.   As Hutt and Hutt have stated: "only direct observations by an observer is both sufficiently flexible and sensitive to record the nuances which ultimately may prove important" (1970: 8).

In this chapter the reduction of behavioural information into factors is discussed because in attempting to describe the whole spectrum of behaviour such a vast amount of information was generated (three volumes of raw data are available on request).   A comparison has been made between an arbitrary formulation of behavioural factors according to the researcher's hypotheses, and factors which were statistically derived from a factor analytic programme without prior hypotheses as to the number and nature of the factors.   The imposed groupings of behaviours have been termed the "functional categories", and the statistically computed groupings of behaviours have been labelled the "derived factors".   It is argued that these two procedures complement one another.   Both sets of factors were used to investigate the social conditions of the subjects, the presence of a troop activity cycle, and the individual differences of the troop-living subjects, as they were superimposed upon this activity cycle.

6.2 LITERATURE REVIEW.

6.2.1 The activity cycle.

> ... not only are species typical characteristics of behaviour subject
> to natural selection, but so also is the order and timing of their
> performance.
>
> McFarland, 1976: 89.

A circadian rhythm of alternating periods of sleeping and waking has
been reported for all primates, and the cycling is linked to optimal
functioning for this vision-dependent group of animals.   Monkeys, apes
and most larger Madagascar lemurs have acute diurnal vision, but are
virtually blind after nightfall, so would soon fall prey to nocturnal
predators if they left their inaccessible sleeping perches in trees or rocks
at night.   Thus these primates are awake during the day and sleep at
night.   This pattern of behaviour works well in the tropics, where most
subhuman primates live, because day and night are of approximately equal
length throughout the year and the daily transition from daylight to dark
is rapid.   At latitude 50°, however, a diurnally adapted primate would
have only eight hours to forage on a midwinter day, the very season that
food is most difficult to find.   Similarly, nocturnally adapted prosimians
would have only seven hours of foraging between sunset and sunrise in
midsummer, and hence they would be at a severe disadvantage compared
with smell-orientated animals like rodents (Chance and Jolly, 1970).

McFarland (1976) emphasised that natural selection operated not only
on species-typical characteristics of behaviour, but also on the order and
timing of their performance.   He has developed a procedure for
formulating a cost-benefit function, representing the balance of costs and
benefits of the various aspects of the behaviour of an animal in its
environment.   He has hypothesised that this "cost function can be used in
optimality computations to predict sequences of behaviour that should occur
under observed circumstances and conditions" (p. 90).   The temporal
regulation of food intake, for example, "is based conceptually on a balance
between the energetic needs of the organism and the availability of food
...   To understand a species's daily pattern of feeding motivation, we
have to be informed about both" (Daan, 1981: 285).   Thus within the

limits set by metabolic requirements to the temporal spacing of food
intake over 24 hours, species have evolutionarily adjusted their daily
foraging to times when optimal foraging is predictable.

Fentress (1976) suggested that the boundaries of different behaviour
patterns may be more fluid than we suspect, and therefore further studies
into the context of occurrence and control of well established species-
typical and acquired stereotyped movement sequences are required. He
maintained that this would help to clarify the integrative dynamics of
organisation in motivational systems and the relationship between transient
expressions of behaviour and more permanent rules of behaviour. Possibly
comprehensive analyses following the theories of functional organisation of
behaviour as proposed by Salzen (1979), Luria (1980) and Satinoff (1982a)
could be usefully applied here. This should enhance our understanding of
the underlying mechanisms of behavioural sequences and their interrelationship
with endogenous and exogenous factors.

Jolly (1970) asserted that the absence of any worked-out method for
recording the daily pattern of activity has led to a somewhat
undifferentiated picture of the behaviour throughout the day. As an
increasing number of studies are reported, and species differences as well
as seasonal differences within the same species become apparent, the
picture still seems blurred. Furthermore, as Sussman, O'Fallan, Sussman
and Buettner-Janusch (1979) pointed out, the 'improper' analysis of data
by various researchers complicates comparisons.

In most species a morning and afternoon peak of activity with a
midday two-hour siesta is exhibited. It has been shown, however, that
among the patas each component activity presents a distinct pattern in
relation to the distance travelled during the day; for example, a morning
and afternoon feeding peak was observed, but only when the distance
travelled was large (Jolly, 1970). Daan (1981) confirmed that in diurnal
species two daily peaks of activity and two daily peaks of food intake "are
not uncommon" (p. 285). The increased level of food intake in the
morning has often been attributed to hunger as a consequence of nocturnal
deprivation and the afternoon peak to storing an extra measure of reserve
in anticipation of the nocturnal fast. Rhythms in activity, eating and

drinking have been reported for many vertebrate species including primates (see Rusak 1981: 186-187). Although there are many reports of different primate species yielding different activity profiles (e.g. Bernstein, 1971); of the same species behaving differently in different environments (e.g. Bishop, 1979); under different weather conditions (Bernstein, 1972; Clutton-Brock, 1974); and in different seasons (Yotsumoto, 1976); the activity-rest rhythm has been found to free-run (Wever, 1982). Thus it seems to be an endogenous cycle, modulated by environmental zeitgebers. Kripke (1982) probed further and stated that "evidence for about 90-120 minute activity cycles in monkeys have come from a gratifying diversity of laboratories ... in chaired and caged solitary monkeys ... in social settings and in free ranging models. These 90-120 minute cycles seem to be dramatic, repeatable and of large amplitude ... These cycles are expressed not only in general activity and rest but specifically in ingestive and oral behaviours, in exploration, and in social interactions. From the ethologic viewpoint, such cycles suggest a profound periodic aspect in the organisation of primate behaviour" (p. 326).

Exploring the interrelationships between different behaviour patterns Bowden, Kripke and Wyborney (1978) studied ultradian rhythms in rhesus monkeys and found that ingestion, locomotion, exploration, self-grooming and resting each exhibited a statistically significant peak during the day. Locomotion, exploration and ingestion were in phase with one another, and tended to occur in that sequence, and these behaviours were out-of-phase, that is reciprocal to, resting. Self-grooming, while perhaps cyclic, "was not significantly related to the orality-locomotion-exploration complex" (p. 929). The authors found a similar patterning of behavioural activities in vervet monkeys. Bowden, Kripke and Wyborney viewed their findings as being "consistent with the view that oral cyclicity is one component of a more general cyclic behavioural pattern. Whether the cycle here should be considered a basic rest-activity cycle remains an open question" (p. 932).

Rusak (1981) cautioned against accepting rhythmicity results too readily – individual differences remained to be identified, and a population average may not reflect the actual activity pattern of any single animal. A second issue he pointed to was the difficulty in developing appropriate definitions of behavioural categories. Kripke (1982) maintained: "we need

to derive a new family of hypotheses that can be more operationally defined in terms of concrete experimental models ... it is likely that some of the phenomena we have been studying are so unstable that they can only be regarded as quasi-periodic" (p. 336).

The daily free ranging activity pattern of the vervet troop being studied has been recorded by the author (Tollman, 1977). It was relatively constant and similar to that described for vervets by other researchers (Struhsaker, 1967b; Gartlan and Brain, 1968; Hall, 1968b; Basckin and Krige, 1973). The author found that the daily activity rhythm consisted of sleeping at night, an active phase in the morning, a rest phase for ± two hours at midday, another active phase in the afternoon, and back to sleeping at night. When the vervets woke at sunrise, they migrated toward the upper branches of the trees to bask in the sun and groom one another, while the younger members of the troop played most of the time. An eating peak followed, punctuated by troop movements towards the various food sources, and this behavioural activity continued until the midday rest period. In the afternoon a similar sequence of activities followed. A period of 'socialising' and 'grooming' with aunting circles, play, and even water games, was followed by a second peak of eating in the late afternoon. It is notable that these cycles and sequences of behaviour reported in 1977 coincided with Bowden, Kripke and Wyborney's (1976) description of ultradian rhythms in individually housed adult male rhesus monkeys. The observations were also consistent with Kavanagh's assertion (in Clutton-Brock and Harvey, 1977) that in *Cercopithecus aethiops* "feeding activity peaks in the first half of the morning and the second half of the afternoon" (p. 548). Despite inter and intraspecies differences, therefore, the behavioural processes do not appear to be exhibited randomly, but seem to follow an organised rhythmic pattern.

6.2.2   The categorisation of behaviour.

It is often forgotten that an animal in an experimental procedure
already has a well established behavioural repertoire and that
knowledge of this repertoire may be essential to understanding the
results of an experiment.

Hutt and Hutt, 1970: 4.

"The first aim of the study of the behaviour of a particular animal is to record it in all its detail", wrote Carthy (1966: 1), a "well-known ethologist" according to Hutt and Hutt (1970).   A major difficulty of this procedure lies in trying to systematise the vast amount of data that is generated.   Simpson and Howe (1980), in studying the social development of rhesus monkey infants, were faced with "a very large number of different measures of the relationships the infants have with their mothers". They reduced their data by analysing the extent to which the different measures could be classed into groups, with members of each group being correlated relatively highly with each other, but less highly with those of other groups.   Clustering "extracts typologies from data which in turn represent a reduction of data complexity and may lead to conceptual simplifications" wrote the statistician Krippendorff (1980: 259).

Fairbanks, McGuire and Page (1978) identified behaviour clusters "through factor analysis of individual behaviour profiles over time and across groups of different composition in a captive vervet monkey *(Cercopithecus aethiops sabaeus)* colony" (p. 335).   The objective, according to these researchers, was to identify which behaviour clusters could best be viewed as social roles, and which are more accurately described as developmental stages or invariant characteristics of individuals.   Fairbanks, McGuire and Page claimed that factor analysis is a "new approach to this problem" (p. 336) because traditionally quantitative studies of social roles have used either a functional or a descriptive approach, which do not produce roles as a complex of related behaviours which have meaning in a social and a biological sense.   The functional approach involves choosing a set of behaviours which are judged to be functional for the social group (e.g. responding threat) and then recording which individuals or age-sex classes perform these behaviours.   The descriptive method is to choose the individuals which constitute the role groups.   Their troop consisted of

eighteen vervets of which four were adult females.   Eighteen behaviours were reduced to six factors.   Each factor was "assessed through examination of (1) the behaviours contributing to each factor; (2) the properties of the factors across groups; and (3) the distribution of individuals along the factor dimensions.   Three of the clusters were judged to represent the social roles of Control Male, Control Female, and Subordinate, and the other three described the behaviours associated with the developmental stages of yearling (playful-protected), juvenile female (infant focus) and juvenile male (sex-play)" (p. 335).   This procedure is useful because behavioural groupings achieved statistically may help to eliminate bias, and can be compared to categories chosen by the researcher. The labelling of the clusters in terms of roles may be promising but, as discussed in the section on roles, needs further examination particularly in terms of ultimate function as advocated by Chalmers (1979);   for example, is 'Subordinate' a role in its own right?   In addition, individual differences are obscured when statistical testing is used to extract an average animal (Slater, 1981).   The papers by Fairbanks, McGuire and Page (1978), and Simpson and Howe (1980), will be considered further in the discussion.

McGuire, Raleigh and Johnson (1983) looked at social dominance in the adult male vervet of St. Kitts.   These researchers have grouped the different behaviours observed according to what they perceive as functional categories for social dominance while acknowledging that differences among investigators concerning functional categories renders cross-study comparisons difficult.   For example, in different studies the number of behaviours associated with social dominance varied from a few to many and overlap was not always achieved, or similar motivations assumed to underlie similar behaviours in two or more species.   McGuire, Raleigh and Johnson asserted that to think in terms of functional categories (e.g. foraging/nutrition) "is attractive, nonetheless, primarily because natural selection may differentially affect subgroupings of behaviours associated with particular activities and/or behavioural consequences" (p. 93).   They added that the use of functional categories has heuristic value, and can facilitate data organisation, cross-species comparisons and the development of theory.   The contradiction regarding cross-species comparisons is confusing.   Perhaps these researchers meant if there was agreement about functional categories meaningful dialogue will be generated.   They applied the following criteria to their

functional categories:

1. Behaviour associated with categories were identified.

2. Environmental and social variables which affected the frequency of behaviour within a category were specified.

3. Conditions under which behaviours occurring in one category influence the frequency and form of behaviours in other categories were identified.

4. Where possible, tests were employed to determine if within-category behaviours have behavioural consequences.

The functional categories used in their study were individual, affiliative, kin-related and social dominance. This procedure is useful, these authors claimed, because the categories selected would relate to the questions bring asked.

Some consensus about the procedures and criteria for establishing behavioural factors seems indicated. Categorisation discrepancies would arise from a variety of sources: individual and species differences, diverse situations, dissimilar age-sex composition and varying statistical procedures.

Nash and Chamove (1981) maintained that all the studies they have reviewed on primate behaviour and personality have isolated a sociable dimension, a fearful dimension, and "two report finding an aggression dimension" (p. 89). They pointed to the early work of selective breeding, where strains of 'hi/lo' emotional rats, 'maze bright' and 'maze dull' rats, and aggressive and non-aggressive rats separated out. Nash and Chamove began their research with a factor analysis of a group of thirteen laboratory-born stump tailed macaques, and this yielded a strong first factor of 'dominance'. The question arose as to whether these characteristics were a function of their dominance position or their personality. More recent studies, according to Nash and Chamove, employ factor analytic techniques in an attempt to parallel the work on human personality. Van Hooff (1970), using a component factor analysis for the behaviour of a captive group of chimpanzees, found four factors: "socially positive"; "play"; "aggression"; and "submission". Chamove, Eysenck and Harlow (1972) identified "three clear behaviour factors: fearful, hostile and affectionate. These patterns of behaviour are not dissimilar to those which give rise to the three major factors in research on human

personality: neuroticism-stability, extraversion-intraversion and psychoticism"
(Chamove, Eysenck and Harlow, 1972: 502).   The 'affectionate' factor has
been interpreted as 'sociable' by Nash and Chamove (1981).   Stevenson-
Hinde and Zunz (1978) produced three main components in a principle
components analysis on ratings of laboratory rhesus monkeys: Confident-
Fearful, Active-Slow and Sociable-Solitary.

The necessity for some agreement about functional categories is
clear.   It is proposed that comparisons between categories that have been
logically imposed upon the data by each particular researcher, and
statistically derived factors from the same data may be useful.   The
former could act as the hypotheses which are then examined by statistical
procedures.

6.2.3   Individual differences.

> Given that variation among individuals is the raw material on which
> natural selection acts, it should certainly not have been neglected
> in the way that it has.
>
> Slater, 1981: 47.

Buirski, Plutchik and Kellerman (1978) maintained that "the idea that
primates show emotions and have definite personalities is widely noted in
the literature (Hebb, 1946; van Hooff, 1962, 1967 and Bolwig, 1964)"
(p. 123).   Nash and Chamove (1981), on the other hand, asserted that
primatologists working in both laboratory and field settings have "largely
ignored the role of personality in an individual's behaviour" (p. 88).   It
seems that although individual differences are acknowledged, in their attempt
to look for general laws researchers tend to average out their data so that
individual differences are lost.   Whenever means are calculated, the
standard deviations must be taken into account, as a first indicator of the
extent of individual differences.

Saayman (1971) pointed to individual differences.   The assertion by
Wilson (1975) that when Saayman spoke of the "roles of three male chacma
baboons in one particular troop as coincident with detailed differences in their
behaviour he stretched the definition too far" (p. 299) does not seem tenable
for any study which attempts to come to grips with the complexity of the
situation.   Nash and Chamove (1981) found their dominant animals (refer to
6.2.2) showed more positive social behaviour, did less visual monitoring,

were more disturbed when removed from the rest of the group, and exhibited more self-aggressive behaviour. Cheney, Lee and Seyfarth (1981) have looked at dominance rank among female vervets. They have identified differences in personality styles and suggest that rank may not reflect an index of fitness, but rather the different personality styles. This data supports Bolwig's (1978) investigation of aggression in several species of African monkeys including the vervet monkey. Individual differences were apparent. "Casual observations", he wrote, "seemed to indicate that the members of the various monkey groups were not equally aggressive and did not distribute their aggression evenly" (p. 78).

Generally, it seems the sociable dimension is more highly developed in the adult females (please refer to the section on females), although several studies have noted marked individual differences. McKenna (1978), working with langurs, wrote that although "adult females initiated grooming at rates significantly different (p < 0.01) than either immature males or females, there is much variation within age and sex classes which deserves attention ... it is important to realise that general interclass distinctions can often differ from the behavioural records of individuals" (p. 504). Dolhinow, McKenna and Von der Haar Laws (1979) also noted that in langur monkeys "inclination to interact varies tremendously among adult females – from low to high regardless of age" (p. 28). Buirski, Plutchik and Kellerman (1978) confirmed these findings for all primates. Using ratings on an Emotion Profile Index they characterised dominant animals as aggressive and distrustful and subordinates as timid. Nash and Chamove (1981) asserted that dominance seems to have such a pervasive and restrictive influence on behaviour that it is only through experimental or statistical control that one can separate dominance from personality. In a follow-up study of their stump tailed macaques they have discovered that some of the behaviours which initially seemed to be correlated with dominance are a function of the individual in that dominance position and not of dominance per se. The problem that now remains is how to separate dominance effects from personality effects, particularly since there is an element of interaction between dominance and personality. In experimental manipulations they found that some animals adapted better than others to positions of dominance and subordinance.

An assessment of the contributions of all the factors that contribute

of enquiry is, the principle of epigenesis needs to be remembered. Environmental influences have been shown to have important and longlasting effects upon behaviour. For example, Johnson, Gilbert and Herdt (1979) carried out ethological observations of maternal and infant behaviours of nine vervet monkey pairs *(Cercopithecus aethiops sabaeus)* and discovered that certain qualities of maternal responsiveness and the frequency of early contact in mother-infant pairs corresponds to attributes of infant competence and social integration at six months of age. "Mothers who were most responsive had infants who were likely to be less competent in the last three months of the study" (p. 31). These authors also mentioned studies which indicate that infant status positions are learned. Will we ever be able to separate personality from all these factors?

Slater (1981) explored the reasons for individual differences in animal behaviour and pointed to various ways in which they deserve closer study. Slater maintained that differences in feeding, mating or fighting behaviour may occur because selection favours the adoption of different strategies by different individuals. Variations in signals may arise through selection for animals to be identifiable as individuals or for their relatedness to others to be assessed. He suggested that variation may arise because the exact form of the behaviour being measured makes little difference from the point of view of selection, and that variability in other cases may come about because in an unpredictable environment the best course of action cannot be forecast.

Slater also dealt with the limitations of statistics. In many studies "statistical testing is used to extract an average animal from each group and provide justification for ignoring those which behaved differently. It is the main contention of this article that individual differences in behaviour should not be treated so lightly and that there are important reasons why they deserve examination in their own right" (p. 36). The author submits that the cost-benefit ratio for this type of study is not favourable: that a one-variable measure validated on a relatively large number of animals, rather than an in-depth ethologically based multilevel examination of three animals seems favoured by most editors even though the actual time spent on collecting data may be equivalent. This is particularly important at the present time of economic stringency, when it is relatively difficult to

obtain research grants.

Slater concluded his article with the following question: "This variation in variability presents a challenge which is particularly important at a time when interpreting behaviour in terms of natural selection is the fashion: does variability exist because it is irrelevant as far as selection is concerned or because selection actively encourages it?" (p. 47).

In this study, marked individual differences were evident, at each of the levels studied.

6.3 PROCEDURE.

More than 760 hours of behavioural observations have been recorded by the author since she first began observing *Cercopithecus aethiops pygerythrus* in 1975 (see Chapter Three).

The present research enquiry began with a pilot study in which a procedure was developed for collecting thermal, behavioural and social information concurrently from a free-ranging subject in an ongoing social situation. This was followed by in-depth behavioural and social studies of each of the five vervet monkeys with temperature-sensitive transmitter implants described in section 5.3.2. In addition to behavioural observations of each of these subjects, the activity of the caged troop had to be monitored because the troop members formed the context within which the troop-living subjects operated.

Interobserver agreement regarding the dominance status position of the three troop-living vervets was assessed in an additional series of observations in conjunction with two other researchers (to be discussed in Chapter Seven). A total of 114 hours of behavioural observations were recorded during this time.

6.3.1 Data collection.

For this study, 840 five-minute focal time-samples of behaviour were

collected in conjunction with T_b. These time-samples of behaviour were rigorously randomised across subjects and over different times of the day (see section 5.3.3 and Table 5.1). A troop scan was conducted before and after each focal time sample.

A five-minute sample was selected following the rationale of Hutt and Hutt (1970) that the smaller the time interval the more representative the sample, and the more comprehensive the report. Five minutes seemed long enough to monitor behavioural sequences including interactions with the rest of the troop, yet short enough to permit several observations of each animal per day.

All data was recorded verbally onto cassette tapes which played continuously to preserve the time sequence. In addition, a stopwatch for timing sequences, binoculars for visibility, videotapes, 35 mm slides, and black and white photographs for recording specific events were used to enhance the accuracy of data collection.

6.3.2   Data processing.

The time sequence of the behavioural information has been preserved, and each five-minute sampling unit has been transcribed on to three different charts: an activity matrix, a 3 x 8 interaction matrix, and a spatial distribution/movement plan. Two further files were compiled. The first, a diary, recording the most important events of each day, and noting any information not encompassed by the charts. The second file contained profile sheets for each animal, so that any behaviour or unusual occurrence specific to a particular animal could be noted.

The activity matrix :

The activity matrix developed by the author is an ethogram which includes as many behaviour patterns as possible. Since its creation, this tool has been used effectively in masters and doctoral research conducted in the Department of Psychology, University of Natal, Durban, and was also adopted by Dr J. Jacobs for her Ph.D. research carried out in the

Psychology Department of University College London (Jacobs, 1983). The activity matrix has been designed to allow simultaneous recording of the frequency, duration and sequence of each behaviour within a time sample, and to permit comparisons between solitary and social, and friendly and agonistic activities. It consists essentially of parallel ethograms each superimposed upon a grid, which can be modified to represent a time scale, or comparisons of recordings, or inter or intraindividual activity. Four charts were designed for this research project (see Charts 6.1, 6.2, 6.3 and 6.4 respectively).

As can be seen in Chart 6.1, the abscissa consists of a range of discrete behaviour patterns, and the ordinate reflects a time sample of five minutes, divided into ten-second time units. This matrix reflects the activity of one individual for five minutes. Charts 6.2, 6.3 and 6.4 provided for the synthesis of information collected during a randomised block of recordings (see Table 5.1; N = 75 per subject). In all these charts the abscissa remains the same and the ordinate is altered. Chart 6.2 is a summary of all the activities of each individual subject at a specific level (period) of the day. The ordinate provides for the frequential and durational totals of each behaviour for each of the fifteen five-minute recordings, in sequence, collected at the same period of the day, during a five-week monitoring block. Chart 6.3 allows the daily activity cycle for each individual subject to be collated. In this matrix, each behavioural score (durational and frequential) at each level of the day can be compared and an overall total can be calculated. Chart 6.4 enables between subject comparisons for each behavioural item within the entire spectrum of behaviour. Space for three subjects was allotted, because that was the maximum concurrent T_b monitoring capacity of the receiver. This chart can be used for between subject comparisons at any particular level (period) of the day, or for comparisons of a composite picture eliminating day-level differences. A visual pattern of activity emerges if the column corresponding to the behaviour is shaded in Chart 6.1 and a number or bar graph is filled in on Charts 6.2, 6.3 or 6.4. By placing three ethograms parallel to one another, comparisons between non-social and social, friendly and agonistic activity is facilitated.

ACTIVITY MATRIX   subj ...5..... tape .13 B.... date 2.6.5.77.. time 11.13... block1. w.4. level 2.5... weather 3...... ambient T .13... intern. T 21.2. mean T 21.369 dist. trav 17... pref. posn. 1.....

1. INDIVIDUAL	NON-SOCIAL										TOTAL D	F	SOCIAL : AGONISTIC participants S3; with TU eyeing S3 seems to be chasing then harassed by subad.										TOTAL D	F	SOCIAL : FRIENDLY participants INF, S3, subad TU eyeing S3										TOTAL D	F	TOTAL D	F	MEAN D	F
activity time(secs)	30	60	90	120	150	180	210	240	270	300			30	60	90	120	150	180	210	240	270	300			30	60	90	120	150	180	210	240	270	300				
1. Approach																			•																			
2. Attacking																																						
3. Attacked																																						
4. Avoiding																	• • • • • •			60	2														60	2		
5. Avoided																																						
6. Biting																																						
7. Bitten																																						
8. Chasing																																						
9. Chased														• • • • • • •			60	2														60	2		
10. Chewing																																						
11. Climbing	•				• •					30	2																								30	2		
12. Coalition																																						
13. Displaying																																						
14. Eating																																						
15. Following																																						
16. Gaping																																						
17. Grabbing																																						
18. Grabbed																																						
19. Grooming (auto)																																						
20. Groomed																																						
21. Huddling																								•									10	1	10	1		
22. Ignoring																									•			•				20	2	20	2		
23. Investigating																																						
24. Interfering																																						
25. Joining																											•					10	1	10	1		
26. Jumping																																						
27. Licking																																						
28. Lying Down																																						
29. Presenting																																						
30. Presented to																									•							10	1	10	1		
31. Protecting																																						
32. Protected																																						
33. Pushing																																						
34. Pushed																																						
35. Redir. Aggr.																																						
36. Running		•	•		•					30	3																								30	3		
37. Scratching																																						
38. Sexual																																						
39. Sitting	•				• • •					40	2													•							10	1	50	3		
40. Sniffing																									•			•				20	2	20	2		
41. Standing			•							10	1														•							10	1	10	1		
42. Submission																																						
43. Supplanting																																						
44. Supplanted																																						
45. Threatening																																						
46. Threatened																																						
47. Touching																																						
48. Touched																																						
49. Trav. Perimeter	• •	• •	• • • • • • •						110	3																								110	3		
50. Vigilant																																						
51. Walking			•							10	1																	•				10	1	20	2		
52. Yawning																																						

NOTES

Sniffed S3, who seemed to invite her to groom, which she ignored...

ACTIVITY MATRIX | Comparative Time Samples | subject ...4... | date 2/1 ... block ...... | level ....

2 INTRAINDIVIDUAL — NON-SOCIAL | SOCIAL : AGONISTIC | SOCIAL : FRIENDLY | TOTAL | MEAN

time samples (5 min) 1–15 each section, with D / F columns.

Activity	NON-SOCIAL TOTAL D	F	AGONISTIC TOTAL D	F	FRIENDLY TOTAL D	F	TOTAL D	F	MEAN D	F
1. Approach			20	2			20	2	1·3	·3
2. Attacking										
3. Attacked										
4. Avoiding			10	1			10	1	·67	·3
5. Avoided			10	1			10	1	·67	·0
6. Biting										
7. Bitten										
8. Chasing										
9. Chased										
10. Chewing										
11. Climbing	130	13					130	13	·87	·8
12. Coalition										
13. Displaying										
14. Eating	1030	113			120	1	1150	114	7·67	·7
15. Following										
16. Gaping										
17. Grabbing										
18. Grabbed										
19. Grooming (auto)	370	8	10	1	30	2	400	10	93·3	·6
20. Groomed					50	2	50	2	3·3	
21. Huddling										
22. Ignoring					20	2	20	2	4·8	
23. Investigating										
24. Interfering										
25. Joining			10	1			10	1	·4	·3
26. Jumping										
27. Licking										
28. Lying Down	50	3					50	3	3·3	·2
29. Presenting										
30. Presented to										
31. Protecting										
32. Protected										
33. Pushing										
34. Pushed										
35. Redir. Aggr.										
36. Running	220	14					220	14	1·47	·9
37. Scratching	140	13					140	13	·93	·8
38. Sexual			20	1			20	1	·3	·0
39. Sitting	1120	29			70	1	1190	31	7·93	2·1
40. Sniffing										
41. Standing	150	5					150	5	33	·3
42. Submission										
43. Supplanting										
44. Supplanted			10	1			10	1	·6	·3
45. Threatening										
46. Threatened			20	2			20	2	1·3	·3
47. Touching					20	2	20	2	1·3	·3
48. Touched					10	1	10	1	·6	·0
49. Trav. Perimeter	850	23					850	23	5·67	1·5
50. Vigilant	280	9					280	9	1·87	·6
51. Walking	190	17					190	17	1·27	1·1
52. Yawning										

NOTES

ACTIVITY MATRIX | Activity Cycle   subject ..3..........   date 24 - 19 5. block ..1.......   int. temp. sA 0,211 : sB 0,233 : sC 0,263 :

INTRAINDIVIDUAL	NON-SOCIAL						SOCIAL : AGONISTIC						SOCIAL : FRIENDLY				TOTAL	MEAN
activity / level	1	2	3	4	5	TOTAL	1	2	3	4	5	6	TOTAL	1	2	3	TOTAL D F	D F
1. Approach															20 1	30 3 50 5	80 9	16
2. Attacking																		
3. Attacked																		
4. Avoiding																		
5. Avoided							20 2 50 3 40 4 70 7 50 4	230 20						10 1			240 21	48
6. Biting							10 1	10 1										
7. Bitten							10 1	10 1										
8. Chasing							30 1 20 1 20 2	70 4									70 4	
9. Chased																		
10. Chewing	30 3					30 3											30 3	
11. Climbing	90 9 30 3 110 11 100 10 60 14					490 47								10 1	10 1	490 47	98
12. Coalition							90 1	70 1 190 2 120 2 40 2 20 2	50 2 520 10	10 1	520 10	122
13. Displaying																		
14. Eating	1000 13 290 4 460 11 510 12 740 49									50 1 100 1 80 1	40 4				
15. Following									10 1 10 20 2 10 1	40 4			40 4	
16. Gaping																		
17. Grabbing									10 1			20 2	4	
18. Grabbed										130 3	260 6	52	
19. Grooming (auto)	420 260 3 40 3 40 3 200 9 700 32									1080 1 240 2 980 25	760 2 460 9 570 26	443 28	
20. Groomed										120 3 100 3 360 7 380 580	820 30 870 30	373	
21. Huddling										80 2 160 3 50 1	210 6 590	
22. Ignoring										10 1 20 2	30 270 6	54
23. Investigating	20 2 80 5 150 10 260 18								10 1	270 9	54
24. Interfering																
25. Joining							30 40 4	10 1 20 2	60 6 60 6	12
26. Jumping	50 5 50 5 30 3 20 2 150 15									150 15 32
27. Licking									10 1	10 2
28. Lying Down	10 1 70 2 20 100 4							30 3 20 2 10 160 6	160 10 32
29. Presenting									10 1	10 1 2
30. Presented to									10 1	10 20 2 20 2 4
31. Protecting											
32. Protected											
33. Pushing							10 1 10 1	120 2			120 2 4
34. Pushed											
35. Redir. Aggr.											
36. Running	20 1 10 1 20 2 10 1 80 6							80 6 16
37. Scratching	10 10 210 84 400 33 330						10 1	1070 9 1200 182
38. Sexual							10 1	40 3 50 3 100 7	100 7 20
39. Sitting	610 24 530 555 3 960 28 610 3100 118						460 10 490 64 490 12 430 11 400 11 270 15 370 17	1074 349
40. Sniffing	20 2 20 2						10 1 20 2	30 3 50 5 10 1
41. Standing	80 8 20 4 80 7 20 330 27						10 1	10 1 20 2 350 29 70 5
42. Submission	10 1 10 1								10 1 2
43. Supplanting							20 2 10 1	30 3	10 1	40 4 8
44. Supplanted							40 1 40 1		40 1 8
45. Threatening	20 2 20 2 90 1	130 5		130 5 26
46. Threatened	10 1 10 1	20 2		20 2 4
47. Touching	10 1 10 1	60 4 60 3 10 1 40 3 170 11	180 12 36
48. Touched										
49. Trav. Perimeter	20 1 20 1						20 1 20 1 40 2 8
50. Vigilant	790 18 280 9 70 4 420 13 280 14 1290 58						10 1 10 1 30 1 50 3 179 6 2358 122
51. Walking	180 14 250 20 380 25 550 34 330 25 1690 118						10 1 20 1 30 2 1720 120 344 24
52. Yawning										

NOTES

CHART 6.4   SPECIMEN OF INTERINDIVIDUAL ACTIVITY MATRIX.   94

ACTIVITY MATRIX subjects 3,4,5 (1,8,2) date 24.-4/5/1977 block ...1... level(s) ...2... int. temp. sA 0,211 : sB 0,233 : sC 0,263 :

INTERINDIVIDUAL activity	NON-SOCIAL	SOCIAL: AGONISTIC	SOCIAL: FRIENDLY	TOTAL	MEAN
1. Approach		20 / 20 2 / 20 1	20 1	40	133
2. Attacking					
3. Attacked					
4. Avoiding					
5. Avoided		50 3 / 10 1 / 110 7 / 170 11	10	180 12	60 4
6. Biting					
7. Bitten					
8. Chasing		30	30 1	30 1	10 3
9. Chased		60 2 / 60 2		60 2	20 7
10. Chewing		10 / 10 1			33 3
11. Climbing	30 3 / 100 2 / 200 19 / 330 34			330 34	110 113
12. Coalition			120 2	120 2	40
13. Displaying					
14. Eating	480 9 / 660 5 / 500 15 / 1640 37		100 1 / 80 3	180 4	1820 46067 137
15. Following			10 1 / 20 2 / 30 3	30 3	10 33 3
16. Gaping					
17. Grabbing					
18. Grabbed					
19. Grooming (auto)	80 3 / 390 / 170 8 / 640 20		2140 22 / 290 5 / 800 / 3230	3870 59	1290 197
20. Groomed			100 3 / 100 5 / 400 / 200 8		67 27
21. Huddling			60 3 / 60 3	60 3	20
22. Ignoring		10 / 10 1	10 1 / 20 2	20 2	50 5 / 60 22
23. Investigating	10 / 40 / 40 4 / 54 9			54 9	18
24. Interfering	10 / 10 1			10 1	33 3
25. Joining			40 4 / 10 1 / 50 5	50 5	167 17
26. Jumping	50 5 / 40 4 / 90 9			90 9	30 3
27. Licking					
28. Lying Down	10 / 100 2 / 110 3			110 3	347 1
29. Presenting		10 1	10 1	10 1	33 3
30. Presented to	10 / 10 1		10 1 / 10 1 / 40 4 / 60 6	70 7	233 23
31. Protecting					
32. Protected					
33. Pushing		10 1 / 10 1		10 1	33 3
34. Pushed		10 1 / 10 1	10 1	20 2	67 7
35. Redir. Aggr.		10 1 / 10 1		10 1	33 3
36. Running	20 1 / 80 / 290 23 / 390 27	10 1 / 10 1		400 28	1333 93
37. Scratching	110 10 / 190 / 180 16 / 480 44			480 44	160 147
38. Sexual					
39. Sitting	390 15 / 1220 30 / 610 36 / 2220 81		490 6 / 410 9 / 160 / 1660	3280 101	1093 337
40. Sniffing	10 / 10 1		20 2 / 20 2 / 40	40 4 / 50 5	67 / 147 17
41. Standing	80 8 / 130 9 / 200 19 / 410 36		10 1 / 10 1	420 37	140 123
42. Submission	10 1 / 10 1 / 30 / 50 3			50 3	167
43. Supplanting					
44. Supplanted					
45. Threatening		70 7 / 70 7		70 7	233 23
46. Threatened		20 2 / 20 2		20 2	67 7
47. Touching					
48. Touched					
49. Trav. Perimeter	820 117 / 840 28 / 1660 35		20 1 / 20 2 / 40	1700 38	567 127
50. Vigilant	280 9 / 550 116 / 150 10 / 980 35		10 1	990 36	330 12
51. Walking	250 20 / 200 13 / 410 33 / 960 66		10 1	970 67	323 223
52. Yawning					

NOTES

Each behaviour pattern was assigned a number. By using these numbers, the information on the Interaction Matrix was extended to include specific behavioural descriptions of the interactions between animals. It also allowed for easy computerisation, although further digits had to be added so that if the same behaviour was performed in varying contexts, each had a separate number, for example, running alone, or running together. A total of sixty-five behaviours were noted and analysed. In an attempt to preserve the gestalt as much as possible, the activity matrices also provided for the inclusion of climatic data, movement patterns, T_b, and the social environment – viz., participants involved in social interactions, and the outcome.

The behaviours tabled in the activity matrix were compiled with the aid of the Primate Group's IBM Computer code, together with the author's field and caged observations.

The Glossary contains a description of each of the behaviours included in the Activity Matrix.

The interaction matrix :

Two interaction matrices were designed (see Chart 6.5 and Chart 6.6). Chart 6.5 allowed for the recording of the individual subject's interactions with the troop during the different levels of the day. Thus, the columns of the abscissa allow for the different troop members, while the rows of the ordinate each represent one level or period of the day. Two matrices are provided, one for agonistic interactions, one for friendly interactions.

The 'Interaction Matrix' of Chart 6.6 enabled a comparison between the interactions of each of the troop-living subjects under study. This interaction matrix consisted of two 3 x 8 grids, one representing 'friendly interactions' and the other 'agonistic interactions' (refer to Chart 6.6). As can be seen, the female subjects were depicted once in a column and once in a row. The remainder of the troop was represented in classes, in the columns only. Thus all interactions of the subjects could be examined in terms of the subjects' relationships with each of the other females in the troop, the adult male, and the classes of subadults, juveniles, and juniors.

CHART 6.5 : SPECIMEN OF INTRAINDIVIDUAL INTERACTION MATRIX.

INTERACTION MATRIX

BLOCK 1

date April 2 – May 4

time sample VERVET B

TROOP	A	B	C	♂	♀	Subad.	Juv.	Jun.
1	4		5,46	44	4			
2					5			
3	4		4,46		5			5
4	44		44(2)		45	5	5(3),44,46	5
5	4(5)				4			
Total	4(7),44		4,5,44(2) 46(2)	44	4(2),5(2),45	5	5(3),44,46	5(2)

DAY LEVEL

AGONISTIC

TROOP	A	B	C	♂	♀	Subad.	Juv.	Jun.
1				14,19,22,39		14,20,25,38 39	14,19,20	14,22,47(2)
2	19(2)			1,19		14,19(2),22, 30,39(2)	19,39(2)	14(2),19,39(2)
3	12,15,18, 19(3)		39	1,19(2),39	1,19,39	19	19(2),20(2) 25(2),38, 39(3),49	12,19(3),28, 39(4),41.
4	19(4),20,25			15(2),19(2) 25,39	12,19(2),38, 39(2)	19(3),22,39	19(2),20(2) 38,39	19(2)39(2) 40,47
5	19(5),39(2)			15(2)19(2) 25,39	12,19(2),38, 39(2)	19(3),22,39	19(2),20(20) 38,39	19(2)39(2) 40,47
Total	12,15,25,18, 19(14),39(2)		39	1(1),14,15(4) 19(6),22, 25(2),39(3)	1,12,19(5) 38(2)39(2)	14(2),19(9), 20,22(3) 25,30,38, 39(5)	14,19(8)20(7) 25(2)38(3) 39(7),49	12,14(3),19(8 22,28,39(10) 40(2),41,47(4)

DAY LEVEL

FRIENDLY

NOTE:

1. Please turn to section 6.3.2 for a description of the matrix. A,B,C refer to subjects 3, 4 and 5 respectively, and the following columns to the classes of subadults, juveniles and juniors respectively.
2. Numbers refer to specific behavioural activities as coded on the interaction matrices.
3. Numbers in parentheses refer to frequency with which the behavioural activity was observed.
4. Dash under numbers denotes passive form, e.g. 1 = was approached; 1 = approachin (These behaviours were given separate numbers in

CHART 6.6 : SPECIMEN OF INTERINDIVIDUAL INTERACTION MATRIX.

INTERACTION MATRIX

date ...April 2 – May 4.......

time sample ...Level 5.........

15h30 – 17h30

TROOP	A	B	C	♂→	♀	Subad.	Juv.	Jun.
A	43			44,46	5(3)	22	5	5
B	4(5)				4			
C	4,44	46			46(2)		35,45	33,46

SUBJECTS (left axis label for rows A, B, C)

AGONISTIC

TROOP	A	B	C	♂→	♀	Subad.	Juv.	Jun.
A		19,20(4),39(2)		19(4),20	17,32	39(2)	1,19(5)20(3)39(4)	1(2),11,18,19(11)20,21(4)22,28,30,39(8)41,51
B	19(5),39(2)			15(2)19(2)25,39	12,19(2),38,39(2)	19(3),22,39	19(2),20(2),38,39	19(2),39(2)40,47
C	1,22			19(5),30,31(3)	19(5),20,31	19	19,20,38,39	1,19,21,39

SUBJECTS (left axis label for rows A, B, C)

FRIENDLY

NOTE: Please turn to Chart 6.5 and section 6.3.2 for a description of the matrix.

CHART 6.7

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SPECIMEN OF INDIVIDUAL MOVEMENT.

RECORD OF SPATIAL DISTRIBUTION / MOVEMENT

DATE .....3 – 4 – 1979.....

TIME .....13h40 : Level 4 Segment 1.....

SUBJEGT 5   36m.....

5 minute time sample.

OBSERVATION
ZONE

CHART 6.8

99
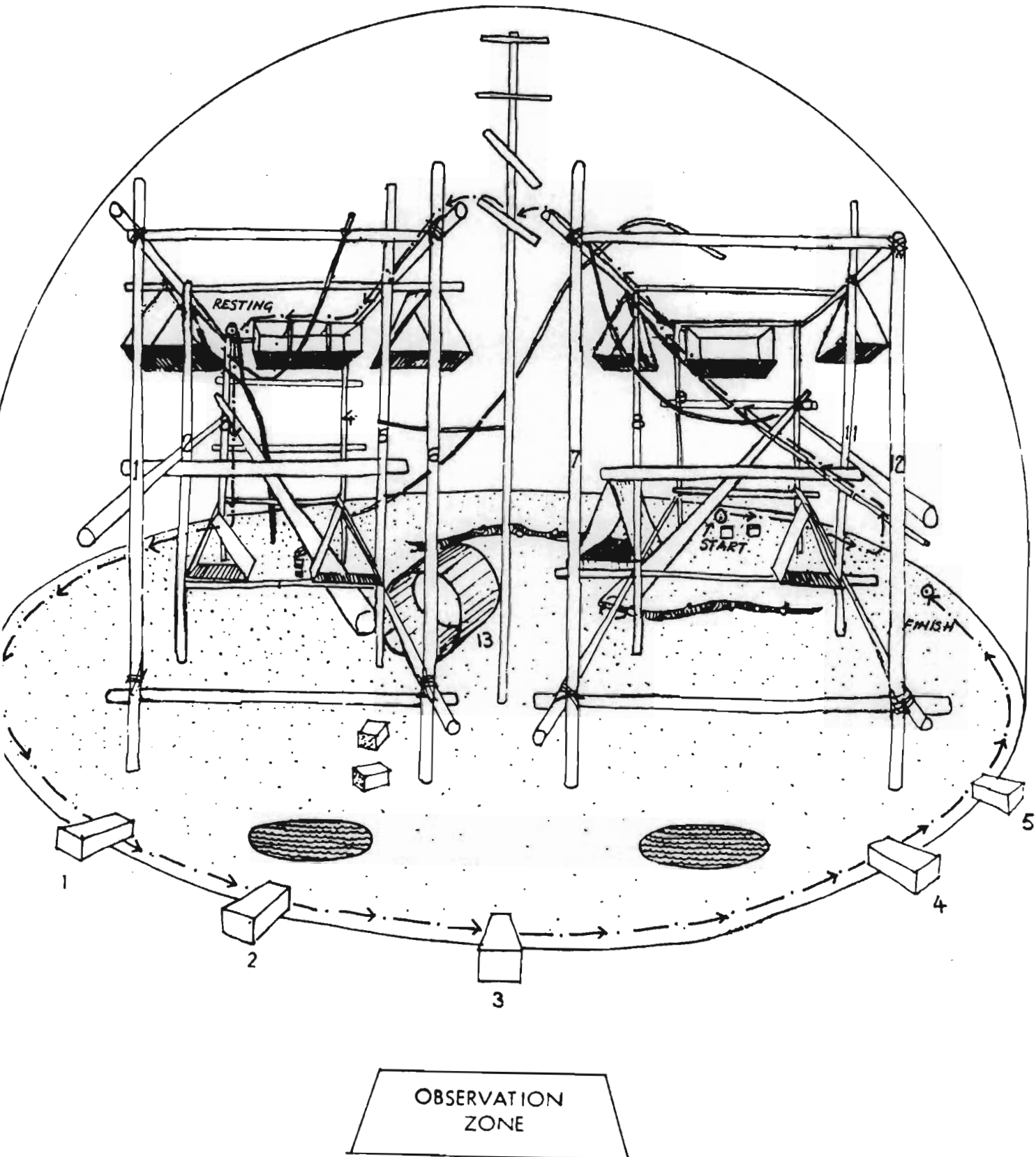
SPECIMEN SHOWING SPATIAL DISTRIBUTION OF TROOP.

RECORD OF SPATIAL DISTRIBUTION / MOVEMENT

DATE . 20 - 4 - 1977 . . . .

TIME . 13h04 : Level 3 Segment 3 . . . .

SUBJEGT . . . TROOP . . . .

Overcast – post rain.

OBSERVATION
ZONE
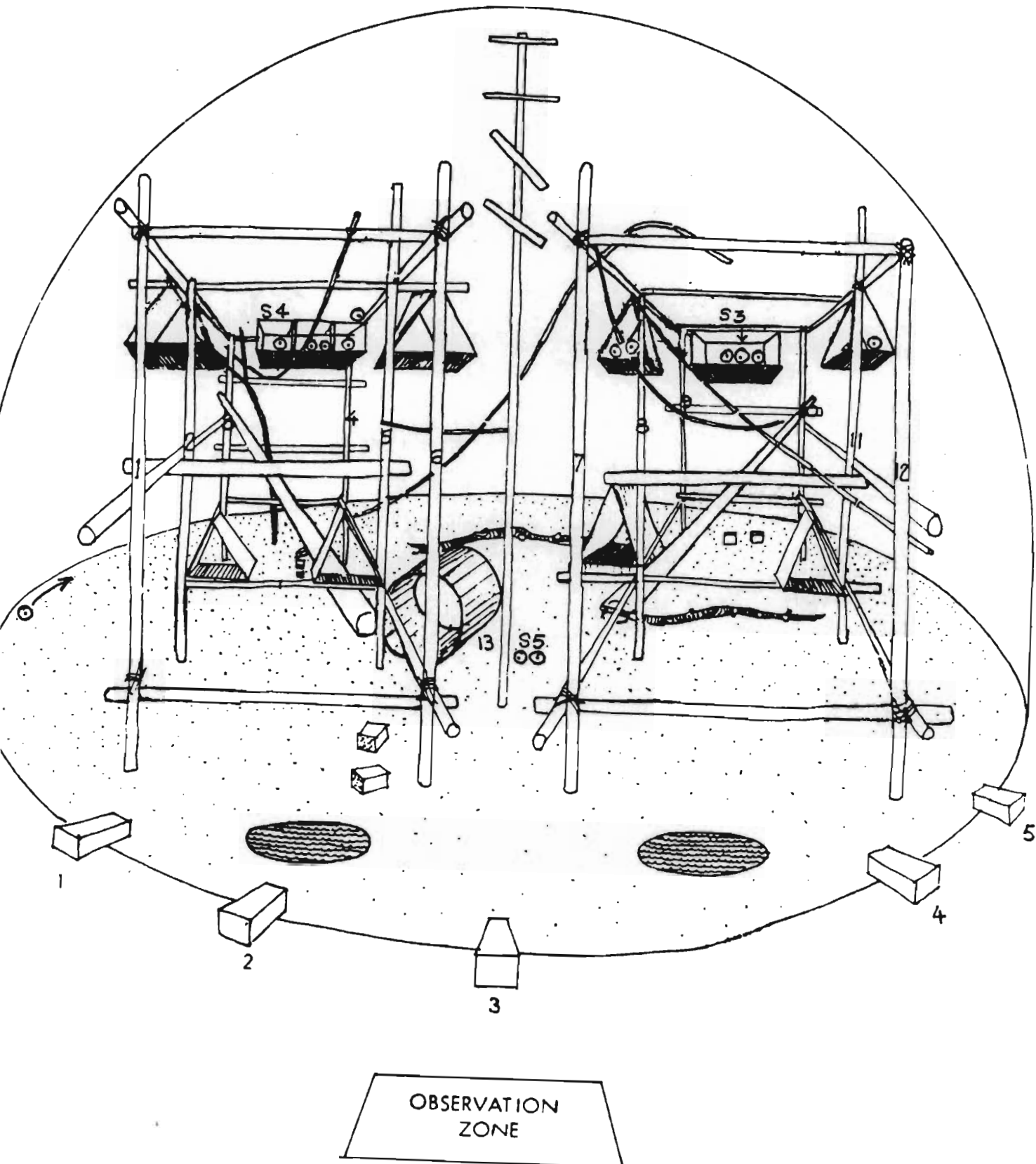
As the tapes were transcribed, all interchanges within and between the troops were immediately recorded in the appropriate square, using the number in the Activity Matrix to describe the type of interaction, and noting the time and the date. One chart was used for every round of timed samples. Morning and afternoon charts were also compiled for interactions not occurring during time sampling.

Movement and spatial distribution charts (refer to Charts 6.7 and 6.8).

The Spatial Distribution Chart consisted of a diagrammatic representation of the inside of the cage, and was used to record individual movement patterns, as well as the troop's distribution in space.

The movement pattern of each vervet during a time sample was traced onto the diagram. Since the size of the dome and frames were known, the distance travelled by each animal during a time sample could also be calculated – thus, for each timed sample, the pattern of movement, and the distance travelled by the individual monkey has been recorded.

The spatial distribution charts are also an effective tool for illustrating the spatial organisation of the troop speedily and efficiently at any moment in time. Each animal has merely to be recorded as a dot on the corresponding position of the chart. A pictorial sequence of the changes in the troop's spatial organisation over time was compiled.

6.4 RESULTS.

The entire spectrum of behaviour observed during each five-minute time-sample was recorded in terms of sixty-five behavioural elements (refer to Appendix 3). The data recorded from the vervets living in the caged troop, that is seventy-five sets of measurements for each animal over five levels of the day, were clustered into two separate sets of factors.

In the first set, each behavioural element was grouped into one of seven factors specified on the basis of the researcher's eight years of vervet study. The factors were hypothesised as being appropriate descriptions of

vervet behaviour, and relevant to the questions under consideration.   These factors have been termed "Functional Categories", after McGuire, Raleigh and Johnson (1983), and the same seven factors were used for the durational and frequential data.   Table 6.1 outlines these factors, and describes the hypotheses in terms of which they were formed.

TABLE   6.1

FUNCTIONAL   CATEGORIES :

GROUPING OF BEHAVIOURAL ELEMENTS TO TEST HYPOTHESES.

Factor No.	Category	Behavioural Elements*	Hypotheses
1 2	ACTIVE PASSIVE	All elements categorised in Factor 1 or Factor 2 except:- coalition = ambiguous trav.per. = recorded in parallel with running or walking.	1. Troop activity and passivity vary over different levels of the day. 2. There are individual differences in activity and passivity.
3	CONTACT	Huddling Touching	3. Troop spatial configuration differs over different levels of the day; between clumping and dispersing. 4. The rhythmic variation in spatial pattern is related to changes in activity and passivity. 5. There are individual differences in contact behaviour.
4 5	SOCIAL NON- SOCIAL	All elements included in Factor 4 or Factor 5, depending whether activity carried out alone or with other animals.	6. There is a variation in sociability over the different levels of the day. 7. The variation in sociability over different levels of the day parallels the rhythmic pattern of activity and passivity, clumping and dispersing. 8. There are individual differences in sociability. 9. The dominant vervet is more sociable than non-dominant animals.
6. 7	SOCIAL FRIENDLY SOCIAL AGONISTIC	26 out of the 29 elements included in Factor 4 distributed into Factor 6 or Factor 7. Exclusions were ignoring, ignored and interfering. It was not clear whether these were friendly or hostile actions.	10. There are individual differences in friendly social encounters. 11. There are individual differences in agonistic social encounters. 12. Friendly encounters are directly related to status - the higher the status, the more friendly encounters. 13. Agonistic encounters are indirectly related to status. The higher the status, the less agonistic interactions.

* For detailed list of activities in each category

In contrast to the first set, all the raw data was also subjected to a factor analysis, without prior hypotheses as to the number or nature of the factors. The durational and frequential data were analysed separately. Before factor analysis was attempted, the behaviour measurements were inspected for independence of means and standard deviations. Suitable transformations were applied to the data to minimise this relationship, and also to reduce the extreme range of measurements.

The Principal axes method of analysis was chosen in preference to a Principal components analysis in order to ensure that only the common variance between behaviour elements was analysed. Initial communality estimates were based on squared multiple correlations of each element with the remaining set and these estimates were then iterated until the final communalities attained stable values. The factors obtained from this analysis have been termed the "Derived Factors".

Four factors emerged from the analysis of the durational data, and five factors from the analysis of the frequential data. It seems that these factors are independent of one another, and are of equal importance in terms of explained variance (see Figure 6.1). The "Derived" factors have been examined in terms of the "Functional Categories" in order to begin to probe the validity of the hypotheses upon which they are based. The factors revealed behavioural mechanisms which it is suggested enhanced an understanding of the complexity of vervet behaviour even though the reasons for the inclusion of particular behavioural elements into a specific category was not always clear.

Factor scores were calculated for each of the "Derived" factors and these were intended to provide the best measure of each behavioural dimension identified in the factor analyses. Similar combined standard scores were calculated for the "Functional Categories" by summing and standardising measurements across all behaviour elements which were grouped together. These measurements were then subjected to a two-way multivariate analysis of variance across subjects and day levels.

Analyses of the relationship between behavioural factors and temperature have been conducted by using multiple regressions, and are described in Chapter Eight.

6.4.1 Factor analytic treatment of the data.

The application of factor analytic methods to the data was not a straightforward procedure owing to the unusual form in which the data was structured. It seemed necessary, therefore, to review possible approaches and indicate the line of reasoning which led to the approach which was finally chosen.

There are two features which make the data unusual when compared with the type of data which is generally used in a factor analysis. Firstly, the data consisted of repeated observations on a very small set of subjects, whereas the format for factor analysis usually consists of scores on a large number of subjects on a set of tests or variables measured at one particular time. Secondly, three different modes of classification (subjects x time x behaviours) are included in the same analysis, whereas the conventional approach uses two modes of classification (typically subjects x tests).

The factor analysis of time series or repeated measurements has been the subject of a number of papers, notably Anderson (1963), Weitzmann (1963), and Ross (1964). Weitzmann and Ross were specifically concerned with the problem of analysing learning data. An important question in the analysis of repeated measurements is whether or not to retain the mean scores in the analysis. The issue in question is whether to use raw score cross products, covariances or correlations in the factor analysis. If the cross products of raw scores are analysed, the mean scores of the repeated measures appear as a factor in the analysis. By using covariances or correlations this factor of means is removed. Ross favours the retention of the means, but overlooks the fact that with most psychological data the mean score is arbitrarily set by the scaling device that is used. This argument would not have the same force in the case of behavioural measures, such as duration and frequency, when the scaling is based on time units. However it is probably more essential to ensure that relative differences between subjects are preserved in the analysis. In order to meet this requirement it would be necessary to include the observations for all subjects in the same analysis.

Tucker (1966) and Evans (1967) propose methods of factor analysis for analysing three mode classifications of data. Levin (1965) has presented some illustrative examples of three mode analysis using Tucker's method. His examples demonstrate the advantages of this approach over the alternative strategy of averaging the data over one mode, thereby reducing the problem to a two mode analysis. It would seem that three-mode analysis is the appropriate method to use for the present study. Unfortunately computing methods for this particular type of analysis are not readily available in standard computing packages, and it did not seem worthwhile to embark on the arduous task of writing programmes to handle this specific investigation.

In summary, two requirements appeared to be imposed on the analytical approach to be followed:-

1. A classical two mode analysis is the only practical alternative which can be readily implemented in computer packages.

2. Averaging the data over the unimportant mode (that is, subjects) would seem to be undesirable, since this strategy would result in a loss of information about individual differences.

Conducting three classical two mode analyses (behaviours x time intervals), one for each subject, would allow different behaviour structures to appear while preserving the subject mode. However, using this approach it would not be possible to make comparisons between subjects over time intervals on common structures, since mean differences would be eliminated. On the other hand, this approach would have the advantage of permitting an investigation of the relationship between factor changes and temperature for each individual animal. This could be an important advantage in view of the difficulties in calibrating the temperature measuring instruments to a common scale.

If we wish to retain three data modes in the classical factor analysis, then it is clear that one mode will have to be a combination of two of the three data modes. There were two feasible possibilities, namely combining subjects and time intervals to generate a "subject-occasions" variable or combining subjects and behaviour categories to produce a "subject-behaviours" variable. The second alternative would seem to be less meaningful than the

first, since it postulates separate behaviour factors for each subject. Intuitively it seems reasonable to postulate a common set of behaviour categories or "states" in which subjects reflect varying levels of intensity over time intervals.

In view of these considerations, it was finally decided to structure the data in the form of a matrix whose rows were the behaviour categories selected for analysis and whose columns were "subject-occasions". Correlating behaviours over "subject-occasions" generates a behaviour correlation matrix which was factored into component states, the loadings of behaviours on these component states being independent of the subject-occasions. This analysis makes it possible to generate factor scores for each component state across all "subject-occasions". These scores may then be used in further multivariate analyses.

In conclusion, it is clear from this discussion that alternative solutions for the analysis are possible. Ideally it would be desirable to explore the more promising solutions in order to develop a clearer view of the structure of the data within the limitations set by available computing packages.

Method of analysis :

The computer programmes utilised in this thesis were from the SPSS (Statistical Package for the Social Sciences), and the relevant printouts were bound and housed in the Department of Psychology, University of Natal, Durban.

The Principal Axes Method was used for grouping the behaviours into factors, using the pooled data collected concurrently from the three troop-living vervets during the first five-week block of measurements (Table 5.1). This data, therefore, consisted of seventy-five repeated five-minute measures of each of sixty-five behavioural elements per subject, that is, of a total of 225 five-minute repeats.

Simpson and Howe (1980) chose and described a Principal Components Analysis for classing measures into groups because "it can suggest new relationships between behavioural variables" (p. 135). They quoted Kim

(1975: 470): "Principal components analysis is a relatively straightforward method of transforming a given set of variables into a new set of composite variables or principal components that are orthogonal (unrelated)". This method finds that linear combination of variables accounts for more of the variance in the items as a whole than any other linear combination. This becomes the first component and the second component is defined as the second best linear combination of variables, or the one that accounts for the most residual variance after the effect of the first component is removed. This process continues for successive orthogonal components, until the variance is accounted for (Nie, Hull, Jenkins, Steinbrenner and Bent, 1975; Stevenson-Hinde and Zunz, 1978). In this analysis the methods for factoring the correlation matrix were applied to a matrix with communalities, when the method of principal components is called "principal axis factor analysis" and produces "principal axis factors". The communality of a variable refers to the proportion of variance that variable shares with other variables.

The advantages of using principal axes (or principal components) include the fact that the principal components are orthogonal to each other – thus the comparisons among subjects with respect to their scores on one principal component do not provide the same information as comparisons of scores on another component. Also the orthogonality property simplifies calculations involved in subsequent analyses involving the set of variables. "At least 90% of all current factor analyses finish with one orthogonal rotation procedure: Varimax" (Hunter, 1980: 240). So it was with this analysis. The effect of this procedure aims to increase the number of loadings of very high and near zero values and to minimise the amount of loadings of moderate size.

Applying the scree test (Cattell, 1965) to the factors derived from the frequential and durational scores, four factors were extracted from the durational data and five factors from the frequential data. Cattell suggested that once the significant common variance had been extracted from the correlation matrix, the subsequent factors would show very little change in the amount of variance extracted. Full details of the Principal Axes Factor Analyses, and the graphs (see Graph 6.1) plotting eigenvalues against factor numbers for the application of the scree test are presented

in Appendix 5. It was found that the variances for each of the durational and frequential factors were similar, suggesting that the behavioural factors were of almost equal importance.

Figure 6.1 depicts the factors derived from the Principal Axes Factor Analyses. Any behaviour with a factor loading less than 0.2 has been excluded because its importance on the factor is minimal.

The factors were labelled in terms of a composite category of behaviour which seemed best to describe the behavioural components. It should be borne in mind that although the varimax rotation of the factors is designed to force them into unrelated groups of behaviour, these measures come from biological systems where everything is to some degree related to everything else, and where criteria for dividing 'related' from 'unrelated' pairs of measures are always arbitrary (Simpson and Howe, 1980). The data showed great complexity (see Appendix 5). The four durational factors together accounted for only 29.4% of the variance, and the five frequential factors for 30%, so that a large number of minor factors are needed to explain the variance more completely. This is discussed in section 6.5.

The durational data and the frequential data have been analysed separately. The following table (6.2) compares the factors that have been statistically derived from the durational data with the factors derived from the frequential data, and explains the author's categorisation of these factors.
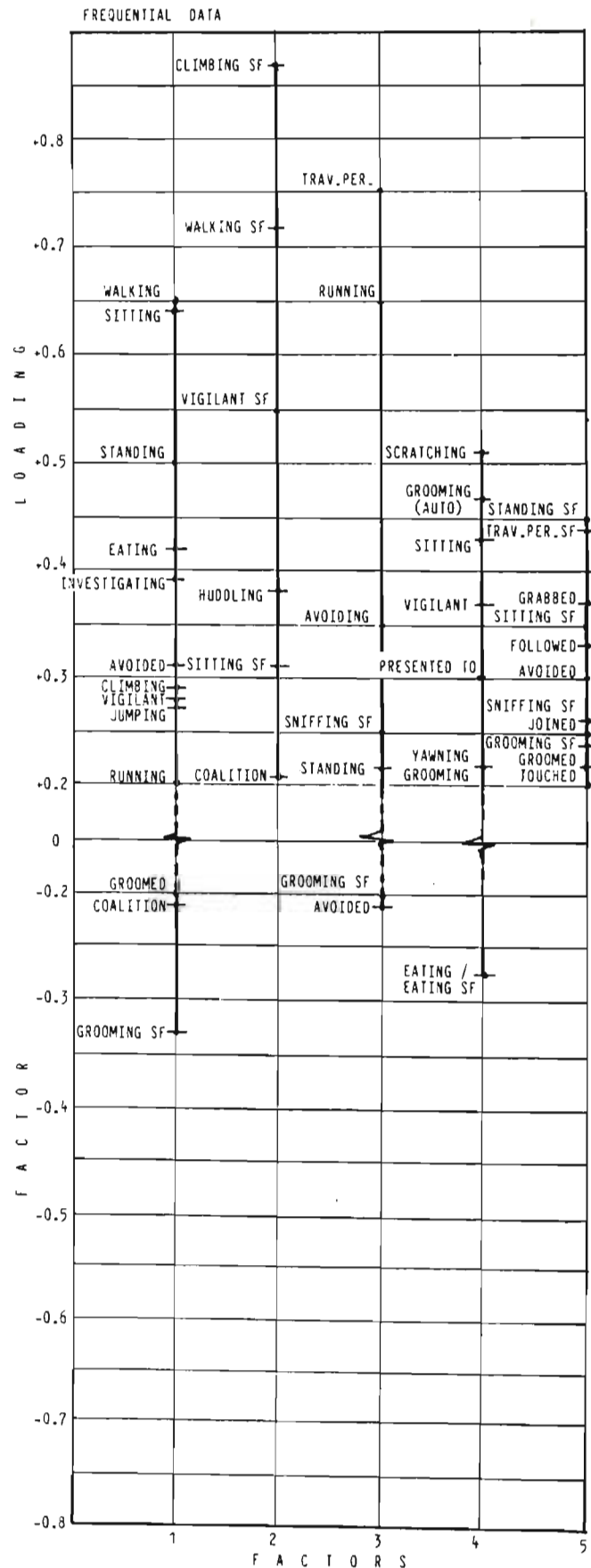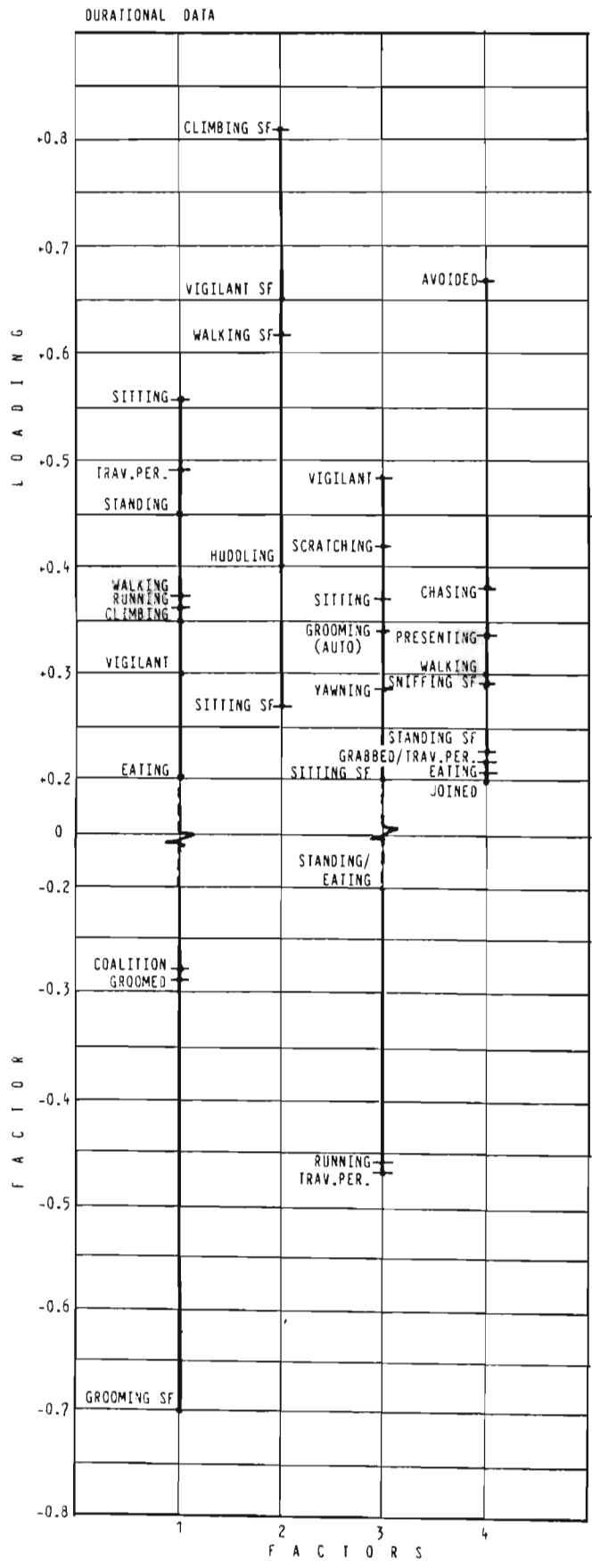
FIGURE 6.1   THE DERIVED FACTORS : STATISTICAL GROUPING OF BEHAVIOURS.

TABLE 6.2

DERIVED FACTORS :

A COMPARISON BETWEEN DURATIONAL AND FREQUENTIAL
DATA FACTORS, DERIVED BY THE PRINCIPAL AXES METHOD.

DURATION FACTORS (D)		FREQUENCY FACTORS (F)		BEHAVIOURAL ELEMENTS			INTERPRETATION
No.	Proposed Category	No.	Proposed Category	Common	Durational Additions	Frequential Additions	
1	+ Solitary	1	+ Solitary	standing sitting walking climbing eating	trav. per running	investigating avoided jumping	The 'solitary' or 'individual' axis seems to be concerned with active behaviours that the animal may carry out alone, and the additional elements support this inter- pretation. It is suggested that inclusion of an 'avoided' element (F) and the fact that each of the behavioural elements could be conducted socially implies a choice on the part of the individual. Could an intraversion- extraversion dimension apply to individual monkeys?
	– Inter- active		– Inter- active	coalition groomed grooming sf	–	–	The 'interactive' or 'social' axis includes behaviour which is asymmetric but co-operative. A bipolar factor. As the animal spends more time on its own, it has less time for interactive activities.
2	+ Coaction	2	+ Coaction	climbing sf vigilant sf walking sf huddling sf sitting sf	–	coalition	A unipolar sociable symmetric factor. Social because the behaviours could be executed alone. The addition of coalition (F) strengthens the sociability, because co-operation is implied.
3	Ecological Resources: acquisition and mainten- ance	4	Ecological Resources: acquisition and mainten- ance				These bipolar factors are not easy to interpret. It seems that durational factor 3 separates into two separate factors with the frequency data. These factors show the individual orientated to the environment. The opposition between apparent territorial activity (display) and eating (Factors 3D+ and 4F) reflect activities occupying different ends of the day. The foci of attention differ. The frequency factor includes 'presented to' and 'grooming sf' which suggests a late afternoon factor allowing for the acquisition of territory and partners for the evening.
	+ Terri- torial		+ Terri- torial	scratching vigilant grooming (auto) sitting yawning	–	presented to grooming sf	
	– Eating and Boundary	3	– Eating + Boundary	eating standing trav. per running		eating sf avoiding sniffing	Boundary pacing (border patrol) is problematic. Is it simply cage behaviour ; an attempt to check out boundary for escape, or a form of territiorial behaviour? The impression is of agitation. Its opposition to territorial display (factor 3D) could be mobile versus immobile activities, ground versus height, and possibly behaviour orientated to the protection of different territorial areas. The opposition between boundary
			– Tension reduction			grooming sf avoided	behaviour and grooming in Factor 3(F) is possibly between tension inducing and tension reducing activities; individual versus social. Can humans ever fully understand human behaviour ?
4	Social Organi- sation	5	Social Organi- sation	avoided sniffing sf standing sf trav.per sf joined grabbed	chasing presenting walking trav. per eating	sitting sf followed grooming sf groomed touched	This factor could be a behavioural mechanism which allows for the integrity of the social structure to be maintained. The combination of hostile and friendly elements symmetric and asymmetric may subserve social status rituals. The additional elements (D) and (F) all possess a 'social action' quality.

NOTE: sf = social friendly.

In both the statistically derived factors (durational and frequential), social elements have separated from non–social or individual behaviours. This was in agreement with the functional categories, reinforcing the contention that ongoing social behaviour occurs together with solitary behaviour. An informed understanding of ongoing behaviour therefore cannot occur if the social environment of the animal is not accounted for.

The manner in which the derived categories were clearly embedded in the functional categories indicated that a pattern of behaviour for the troop's adult female vervets was emerging (see Table 6.3).

TABLE   6.3

COMPARATIVE TABLE ILLUSTRATING HOW THE FACTORS
DERIVED FROM A STATISTICAL ANALYSIS ARE EMBEDDED
IN THE FACTORS DEDUCED THROUGH OBSERVATION.

FACTORS FROM FACTOR ANALYSIS				FACTORS FROM OBSERVATION	
Durational Factors		Frequential Factors		Functional Categories	
No.	Category	No.	Category	No.*	Category
1	Solitary-Interactive	1	Solitary-Interactive	5	Non-Social (Solitary) and
				6	Social friendly
2	Coaction	2	Coaction	2	Social Passive and
				3	Contact and
				6	Social friendly
3	Ecological Resources Territorial-Boundary Eating	3	Ecological Resources Boundary-Tension	1	Active
		4	Ecological Resources Territorial-Eating		
4	Social Organisation	5	Social Organisation	6 + 7 ie 4	Social friendly Social Agonistic

* The statistically computed factors are embedded in rather than

6.4.2   Multivariate analysis of variance of behavioural factors.

Subject and day level differences were investigated by subjecting the factor scores derived from the Principal Axes Analyses and the scores based on Functional Categories to a Multivariate Analysis of Variance, durational and frequential data being analysed separately.   (All the computer sheets have been lodged with the Department of Psychology, University of Natal, Durban, and are available for inspection.)

The following table outlines the overall results.

TABLE   6.4

MANOVA ANALYSIS OF FACTORS FOR MAIN EFFECTS

OF SUBJECTS AND DAY LEVEL.

FACTOR CATEGORY	DATA	EFFECT	WILKS LAMBDA	SIGNIFICANCE
Derived	Durational	Subject x Level Level Subject	$\lambda = 1.921$ $\lambda = 2.467$ $\lambda = 7.928$	P < .002 P < .001 P < .0005
Derived	Frequential	Subject x Level Level Subject	$\lambda = 1.827$ $\lambda = 2.399$ $\lambda = 7.956$	P < .002 P < .001 P < .0005
Functional	Durational	Subject x Level Level Subject	$\lambda = 1.206$ $\lambda = 1.617$ $\lambda = 5.433$	P < .146 P < .024 P < .0005
Functional	Frequential	Subject x Level Level Subject	$\lambda = 1.330$ $\lambda = 1.890$ $\lambda = 5.237$	P < .056 P < .004 P < .0005

NOTE:

1.   **Derived Factors:** There is a first-order interaction for frequential and durational data, i.e. when behaviour is viewed in terms of the derived factors, there are significant differences in the behavioural profiles of the subjects across the five levels of the day.

2.   **Functional Categories:** There is no interaction effect between subjects and day level, and therefore the tests for main effects have been investigated, both level and subject effects being significant.

The following techniques have been used in order to probe the overall significant differences revealed by the MANOVA:

1.   Univariate F-tests.

2.   Discriminant Analysis: standardised discrimination function coefficient.

3.   Graphs.

6.4.2.1   Multivariate analysis of variance of functional categories.

According to a MANOVA, there was no significant interaction between subjects and day levels, thus the subjects displayed the same trend over the day for each of the functional categories, and the main effects could be explored.   In contrast to the derived factors, the durational data and the frequential data yielded comparable results even though the data were analysed separately.

Level differences :

Factor profiles over the day were similar for each subject, but there were significant differences durationally ($P < .024$) and frequentially ($P < .004$) in the behavioural profiles at different levels of the day.

Table 6.5 and Graph 6.2 attempted to identify the prominent factors in these differences (refer to Appendix 7 for mean z scores).

Subject differences :

Factor profiles were similar over the day (no S x L interaction) but there were highly significant differences durationally and frequentially ($P < .0005$) in the behavioural profiles of the subjects.

According to the Univariate F-tests for both the durational and the frequential data, the subjects differed significantly on all factors except factor 7 – and the strength of the differences was supported by two independent discriminant functions, except for factor 3 which did not seem to have a strong coefficient weighting (see Table 6.6 and Table 6.7).

TABLE   6.5

STATISTICAL COMPUTATIONS FOR ASSESSING THE
FUNCTIONAL CATEGORIES RESPONSIBLE FOR THE
SIGNIFICANCE OF DAY LEVEL DIFFERENCES.

DATA	FACTOR NO.	STATISTIC	RESULT	COMMENT
Durational	1 Active	Discriminant Analysis	Standardised Discr. function Coeff. = 1.708	Factors 1, 4 and 5 were the most important in describing the level differences and these were
		Univariate F Test	F = 3.259 P < .013	supported by the Univariate F tests. Factor 1 was positive,
	4 Active Social	Discriminant Analysis	Standardised Discr. function Coeff. = -1.591	but factors 4 and 5 were negative, indicating that they went together on this
		Univariate F Test	F = 3.087 P < .017	discriminant.
	5 Active Non-Social	Discriminant Analysis	Standardised Discr. function Coeff. = 1.450	
		Univariate F Test	F = 3.560 P < .008	
Frequential	.1 Active	Discriminant Analysis	Standardised Discr. function Coeff. = -5.073	Factors 1 and 5 were important in describing the differences and carry opposite signs.
		Univariate F Test	F = 1.438 P < .222	
	5 Active Non-Social	Discriminant Analysis	Standardised Discr. function Coeff. = 4.403	This was not supported by the Univariate F Tests. It seemed strange the Univariate F tests
		Univariate F Test	F = .243 P < .914	were not significant for any of the factors, even though level differences were highly significant overall.

NOTE:

There was a relatively good agreement between the durational and frequential data regarding the factors which were important in describing level differences, i.e. factors 1 and 5.   That factor 4 was important durationally but not frequentially can be explained because this factor, Active-Social, included behaviours of long duration but relatively low frequency, e.g. grooming and sitting together, and excluded several high frequency low duration behaviours, e.g. scratching, which were included in factors 1 and 5.

TABLE 6.6

STATISTICAL COMPUTATIONS FOR DESCRIBING

SUBJECT DIFFERENCES ACCORDING TO MANOVA.

FACTOR		DURATIONAL DATA				FREQUENTIAL DATA			
No.	Category	Univariate F-test		Stand. discr. function coeff. 1	Stand. discr. function coeff. 2	Univariate F-test		Stand. discr. function coeff. 1	Stand. discr. function coeff. 2
		F	P			F	P		
1	Active	5.169	< .006	-1.093	-0.231	7.924	< .0005	-3.952	-0.271
2	Passive	5.584	< .004	-0.500	0.881	4.336	< .014	0.465	-0.487
3	Contact	4.428	< .013	-0.062	-0.179	4.231	< .016	0.173	0.264
4	Social	19.698	<.0005	1.372	7.472	9.441	< .0005	-1.453	-1.573
5	Non-social	16.309	< .0005	1.629	0.412	10.169	< .0005	-3.945	-0.508
6	Social friendly	18.030	< .0005	-0.444	-7.358	9.291	< .0005	-0.009	1.058

TABLE 6.7

FUNCTIONAL CATEGORIES AND SUBJECT DIFFERENCES.

FUNCTIONAL CATEGORY No.	LABEL	SUBJECT MEANS		
		3	4	5
DUR 1 FREQ 1	Active	+.279 (1) -.140 (2)	-.212 (3) -.218 (3)	-.068 (2) +.358 (1)
DUR 2 FREQ 2	Passive	+.025 (2) +.184 (1)	-.273 (3) -.261 (3)	+.248 (1) +.077 (2)
DUR 3 FREQ 3	Contact	+.081 (2) +.21 (1)	-.264 (3) -.243 (3)	+.183 (1) +.030 (2)
DUR 4 FREQ 4	Social	+.469 (1) +.242 (1)	-.467 (3) -.388 (3)	-.007 (2) +.147 (2)
DUR 5 FREQ 5	Non-Social	-.445 (3) -.360 (3)	+.404 (1) +.016 (2)	+.041 (2) +.344 (1)
DUR 6 FREQ 6	Social friendly	+.464 (1) +.307 (1)	-.428 (3) -.360 (3)	-.036 (2) +.053 (2)

NOTE:

1. DUR refers to results based on the durational data; FREQ refers to results based on the frequential data.

2. Numbers in parentheses denote ranking: 1 = highest score; 2 = middle score; 3 = lowest score

INFERENCE: Individual differences for every category measured, except category 7 (Social Agonistic).

FUNCTIONAL CATEGORIES
1. ACTIVE

Durational Data — Frequential Data

4. ACTIVE SOCIAL

Durational Data
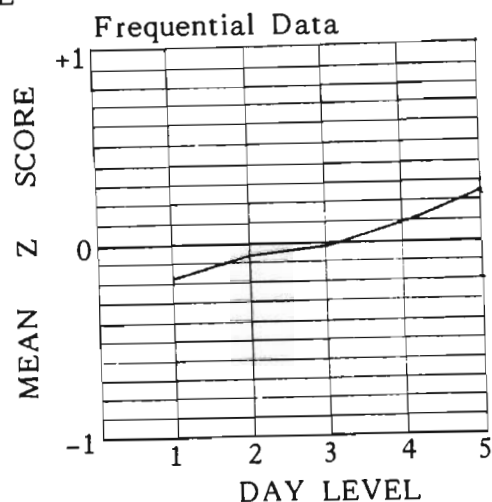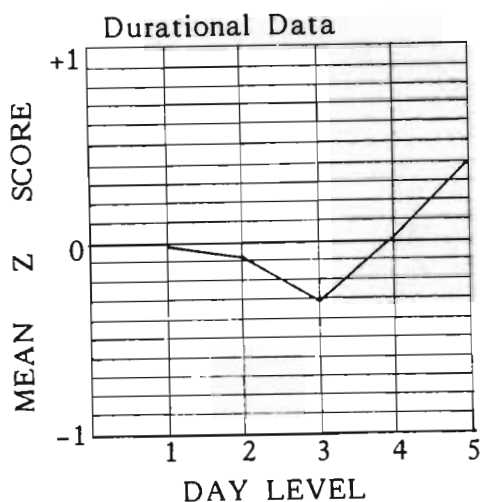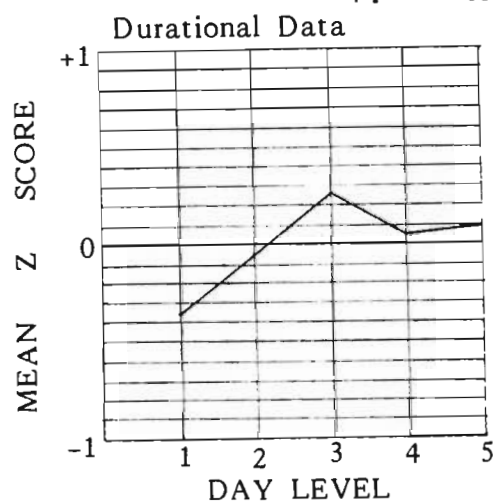
Frequential Data

non-significant
(see Table 6.5)

5. ACTIVE NON-SOCIAL
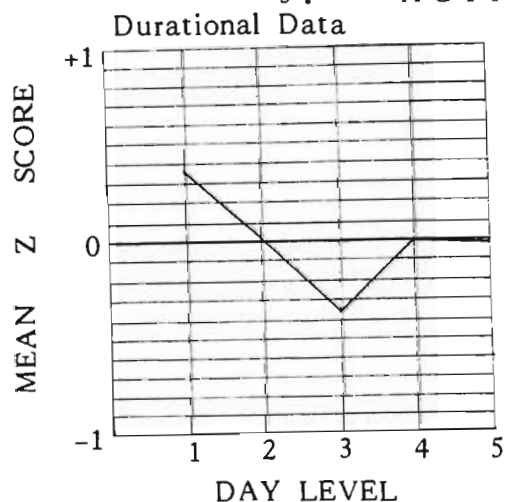
Durational Data — Frequential Data
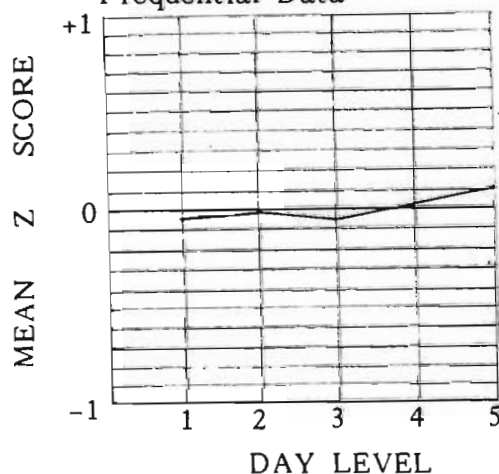
Day levels :
1. 07h30 – 09h30
2. 09h30 – 11h30
3. 11h30 – 13h30
4. 13h30 – 15h30
5. 15h30 – 17h30

n (per level) = 45
N (total) = 225

NOTE:
1. Fluctuations in behaviour which generally peaks or troughs at level 3 (around midday).
2. Level 3 : factor 5 least active; least active non-socially but most active socially.
3. Opposite trends in factors 4 and 5.

GRAPH 6.2

The behavioural profiles of subjects 3 and 4 appeared to be different for each one of the factors, and subject 5 seemed to be more similar to subject 3 than to subject 4.   Subject 3 exhibited the most 'active' behaviors, in terms of durational scores, and subject 5 was the most 'active' in terms of frequential scores, while subject 4 displayed the least amount of 'active' behaviours for both types of data.   As may be expected, the trend was reversed for 'passive' behaviours, with subject 3 displaying passive behaviour more frequently than subject 5, but subject 5 spending more time on passive behaviours.   Subject 4 once again had the lowest score.   Passive and contact behaviours are virtually synonymous – thus subject 3 touched other animals more frequently than subject 5 but not for as long a time.   The differences between subjects 3 and 5 clarified when the functional categories 4 and 6, which deal with social and social friendly behaviours respectively, were examined.   Subject 3 was the most 'social' and the most 'social friendly' of the animals, which meant that the high scores of subject 5 on the active dimension were made up of a larger number of non-social activities than subject 3.

This was consistent with the findings on category 5.   Subject 3 was the least 'non-social' vervet.   Subject 4 showed the greatest amount of 'non-social' activity on the durational data, but subject 5 displayed the greatest amount on the frequential data (elevating her frequential score for activity).

A further summary of these results appears in the discussion.

6.4.2.2   Multivariate analysis of variance of derived factors.

A MANOVA probing the relationships between subjects, time of day, and the statistically computed DERIVED FACTORS, revealed a significant two-way interaction between subjects and day levels for both the durational and the frequential data, which were analysed separately, $P < .002$ (see Table 6.4).

According to Monge and Capella: "Finding an interaction significant, we would stop testing and attempt to interpret the interaction.

Significant interactions do not invalidate main effects, but they do complicate interpretations" (1980: 166).   (Scheffe (1959: 110) agreed with this viewpoint.)

In an attempt to understand the factors most responsible for the significant difference in the behavioural profiles of subjects across the five levels of the day, the discriminant analyses and the univariate F tests were examined.

Graph 6.3 of the factors pointed to in Table 6.8 helps to elucidate further the differences in behavioural profiles of the subjects across the five levels of the day (refer to Appendix 7 for mean z scores).

These results, as with the functional categories, emphasised differences in sociability.   The different factors highlighted by frequential and durational data seemed to be accounted for in the characteristics of activities involved.   Frequential factor 3 comprised behaviours of short duration, while activities within factor 1 (durational and frequential) tended to be of longer duration.   It is noteworthy that factor 2 – Coaction – is stressed by both durational and frequential data analysis as being significantly different among subjects.   The activities in factor 5 are also generally of short duration.

The derived factors revealed that subject 3 was concerned with social behaviour, subject 4 concentrated on individual activities and subject 5 was in between.

Subject 3 seemed to display significantly more asymmetrical social behaviour than her two conspecifics, that is, of the factors categorised as SOCIAL INTERACTION and SOCIAL ORGANISATION (see data DUR 1 and FREQ 3, Table 6.7).   For the symmetrical social behaviour COACTION (factor 2, durational and frequential), subject 5 scored higher on the durational factor and subject 3 on the frequential factor, indicating that subject 3 socialised more frequently but for a shorter time.   Subject 4 was less sociable than the other two in all three types of interaction.   In contrast vervet 4 displayed significantly more individual activities, that is, she scored higher on factors SOLITARY (DUR 1) and BOUNDARY (FREQ 3).

Thus subjects 3 and 4 were at opposite ends of a social–solitary continuum, with subject 5 vacillating between the two types, and showing contrasting trends to subject 3 for social behaviour and to vervet 4 for individual behaviour.

TABLE 6.8

STATISTICAL COMPUTATIONS FOR THE SIGNIFICANT BEHAVIOURAL DIFFERENCES IN SUBJECTS, WHEN MEASURED ACCORDING TO THE DERIVED FACTOR DURATIONAL DATA, AND DERIVED FACTOR FREQUENTIAL DATA.

Table 6.8.1   Durational Data

FACTOR NO.	STANDARDISED DISCR. FUNCTION COEFF.		UNIVARIATE F TEST		COMMENT
	1	2	F	P.	
1	.351	−.785	2.279	<.023	Two independent discriminant functions helped to describe the differences in subject profiles over the day. The first was based mainly on factor 2 scores and the second stressed the importance of factor 1. These are supported by the Univariate F Tests.
2	−.878	−.412	2.293	<.003	
3	−.364	.493	1.663	<.109	
4	.220	.230	.630	<.752	

Table 6.8.2   Frequential Data

FACTOR NO.	DISCRIMINANT ANALYSIS STANDARDISED DISCR. FUNCTION COEFF.	UNIVARIATE F TEST		COMMENT
		F	P	
1	.262	.100	<.436	Factor 3 is stressed.
2	−.048	2.390	<.017	
3	.871	3.780	<.0005	
4	−.037	.780	<.621	
5	.409	1.350	<.220	

DURATIONAL DATA

Factor 1
Solitary–Interactive
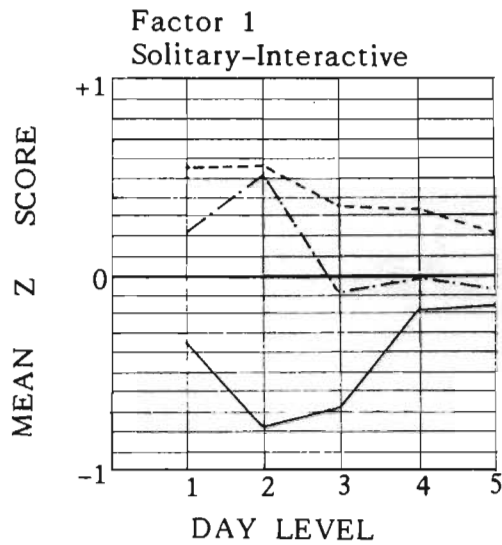
$\bar{X}$ S3 = –.440
S4 = +.331
S5 = +.110
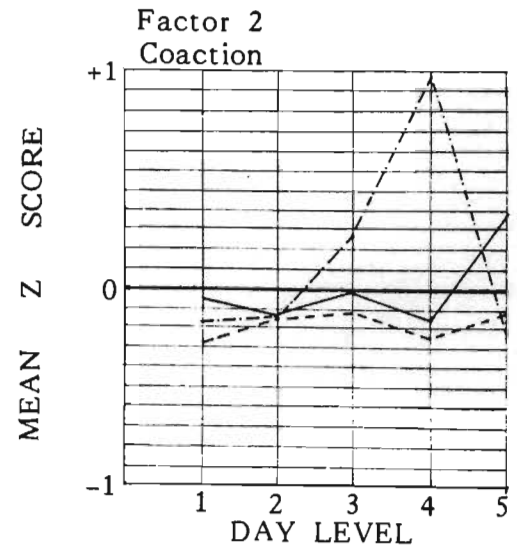
Factor 2
Coaction

$\bar{X}$ S3 = +.026
S4 = –.188
S5 = +.162

FREQUENTIAL DATA

Factor 3
Boundary–Tension Reduction
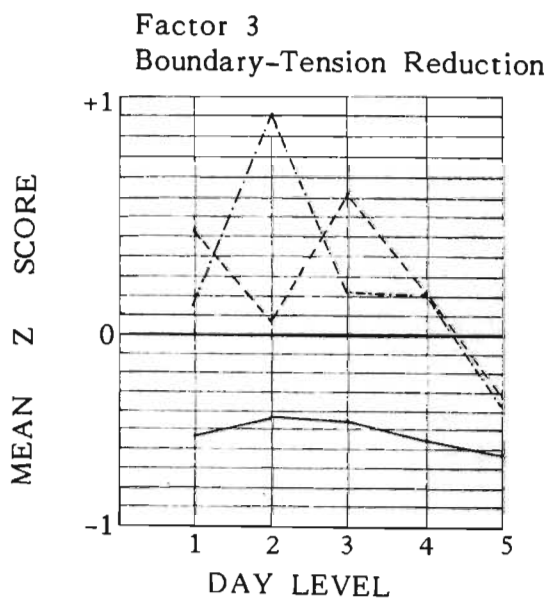
$\bar{X}$ S3 = +.526
S4 = +.247
S5 = +.277
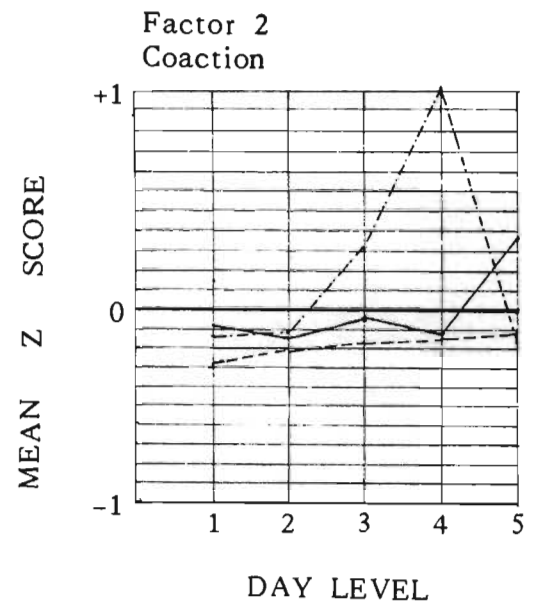
Factor 2
Coaction

$\bar{X}$ S3 = +.012
S4 = –.190
S5 = +.202

DAY LEVELS:

1. 07h30 – 09h30
2. 09h30 – 11h30
3. 11h30 – 13h30
4. 13h30 – 15h30
5. 15h30 – 17h30

NOTE:

This factor has a significant univariate interaction, but does not seem important in producing the S x L interaction (see Table 6.8).

KEY Subject 3 ————
Subject 4 – – – – – –
Subject 5 –·–·–·–·

GRAPH 6.3

COMPARATIVE BEHAVIOURAL TRENDS : SIGNIFICANT BETWEEN SUBJECTS

TABLE 6.9

A COMPARISON BETWEEN THE SIGNIFICANTLY
DIFFERENT DERIVED FACTOR TRENDS FOR
THE CAGED ADULT FEMALE VERVETS.

FACTOR		GENERAL	SUBJECTS		
No.	Category	Comment	3	4	5
DUR 1	Solitary Interactive	S3 different to S4 and S5 $\bar{X}$ 3 = -.440 4 = .331 5 = .110	Below average means throughout day. Therefore greater concern in social activity. U-shape trend for level means indicates grooming is mainly done in L2 and L3.	Decline in solitary activity over the day. Mean = above average at L1.	Similar to S4. Shows less grooming activity than subjects 3 and 4.
DUR 2	Coaction	3 different trends. $\bar{X}$ 3 = .026 4 = -.188 5 = .162	Increased coaction at L5 only	Little variation in coaction over the day = Below average throughout.	Sharply increasing trend up to L4, and then declines to an average level at L5.
		NOTE: Contrasting trends for factors 1 and 2 for subjects 3 and 5.			
FREQ 2	Coaction	As per duration, strengthening the conclusion. $\bar{X}$ 3 = .184 4 = -.261 5 = .077	As per DUR 2	As per DUR 2	As per DUR 2
FREQ 3	Boundary Tension reduction	All animals exhibit decreased boundary activity from L3 to L5. i.e. Increasing tension reduction activity towards evening. 3 different trends. $\bar{X}$ 3 = -.562 4 = .247 5 = .277	Low level throughout. Concentration on social tension reduction mechanisms.	Peak L1 and L3 (L1 - see S5). Is this behaviour 'checking out' territory?	Contrary to S4, peak L2. Maximum when eating. Maybe food, outside disturbance and vulnerability while attention directed to food triggers this behaviour?

6.4.3   Individual behaviours.

The durational and the frequential behavioural data of eating, grooming (allo and auto), huddling and traversing perimeter were each subjected to a two-way subject by levels of the day univariate ANOVA. It was hypothesised that an in-depth study of the trends underlying their manifestation may shed further light upon subject differences and the diurnal fluctuations in behavioural activity.

TABLE   6.10

INDIVIDUAL   BEHAVIOURS :

Effects of Day-Level and Subjects according to a 2-way ANOVA.

EFFECT	DURATIONAL DATA (N =225)		FREQUENTIAL DATA (N = 225)		DAILY TIME BUDGET (% time per sample)	COMMENT
	F	P	F	P		
1. EATING.					12	No S x L interaction.
S x L	.375	< .933	.850	< .560		
Subject	1.260	< .286	.195	< .823		No significant difference.
Level	2.784	< .028	1.312	< .266		Significant diff. (Dur.)
2. ALLOGROOMING ACTIVITY.					26	No S x L interaction.
S x L	1.281	< .255	.690	< .700		
Subject	12.844	< .0005	11.528	< .0005		Significant diff. (Dur. and Freq.)
Level	2.825	< .026	1.868	< .1115		Significant diff. (Dur.)
3. AUTOGROOMING.					5	Significant S x L interaction (Freq.)
S x L	1.470	< .170	2.155	< .032		
Subject	1.947	< .145	2.225	< .067		Different trends per day in frequency but not for
Level	1.450	< .219	1.463	< .234		total duration.
4. HUDDLING.					3	No S x L interaction.
S x L	1.976	< .051	1.918	< .059		
Subject	4.738	< .010	5.406	< .005		Significant diff. (Dur. and Freq.)
Level	1.563	< .185	1.843	< .122		No significant difference.
5. TRAVELLING PERIMETER.					8	Significant S x L interaction (Dur. and Freq.)
S x L	2.375	< .018	4.074	< .0005		
Subject	22.339	< .0005	6.311	< .0005		Different trends per
Level	5.114	< .001	25.331	< .0005		subject per day.

NOTE: Dur. refers to durational results.

Freq. refers to frequential results.

1. Subject trends similar, but significant level differences in behaviour.

ALLOGROOMING

EATING
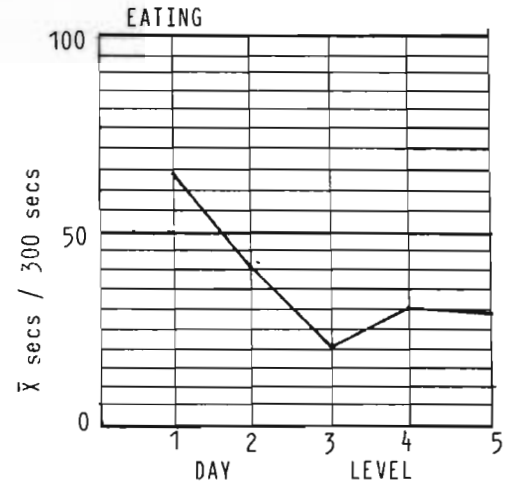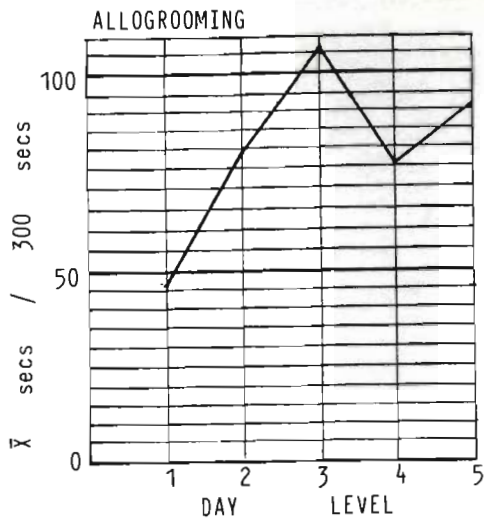
2. Behavioural trends similar, but significant quantitative differences between subjects.
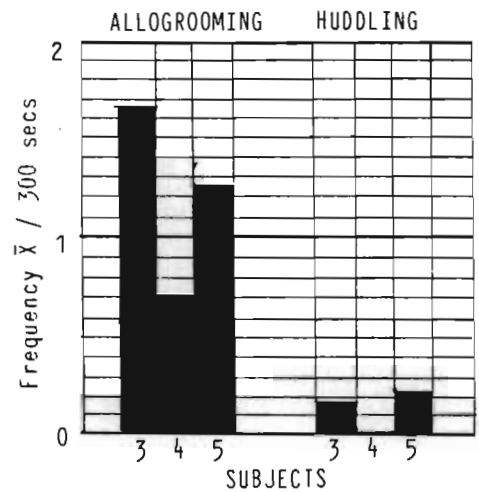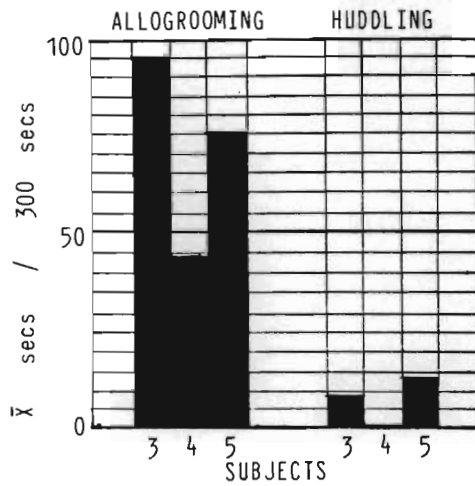
3. Significant trend differences between subjects.

TRAVELLING PERIMETER
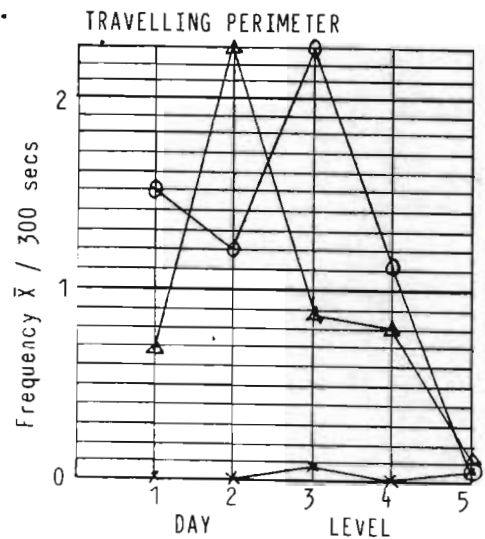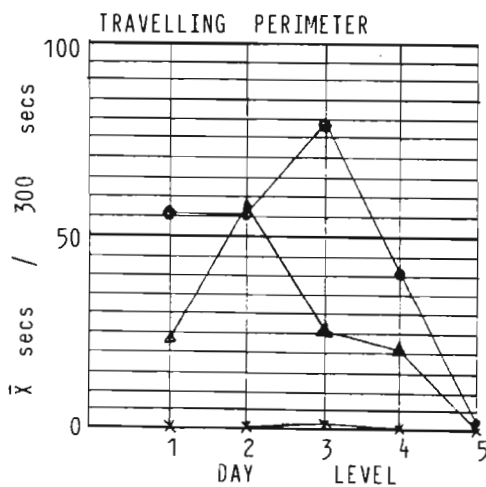
AUTOGROOMING

No apparent durational differences between subjects.

KEY × Subject 3
     o Subject 4
     △ Subject 5
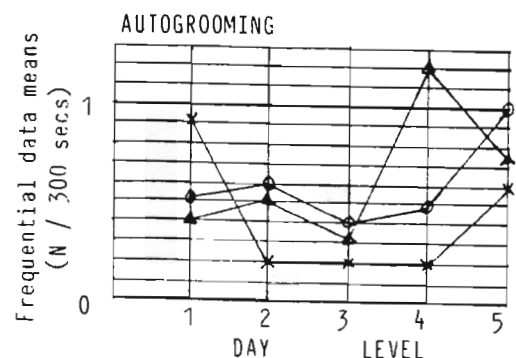
GRAPH 6.4

INDIVIDUAL BEHAVIOURS : SIGNIFICANT FINDINGS OF A

The results in Table 6.10 and Graph 6.4 confirm:-

1.   Significant overall differences in the amount of eating activity and allogrooming activity at different levels of the day.   The middle of the day (L3) was characterised by a trough and a peak respectively, suggesting a change in behavioural emphasis during midday.

2.   Significant differences between subjects in behaviours that followed the same trend over the day, allogrooming and huddling, and in behaviours where the trend varied with each subject (travelling perimeter and autogrooming).

3.   Subject 3 appeared high in 'social activities' (grooming and huddling), and low on individual activities (travelling perimeter and autogrooming).   Subject 4 displayed an opposite trend, while subject 5 seemed to be intermediate between the two.

(Please refer to Appendix 7 for time sample means as illustrated in Graph 6.4.)

Feeding behaviour :

Although the ANOVA for feeding behaviour revealed no significant differences, estimates and interobserver agreement on subject rank which included eating as a parameter were high (see Chapter Seven).   A dominance ranking placed subject 3 on the top of the hierarchy, then subject 4, and ranked subject 5 lowest.   The ANOVA may have failed to reveal subject differences because the division of day levels into two-hour periods was too gross to pick up an order effect.   Most eating was done during Level 1:   between 07h30 and 09h30.   Subject 3 was consistently seen to be eating first, often together with the dominant male.   Subject 4 would begin eating only after subject 3 was well established in her eating activity, while subject 5 would only start eating after most of the other troop members were already eating, or finished, and she rarely approached the food source.   She seemed instead to rely on the food particles discarded by her troop co-members.

A comparison of intraindividual durational and frequential mean scores indicated that subject 5 had the lowest durational score, yet the highest frequency score (see Table 6.11).   This means that subject 5 was seen to eat much more frequently than her conspecifics, but for shorter periods,

coinciding with observations that she was frequently threatened during eating causing her to drop her food and retreat. It is suggested that this erratic feeding behaviour due to harassment may have implications for internal temperature fluctuations (see Chapter Eight).

TABLE 6.11

BETWEEN SUBJECTS COMPARISON OF MEAN DURATIONAL AND MEAN FREQUENTIAL FEEDING SCORES, AT DIFFERENT LEVELS OF THE DAY.

LEVEL	Mean Durational Score per time sample (300 secs)			Mean Frequential Score per time sample (300 secs)		
	SUBJECT			SUBJECT		
	3	4	5	3	4	5
1	70.0	76.67	46.67	13.07	13.07	15
2	38.67	49.33	33.33	9.07	13.2	15
3	19.33	22.0	19.33	4.0	6.0	10
4	36.0	49.33	5.33	11.07	14.07	4
5	34.0	23.33	30.67	12.0	7.0	17
Total	198.0	220.67	135.33	49.21	53.33	61

The feeding pattern of subject 3 seemed to approximate free-ranging vervet behaviour most closely — with peaks at the first and last period of the day.   Subject 4 showed a similar trend to subject 3 durationally, but the frequency with which she ate at levels 1 and 2 are equivalent.   This strengthens the impression that subject 3 ate until she was satisfied, while subject 4 had to rely more on left-overs and discards.   Thus her food portions were smaller and she had to move and find food more frequently. Vervet 4 ate relatively little during level 5 — she concentrated on social behaviour at this time   — was she strengthening bonds that she had failed to consolidate earlier in the day?

It seems that only a detailed account of the entire behavioural spectrum of each animal will be adequate to explain the subtleties of vervet behaviour.

6.5 DISCUSSION.

The results of this intensive in-depth probe into the behaviour of the troop-living female subjects points to significant individual differences, to social activity as an integral part of the behavioural repertoire, and to variations in the behavioural spectrum at different times of the day. These findings are consistent with the literature.

Each five-minute time sample consisted of a complete description of the ongoing behaviour of the target animal, and the behavioural spectrum was divided into sixty-five different behavioural items for scoring.   While this procedure facilitated preservation of the subtle nuances of behavioural activity with its context, a large amount of complex data was generated. The first step in analysis, therefore, was an attempt to render the data manageable by grouping the behavioural items into factors.   As illustrated in Tables 6.1 and 6.2, the behaviour was grouped twice.   In the first set of factors, behaviours were grouped according to categories imposed by the researcher and termed functional categories;   in the second, the factor groupings were derived from a statistical treatment of the behavioural data and labelled derived factors.   The usefulness of functional categories imposed upon the data has been outlined by McGuire, Raleigh and Johnson (1983)   – in particular, factors can be organised to answer the issues under consideration.   It seems that a comparison of functional factors with statistically derived factors would be fruitful because factor analysis makes no assumptions based on the experimenter's judgments.   It is thus probably less amenable to bias, and may also reveal behavioural connections not previously considered by the researcher.

The experimental situation seemed ideal for pursuing an intensive examination of the individual operating as a dynamic system incorporating a physiological level, an individual behavioural level, and a social level of functioning.   The advantage of working within the indigenous environment of the monkey subjects meant that physical conditions did not have to be simulated.   The intensive and rigorously randomised data was collected from relatively undisturbed freely moving animals of the same age-sex category, who were members of a 'natural' troop with social bonds intact.   This is in contrast with, and should, therefore, complement the vast majority of

studies, in which data is taken from monkeys of diverse sources that have been thrown together to form groups, and then these groups have been further manipulated to preserve a particular age-sex category. The data from various researchers is usually pooled, which complicates by introducing interobserver differences even though it may increase data. Following this the behavioural factors usually seem to be formed from data collected from a variety of age-sex categories, each of which may have its own 'typical' behavioural profile (see Literature review: e.g. Chamove, Eysenck and Harlow, 1972; Stevenson-Hinde and Zunz, 1978; McGuire, Raleigh and Johnson, 1983). Fairbanks, McGuire and Page (1978), for example, use data from eighteen monkeys for a factor analysis (similar to the one used in this thesis) of the behaviour of vervet monkeys *(Cercopithecus aethiops sabaeus)*, yet only four are adult females and their ages range between 10+, 8+, 7 and 4 respectively. Simpson and Howe (1980) have highlighted the problems of pooled data and the importance of context, in their investigation of male and female profiles.

A discussion of the behaviours as categorised in this study is followed by a consideration of the activity cycle, and then attention is focussed upon differences between subjects. That individuals are different is a basic tenet of evolutionary theory; thus Slater (1981) asserted that this phenomenon "should certainly not have been neglected the way that it has" (p. 47). Lomnicki (1982) has examined the development of ideas in evolutionary theory, and he asserted that: "If natural selection operates on the individual or gene level, not on the level of entire populations, then it seems reasonable to consider population members more as independent entities, and entire populations less like integrated systems than was previously assumed" (p. 154).

6.5.1 The factors.

A discernible pattern in the behaviour of the troop-living adult females seemed to emerge. The factors formed from a statistical analysis of the frequential data corresponded closely to the factors formed from the durational data (see Figure 6.1). Furthermore, the statistically 'derived factors' were clearly embedded in the 'functional categories' (see Table

6.3).   Thus the statistically derived factors supported the author's hypotheses (see Table 6.1: Functional categories).

A prominent result, cutting across all analyses, was the separation of social behaviours from individual behaviours into different categories, and this is consistent with the literature (see section 6.2.2).   According to the statistical analyses, the social and the individual categories of behaviour were equally important, and occurred together.   Following this, it is submitted that the vervets living alone belonged to a different behavioural sample from the vervets living in a troop.   Thus these two samples of subjects differed, not only physiologically as indicated by the body temperature data, but also behaviourally.   The monkeys living alone were deprived of social contact and, consequently, were denied the advantages and the disadvantages of functioning within a social context.

A relatively large amount of common variance was not accounted for in this factor analysis, highlighting the complexity of the data (see section 6.4: Appendix 5).   It is proposed that this variance stemmed firstly from the comprehensive and therefore large number of relatively low level behaviours listed in the ethogram (65) which produces 'noise' on the one hand, but facilitates accurate judgments on the other (it is relatively easy to estimate unequivocally, for example, how frequently or for how long an animal will run or sit or climb, etc.).   Secondly, in this research project the raw data was used for computations.   In contrast, Fairbanks, McGuire and Page (1978) for example, used averages which wiped out variances, and Stevenson-Hinde and Zunz (1978) used a rating scale, which would also effectively smooth out some of the error variance.   Simpson and Howe (1980) suggested that in their study "much of the variance remaining to be accounted for may be the result of unreliable observation" (p. 138).   It is believed that this explanation cannot account for all the unexplained variance in the present project.   All the data was recorded by the author, a relatively experienced observer prior to the commencement of this study (see Tollman, 1977).   Indeed, Coelho and Bramblett (1981) have demonstrated that with 'sufficient training' (three to four months) high levels of interobserver agreement are attainable.   It is notable that each of the factors extracted from the data accounted for roughly the same proportion of the explained variance, indicating that social and solitary

behaviour are of equal importance.

The difficulties involved in interpreting and categorising behavioural clusters derived through a statistical analysis is clear to any reader of the literature, and has been pointed to in section 6.2.2. These difficulties explain why some researchers, for example McGuire, Raleigh and Johnson (1983) preferred to use functional categories, and the author chose to look at both functional categories and derived factors. As argued in section 6.2.2, there are many unanswered questions. For example, is it legitimate as Fairbanks, McGuire and Page (1978) did, to refer to behavioural clusters as roles? Is the term 'control female' a role? What happens to individual differences (personality)? Statistically, can behavioural data from diverse age-sex categories be pooled to obtain a behavioural factor? Does that not produce not only an 'average animal' which doesn't exist, but an average 'ageless hermaphrodite'? The author is also puzzled at the apparent failure of researchers to examine the negative dimension in bipolar factors (e.g. Fairbanks, McGuire and Page, 1978; Simpson and Howe, 1980). It would seem that these matters need consideration. Yet despite these queries, the dimensions of sociability, of fearfulness (submission) and of aggression characterise all studies (Nash and Chamove, 1981), and therefore all age-sex categories. In this study sociability is emphasised, and submission and aggression also emerged as important facets of functioning (see Chapter Seven).

Each set of behavioural clusters seemed to enhance an understanding of the others. Difficulties in interpretation arose for both the functional categories and the derived factors. On the one hand, all the behavioural elements observed did not clearly fall into a specific category, and on the other, the computerised cluster of behaviours did not always seem to fit together; for example, for functional categories: Is 'avoiding' a 'hostile' or a 'friendly' action? and for the derived factors: Why do 'eating' and 'travelling perimeter' fall into the same factor?

The derived factors in the present study not only pointed to a separation between social and solitary behaviour, but revealed an underlying structure in the social and in the individual behaviours which, it is suggested, points to a form of regulation of social and individual activity

within the group (see Figure 6.1, Table 6.2).

Social behaviour :

Three different factors emerged suggesting that there are three
different social mechanisms operating during ongoing behaviour: an
interactive mechanism, a sociability mechanism, and a social organisation
mechanism.

1. Interactive Mechanism (Factor 1 (Dur*); 1- + 3- (Freq*). The
    behaviours in this factor cannot be performed by one animal. They
    require cooperation and are asymmetric, for example grooming. This
    factor appeared important for efficient functioning: keeping clean,
    reducing tension and reinforcing social bonds. Perhaps social and
    physiological homeostasis is maintained by this mechanism?

2. Sociability Mechanism (Factor 2 (Dur and Freq)). These behavioural
    elements may be performed alone or socially – thus providing the
    individual with a choice? This sociability mechanism would then
    allow for individual differences (or intraversion and extraversion, as
    suggested by Chamove, Eysenck and Harlow, 1972), flexibility and
    initiation of bonds.

3. Social Organisation Mechanism (Factor 4 (Dur); Factor 5 (Freq)).
    The cluster of behavioural elements in this category may allow for
    the status rituals required to maintain dominance hierarchies and a
    social order.

Individual behaviour :

Three different categories of individual or solitary behaviour also
emerged, a solitary mechanism and two mechanisms for dealing with the
acquisition and maintenance of ecological resources.

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* Dur refers to the durational data.
  Freq refers to the frequential data.

1. Solitary Mechanism (Factor 1+ (Dur and Freq)).   The behaviours in this category were performed alone, but could be carried out in company, complementing the elements in the sociability dimensions. However, even though the individual may have a choice as to how to conduct these elements they are an indispensable part of any behavioural repertoire (for example walking, sitting, standing, etc.).

2. Territorial Mechanism (Factor 3+ (Dur); Factor 4+ (Freq)).   These behaviours occurred in a spatially elevated location (equivalent to high up in the trees), were immobile and allowed for territorial display.

3. Eating and Boundary or Border Patrol Mechanism.   In the durational data analysis this mechanism appeared to subserve both these functions (Factor 3 Dur).   The reason for this was not quite clear, except that both occur on the ground (that is, food is found on the ground).   It also pointed to the complexity of travelling perimeter behaviours: has it a territorial function, or is it simply an artefact of cage behaviour? The frequential data provides an extra factor, and separates these two mechanisms (Eating = Factor 4-; Boundary = Factor 3+).

Apart from the sociable-solitary division examined in this thesis, the author hypothesised a divison between active and passive behaviours (functional categories 1 and 2).   This would seem to correspond with an Active to Slow behavioural component identified by Stevenson-Hinde and Zunz (1978), which was stable in individual animals over three years, and on which adult males score higher than adult females.

The behaviours describing outright aggression were not common to all three females, or even to two of them, so these behaviours did not appear in the analysis.   For example, behaviours such as Attacking and Attacked, Redirected Aggression and Chewing, are confined to subject 5, while Biting, Bitten and Grabbing were confined to subject 3.

The behavioural analyses carried out in this study seem to illustrate that if the underlying structure of behaviour is to be clarified, the entire spectrum of behaviour should be subjected to alternate forms of analysis. Imposing categories upon the data was useful, but it was the statistical

analyses which suggested novel combinations of behaviours, thus enhancing the scope of data interpretation and generating further hypotheses for testing.

Multivariate analysis of variance of behavioural factors :

The behavioural factors were analysed in terms of the duration and frequency with which they were exhibited at different periods (levels) of the day, and by the individual subjects.

According to Table 6.4 (section 6.4.3), when the behaviour is analysed in terms of the statistically derived factors there are significant differences in the behavioural profiles of the subjects across the five levels of the day, yet when the researcher imposed her own categories upon the data, there was no interaction between subjects and day levels. Thus, for the functional categories the behavioural trends were similar, even though significant behavioural differences between subjects and at different levels of the day were revealed. It is argued that for the functional categories, that is for the categories as perceived by the observer, the built-in computer (the brain) filtered and organised incoming stimuli in a way that generated the hypotheses in the first place. Consequently, unlike a statistical manipulation of data, the behaviours became clustered into discernible trends. This seems to support the proposal that these two different ways of dealing with the data complement one another.

6.5.2   The activity cycle.

Consistent with the literature review, the author (Tollman, 1977) noted that the activity cycle of the free-ranging vervets in the Durban area displays a circadian rhythm of alternating periods of rest and activity. These appear to be attuned to the movements of the sun which are considered by Wever (1981) to modulate a free-running cycle. This finding is in agreement with the conclusions of previous authors (see section 6.2.1) that there is a profound periodic aspect in the organisation of primate behaviour. The statistical analysis suggests that the caged female vervets have retained this cycle (Table 6.5). Level differences for functional

category 1 - Active behaviour - are significant. As illustrated in Graph 6.1, the active behaviours were at a minimum at level 3 (11h30-13h30) that is, the monkeys were least active at noon, and they slept at night: thus active in the morning, rest at midday, active in the afternoon and sleep at night. This persistence in the cycle even after caging is important when the validity of extrapolating from caged to field conditions is being considered. In this case, the cage is in the open, so cues arising from the light/dark cycle had remained unchanged. Functional categories 2 and 3 (passive and contact) were not found to vary during the various levels of the day, suggesting that the perceived day-level fluctuations in activity resulted from the females being more or less active.

Functional categories 4 and 5, active social and active non-social (individual) behaviour respectively, were also found to be important factors in day level differences. Not surprisingly they displayed opposite trends, for example social behaviour was at a maximum at noon (level 3) and non-social factors were at a minimum. Non-social behaviours seemed to account for the morning's activity, while in the afternoon period, which is characterised by a sharply increasing level of activity, a combination of active social and individual behaviours occurred. As with activity, there was a regular pattern to the occurrence of social and non-social behaviours, and this rhythm seemed to be coincident with the activity rhythm, and with the varying positions of the sun.

An analysis of the individual behaviours produced further evidence for a changing matrix of behaviour during the day. Significantly more eating occurred in the early morning (level 1: 07h30-09h30) than at any other time during the day, and was at its lowest at noon (level 3: 11h30-13h30). In contrast, level 3 was a social time - it was the time during which most allogrooming was observed. These results are consistent with the observations of Bowden, Kripke and Wyborney (1978).

Behaviour as depicted by the derived factors also pointed to the importance of social interaction at level 5 (3.30 p.m. to 5.30 p.m.; see Graph 6.2). In addition, the frequency of tension-reduction behaviour (that is, grooming) increased at level 5. Is the increase in interaction and in tension-reduction a behavioural mechanism to enhance social bonds, and

thereby facilitate group action such as huddling, when it is most likely to be necessary? For example, huddling for warmth and being close together in case action against predators is needed. This mechanism would be particularly relevant at night when sleeping increases vulnerability to predation and reduces vigilance.

6.5.3   Individual differences.

In the previous chapter, subject differences were revealed at a thermoregulatory level. Behaviour, too, has now been revealed to be significantly different. Yet Rubenstein (1982), supporting Slater (1981), asserted: "a principle so central to evolution – that individuals are different – has largely been omitted from ecological theory" (p. 88). This failure to examine individual differences may arise from the adverse cost-benefit ratio of executing in-depth case-studies, with randomised repeated measures over the day to allow for the daily rhythmic fluctuations in behaviour, as well as to capture the entire spectrum of behaviour – a task which Rusak (1981) called heroic. Unfortunately, averaging behaviours over large numbers of animals tells us nothing about individual variations (Slater, 1981), and any study is limited to the number of parameters monitored.

The three subjects whose individual profiles have been probed in detail were significantly different, both when the different behaviours were categorised by the researcher and when they were categorised by a statistical procedure. In particular, striking differences appeared on a social-non social and an active-passive dimension (see Subject Results: sections 6.4.3.1 and 6.4.3.2).

According to the functional categories, subject 3 was unequivocally the most 'social' of the animals. She displayed the most 'social friendly' interactions and was the least non-social. She also exhibited the highest frequency of passive and contact behaviours. Overall, according to the durational data, she exhibited the most 'active' behaviour.

Subject 4 appeared to be a non-social animal. She engaged in the most 'non-social' activities, according to the durational data, but was second

to subject 5 in the frequential data. It seems that she exhibited solitary behaviour most of the time, because she has the lowest scores for all the other factors: active, passive, contact social, and social friendly.

Subject 5, judged to be the vervet lowest on the hierarchy, seems to be intermediate between subject 3 and subject 5 for every factor scored.

As pointed out in the previous section, for the statistically computed behavioural factors a significant interaction occurred between the subject and the different levels of the day. A graphical examination of the different behavioural trends supported the results of the functional categories analysis. Emphasis was on the social-solitary continuum, with subjects 3 and 4 at opposite ends, and subject 5 vacillating between the two. Differences in the quality of social interaction are explored in the following chapter (Chapter Seven).

It was interesting that the only functional category showing neither level nor subject differences was social agonistic (functional category 7) and is compatible with the 'aggression' factor identified by several authors (e.g. van Hooff, 1970; Chamove, Eysenck and Harlow, 1972; Nash and Chamove, 1981). This factor did not separate aggressor and aggressee, and is further explored in Chapter Seven. Possibly agonistic behaviour is a mechanism for maintaining social order and is, therefore, displayed equally over the day and by all subjects, as suggested by Nagel and Kummer (1974).

6.6 CONCLUDING COMMENT.

A factor analysis of the entire spectrum of behaviour exhibited by the troop-caged female vervets revealed that social interaction was an integral aspect of their ongoing behavioural functioning, and equally important. Singly caged vervets are deprived of this activity.

The persistence, in the cage, of an underlying activity cycle was confirmed by the statistical analyses. Even so, significant differences between subjects were revealed, with activity and sociability emerging as important variants. The next task, it seemed, was to examine the social group in an attempt to elucidate the individual variation in social function, and then to integrate the thermoregulatory data with the individual and social behaviour of each subject.

PLATE   4.0

BEHAVIOUR.

4.1 Environmentally induced modifications.
Bread moistening   –   acquired
behavioural pattern of caged troop in
response to ever-present pools.

4.2 Cyclical behavioural patterns.
Late afternoon, an active period.

4.3 Individual differences superimposed
upon underlying behavioural
fluctuations. Some are sociable,
some remain alone.

CHAPTER   SEVEN

THE   SOCIAL   GROUP

7.1   INTRODUCTION.

Individual variation in the extent to which vervet body temperature
oscillates around its mean has been pointed to in Chapter Five.   In
Chapter Six, these subjects were found to exhibit significant differences in
behaviour, which was not only contingent upon varying social conditions,
but existed among individuals living within the same environmental situation.

An analysis of the behaviour of the troop-living female subjects
revealed that these individuals engaged in both social and solitary behaviours,
that these behaviours occurred together, and were of equal importance.

"Social systems evolve in close relation to ecology" (Crook, 1980: 58),
and each individual vervet is born into, develops and lives within a social
system.   The construction of a behavioural profile, therefore, would not be
complete without an examination of each subject in interaction with her
troop conspecifics.

This chapter commences with a detailed literature review probing the
intricacies of social organisation, the position of the adult female therein,
and the social behaviours of aggression and grooming.   This is followed by
a detailed examination of the social behaviour of each of the three troop-
living female subjects.   A sociogram has been developed which, it is
proposed, facilitates an analysis of the social network of each individual.
This sociogram provides a pictorial representation of both friendly and
hostile interactions, in terms of attraction to and repulsion from the
personal spaces of all its conspecifics.   These subjects were ordered into
a dominance hierarchy.   Lomnicki, after examining the factors which
produce individual variations has concluded that dominance hierarchies "are
probably the final result of the action of all the processes mentioned above.
They can result from individual differences in age, hereditary traits,
environmental variations in the time of hatching, stochastic growth and
dispersal" (1982: 159).

7.2   LITERATURE   REVIEW.

7.2.1   Social organisation.

> The most striking feature of our primate heritage is life in social
> groups. The higher primates, that is, Old World monkeys, apes and
> humans, all solve the major problems of existence in a social context.
>
> Lancaster, 1975: 12.

The strong point of primate adaptation, according to Kummer (1971),
does not lie in the motor skills of the individual but in the way things are
done in groups.   Rowell (1979) observed: "It is obvious to anyone watching
monkeys that it is subjectively very important to the individual to be part
of a group" (P. 5-6).

The definition of a society may be intuitively obvious, yet it is
difficult to verbalise (Bernstein, 1971).   Sarbin (1954) defined a society as
a set of interrelated roles, Altmann (1962b) by its communication network.
Wilson (1975) defined a society broadly as "a group of individuals belonging
to the same species and organised in a cooperative manner.   The diagnostic
criterion is reciprocal communication of a cooperative nature, extending
beyond mere sexual activity" (p. 595).   It seems that both the negative
and the positive aspects need to be considered.   Tinbergen's (1965)
description of a social organisation clarifies further, although he has, perhaps,
neglected the importance of the cooperative aspects involved.   He wrote
that the essence of social organisation is interaction because both negative
(disruptive) and positive (cohesive) factors are involved.   He explained that
members of the society attract and repel each other, their interests coincide
or are incompatible.   Thus, Darwin recognised the functions of
interindividual competitive struggle in evolution – however, if individuals
only repel each other there would eventually be no interaction, society and
individual.   Social organisation, therefore, is an integration of positive and
negative forces, a patterned succession of interactions.

Struhsaker (1969) found that membership in the same social network
is the major feature distinguishing group members from extragroup
conspecifics.   Members of the same social network are all directly or

indirectly associated with each other, do not necessarily have to interact with all the other members , but direct at least 80% of their non-aggressive social interactions within this social network. According to Rowell (1979) social organisations are a high-order, integrative phenomenon. She separated social structure from social organisation, limiting the latter to "the pattern of interactions between individuals; a description of behavior" (p. 5).

Measures of demographic character, population density and group size were included in her conception of social structure. Chalmers (1979) also separated the terms, but defined social structure as "the collection of all patterns of behavioral interactions that occur in a group" (p. 61), and referred to topics such as "group size, population density, home range, size and body size ... collectively as social organisation" (p. 188-189). Asquith (1978) pointed to the "crying need for closer approximation between the concepts and terminologies of different students in the field of primate behavior if a true meshing of ideas and data presented by different workers is to be achieved." He correctly called for "fixed criteria definitions of terms that describe the social organisation of nonhuman primates" (p. 201). It is surprising that Asquith separated nonhuman from human behaviour, since many students of behaviour focus on monkeys for their social behaviour which has special features which we share (Rowell, 1972). Asquith maintained that social organisation has four levels of description: the physiological level, the level of behavioural units, the level of relationships, and the level of social organisation. He hypothesised that if behaviour-based factors were the criteria on which a type of social organisation was labelled we would attain consistency, because "where demographic factors such as group size, home range and so on have been the basis for the definition of a social organisation term, there has been no constancy of definition" (p. 203).

In this section, 7.2.1, the overall features of social organisation and the attendant modulating factors are discussed. In the following section, 7.2.2, entitled "social structure", the focus narrows, and deals with the structure of specific social organisations and, in particular, with the social structure of the vervet monkey. Because social structures do not function in isolation, an examination of the apparent adaptations to a dynamic

environment (physical and social) follows.   Thus it was found that these two sections overlapped, pointing to the difficulty in delineating a clear boundary between the two concepts.   This may stem from the fact that neither social organisations nor social structures are static phenomena, but must be considered in interaction with their surroundings, both physical and social, and these features coincide.

The rapid accumulation of primate field studies published over the past fifteen years points increasingly to the complexity of primate social organisations.   Inter and intraspecies comparisons revealed that social organisation varies not only among different species of primates within the same habitat (e.g. Kummer, 1971a, 1971b; Bernstein, 1972; Chalmers, 1979; Eisenberg, 1979; Coelho, Bramblett and Quick, 1979), but also within the same species inhabiting different environments (e.g. Rowell, 1967; Kummer, 1971a, 1971b; Bernstein, 1972; Estrada and Estrada, 1978; Watanabe, 1978; Suzuki, 1979; Koyama, Fujii and Yonekawa, 1980), and even within the same troop at different times of the year in parallel with environmental changes, natural (climatic), or imposed (e.g. Bishop, 1979; Tollman, 1981).   Convergence further complicates the issue.   For example, nocturnal species of primates have smaller bodies than diurnal species, while terrestrial species living in open country tend to be larger than arboreal species (Clutton-Brock and Harvey, 1977; Eisenberg, 1979). Clutton-Brock and Harvey postulated that the open country primates may be larger because they often have to move considerable distances when travelling from one food source to another, and may be better able to defend themselves against predators than smaller animals.   In fact, the analysis carried out by Clutton-Brock and Harvey has failed to show clear correlations between ecological features and group composition (Chalmers, 1972), so as Barash (1977) declared, "we are only beginning to appreciate the complexity of environmental factors relevant to each species, as well as the range of potential responses of each species, and the adaptive consequences of these responses" (p. 134).

Cercopithecus aethiops has been observed in a variety of habitats. For example, Gartlan and Brain, on the basis of their work in 1968, contrasted the social behaviour of vervets in two areas of East Africa and compared both of these with the behaviour of two captive colonies in

Salisbury and Johannesburg respectively. Struhsaker (1967a, b, c) observed vervets in Amboseli Park in East Africa, and Lancaster (1975) observed vervets in Zambia. More recently Wrangham (1980, 1981), Henzi (1980), and the author have reported on their field work with vervets in Kenya and in Natal respectively, confirming Rosen's (1974) comment that "the behaviour of the vervet has begun to receive considerable attention in recent years because of its behavioural plasticity" (p. 94). Many studies have contrasted the behaviour of the vervet with other primate species (e.g. Hall, 1968a, 1968b; Bernstein, 1971; Hinde, 1971; Chalmers, 1972, 1978; Lancaster, 1975; Clutton-Brock and Harvey, 1977; Henzi, 1982), while still others have attempted to elucidate the relationships between ecological conditions and correlated social structure (e.g. Hall and Gartlan, 1968; Kummer, 1971; McGuire, 1974; Crook, 1980). Apparently *C. aethiops* is socially very different from other Cercopithecines despite the fact that it is ecologically similar (Wilson, 1975), and vervets at Chobi behave differently to those at Lolui (Gartlan and Brain, 1968).

Interpretation of the vast amount of data accumulated seems to be presently undergoing reexamination. As early as 1971, Kummer began to question the emphasis on function which had eclipsed the causal viewpoint, and suggested a combination of these outlooks. Kummer also criticised discussions of adaptiveness which "sometimes leave us with the impression that every trait observed in a species must by definition be ideally adaptive, whereas all we can say with certainty is that it must be tolerable, since it did not lead to extinction and evolution, after all, is not sorcery" (p. 90). Rowell (1979) challenged researchers further by reminding them that if natural selection is to act, there must be a range of viable forms. "The null hypothesis which must be accepted until an alternative can be demonstrated to fit the observations better, is that the differences in social organisation are the result of random drift, by which I understand that each species could use the same food sources and avoid predation as successfully if it were organised like one of the others" (p. 20). She urged us to go beyond 'parlour games' because "evolutionary processes do not invariably produce optimal adaptations" (Bernstein and Smith, 1979: 349). In the same way as genetic drift exists, is it not likely that there is social drift?

Rowell (1979) raised another issue which has recently been addressed by several research workers (e.g. Bernstein and Smith, 1979; Mason, 1978), that is, the "article of faith among primatologists that social organisation is determined by ecological influences" (p. 2). It is far more complicated than that. Mason (1978) distinguished three causal levels that influence the ontogeny of a social system: the individual, the social setting and the environment. He declared that "behaviour per se offers a rather inadequate basis for understanding the genesis of social organisation. The traditional focus on 'who does what to whom' is less useful than a focus on 'who likes to be with whom'" (p. 7). A social system is made up of behavioural interaction patterns – and is defined by the pattern of expression of such behaviour, and a feedback loop exists between a social organisation which influences social behaviour and which, in turn, is influenced by the behaviour of its members. Masters (1979) elaborated by reminding us that just as emotion can sometimes 'cause' behaviour, equally evident are cases in which social organisation is a 'cause' of individual emotions and behaviour. The boundaries of a social organisation are difficult to define because of phenomena such as intergroup contact and migration, both seen in vervets (e.g. Wrangham, 1981; Henzi, 1982).

The efficiency with which different social systems are adapted to the environment will vary if social organisations are subject to random drift, and so Rowell posed the question: "How would we know if social organisation were not adaptive?" (1979: 1). She suggested we ask: "How would the environment affect what?" (p. 5), and challenged us to look again more critically at some of the widely quoted examples of adaptiveness of social behaviour. She herself demonstrated that current conceptions of the different modes of parenting, and dominance-subordinacy relationships, may be simplistic.

It seems that studies of adaptiveness require long term follow-up, because the criteria for 'fittest' is reproductive success, and reproductive success can surely only be assessed when the number of surviving adult offspring can be counted. Malnourished or foolish offspring may not survive for long. It is also pointed out that although a range of adaptiveness exists at any one time, each system at a particular moment in time has survived over alternate systems, and so comparison with 'precursor' systems would be useful.

According to Rowell (1979), the following parameters have been shown to contribute to the unique quality of each social system.

1.   The immediate environment; for example, living space and food availability.

2.   The demographic and kinship structure which develops as a consequence of environmental pressures, life history and reproductive rates; for example, genealogical bonds have far-reaching effects (Sade, 1972; Snowdon, 1983).

3.   The random drift of cultural and/or genetic factors - factors which may be inextricably linked.

In the book **Primate ecology and human origins** (1979), edited with commentaries by Bernstein and Smith, papers by some of the key researchers probed and assessed the above parameters.   Bourliere (1979), using a bioenergetic approach, suggested criteria based upon definite physiological and evolutionary advantages for assessing environmental quality, in place of "a purely intuitive basis" (p. 41).

Altmann and Altmann (1979) explained how demographic processes affected group size and composition and these, in turn, had important effects upon behaviour, for example, increased population density results in an increased demand for food and a decreased availability of land per person, leading to increased competition.   "The single most widespread response to increased population density throughout the animal kingdom is emigration" (p. 55).   It has also been found that the rate of aggression in a group will depend on its adult composition, since "the expected number of females simultaneously in oestrus is a probabilistic function of the number of females in the group" (p. 57).

Dunbar (1979) continued this theme and described how changes in the age-sex structure of a group influenced the mating strategies available to an individual.   Snowdon (1983) maintained that "the introduction of age structure and its attendant constructs suggests for animal behaviour a whole new set of hypotheses about behaviour development within a social group.

Little work in this area has been done so far" (p. 73). Baldwin and Baldwin (1979) reviewed ontogenetic and phylogenetic variables and emphasised the importance of ontogenetic factors and learning in the life of the individual and therefore the group. When dealing with a group as behaviourally flexible as the primates, "we need new theoretical models that give due weighting to both phylogenetic and ontogenetic causes of behavior. This will be the ultimate synthesis" (p. 110).

In the final chapter, Nagel presented a theoretical model for analysing the interactions and relationships of primate group members. He used an inductive, in contrast to a sociobiological or sociological approach, starting from a descriptive catalogue of basic patterns of ecosocial interactions among the 'group system' members, and explored dimensions of variability of such interactions in different relationships. "It appears to be too early, however, for the formulation and testing of predictions about the functional value of such interactions and relationships" (p. 316). This model allows for some of the complexity of the situation and the intimate relationship with the environment. Ecosocial behaviour is defined as every behaviour of Mi towards Z, which is influenced by other group members, and which in turn influences their behaviour towards M (group members are symbolised as M_1 M_2 ....M_n , environmental situations as Z_1 Z_2 .... Z_n , with Z standing for the environment in general). An ecosocial activity profile was defined as the totality of all ecosocial interactions toward Z between Mi and Mj. The complexity of a social interaction network makes it difficult to study; for example, Simpson (1973) has outlined two kinds of events in an interaction: those contributing to the relationship aspect and those contributing to the content aspect, while Kummer, Gotz and Angst (1974) reviewed data revealing that interactions between two monkeys can be strongly altered by a third.

It is evident that the social organisation of any primate group has to be dynamic in order to adapt to everchanging circumstances which consist of a multiplicity of factors buffeting it, and unitary explanations of primate social evolution are being discarded. Care must be taken, however, not to forget the importance of each of the phenomena that have been considered the focus for social organisation; for example, Zuckerman's (1932) theory of sexual attraction, and Chance and Jolly's (1970) conception of attention structure.

Chalmers (1979, after Hinde, 1975) identified three levels of social behaviour which he felt needed to be investigated from an adaptive or functional point of view: the kinds of interactions, the relationships between two or more individuals, and the social organisation.   Presently the majority of researchers are concentrating upon individual rather than group selection. The unit upon which natural selection operates is controversial: is it the gene (as heuristically suggested by Dawkins, 1976a), the individual or the group?   According to Rasmussen (1981) investigations into genetically based differences in social behaviour is a much neglected area.

Behavioural flexibility and, therefore, the importance of learning is increasingly being emphasised.   Yet a 'phylogenetic set' persists – the same species reared in different environments show "remarkable similarity in behaviour" (Seay and Gottfried, 1975: 5).   It seems that the distinction between genotype and phenotype is as important for the social organisation as it is for the individual, and that the principle of epigenesis must be remembered if the social organisation is to be understood.

7.2.2 Social structure.

> More recently, comparative studies have focused on social structure as a product of the adaptive strategies of individuals interacting with each other as well as with other aspects of their environments.
>
> Vaitl, 1978: 28.

Wilson (1975) wrote that troops of vervet monkeys are highly variable in size, and that the largest troops dominate the smallest, which are forced into less favourable terrain and must, therefore, defend larger areas in order to satisfy their needs.

The size of the troops reported by different workers have indeed varied.   Hall and Gartlan (1965) studied forty-six groups at Lolui, and found that the troop size ranged between six and twenty-one animals. Gartlan and Brain (1968) found groups of more than fifty animals north of the equator, while groups of up to a hundred were not uncommon south of the equator.   They noted that group size within *C. aethiops* correlated

with ecological conditions.   Rowell (1972) also found troop size differed according to locality.   Troops were smaller and population density higher in the more densely forested locality.   The "vervet troops", she wrote, "are much larger in Rhodesia and Zambia than in East Africa" (p. 62). Three troops of vervets living at Burman Bush in Durban were found to exhibit the following changes in size and composition between June 1974 and June 1978 (Henzi, 1982).   One reason for the increase observed is that the vervets in that area live in a protected park, and are constantly being provisioned by tourists.

TROOP SIZE OF VERVETS LIVING AT BURMAN BUSH, DURBAN :
1974 AND 1978   (AFTER HENZI, 1982: 88).

				Ratio of adult males to adult females	
Troop	June 1974	June 1978	Annual Increase %	June 1974	June 1978
Upper Troop	28	37	8.0	3 : 7	4 : 11
Lower Troop	23	33	10.9	1 : 7	3 : 10
Third Troop	8	19	34.3	1 : 3	2 : 7

The subjects in the present study were part of a troop which had the following composition (Tollman, 1981).

Category	No. of Individuals
Adult male	2
Adult female	9
Immature vervets	25
Infants	4
Total	40

Clutton-Brock and Harvey (1979) contended that the Cercopithecoidea show relatively small ranges and high densities compared to Ceboidea and Hominoidea.   They have provided evidence that although there are exceptions "across the order as a whole: home-range size is positively related to group weight and negatively to the proportion of foliage eaten" (p. 208).   The following mean values for *Cercopithecus aethiops* were presented:-
Body weight: adult   male   5.0   kg,   adult female 3.75 kg;
Population group size: 15;   % foliage in diet 12;   population density 112/km²;   and Home range size 0.37km².   r and K selective circumstances have been identified,   r being the intrinsic rate of natural increase and K the carrying capacity of an environment (Crook, 1980;   Wilson, 1975;   Barash, 1979).

Rowell (1967) suggested that observer bias and duration of study may contribute to the vast diversity in the pattern of living reported by the different workers.   These are important considerations because "monkeys and apes are so intelligent, their brains so advanced, their social organisation so intricate and variable, that the student of animal behaviour can easily become dazzled by the complexity of the scene" (Morris, 1967: 1).   Studies are revealing an ever-increasing number of variations in social structure and social organisation even within the same species, and giving weight to Bernstein's (1972) assertion, echoed by authors such as Wilson (1975), that "we should not be surprised if we fail to find a single universal principle upon which all primate societies are based" (p. 400).   Possibly both of these authors are pointing to different aspects of the same problem, and attempts to tease out the phylogenetic and the immediate environmental influences are still in their infancy.   Hinde (1978b) articulated these concerns when he compared the views expressed in papers forming part of a symposium in 1978 (Kummer, Abegglen, Bachman, Falett and Sigg;   Mason;   Vaitl; Seyfarth, Cheney and Hinde) and concluded: "... there is a remarkable degree of agreement amongst them on two crucial issues. First, it is basic for all of them that interactions within a primate group can be understood only in terms of the long-term relationships between the individuals concerned.   And second, all take the view that understanding requires coming to terms not merely with the 'surface structure' as measured for example by 'who does what to whom' and 'who sits next to whom', but with the 'deep structure', that is the principles in terms of which the observed patterning can be understood" (p. 2).

Research workers seem to agree that vervet troops consist of several adult males with adult females and young of all ages (Dolhinow and Bishop, 1972). "The vervet monkey lives in heterosexual groups in all the localities in which it has been studied" (Rowell, 1972: 62). The composition reported is highly diverse. Vervets are generally referred to as living in 'multimale' troops. Kummer (1971b) described vervets as being organised into 'multimale' groups. "Their social structure", he added, "permits any number of males per group, even just one" (p. 111). The current view is that the vervets are best described as territorial, multi-male, female-bonded societies (Wrangham, 1980). Eisenberg, Muckenhirn and Rudran in 1972 recommended that 'multimale' is a concept that has been applied too broadly, and an intermediate form of social organisation between the 'unimale' and the 'multimale' structures should be recognised. "This may be termed the age-graded male troop. Although several males of varying ages coexist in such troops, there are proportionately fewer males in these troops than there are in multimale troops (whose sex ratio may approach 1:1) ... the lack or absence of fully adult males of equivalent age is the characteristic that defines an age-graded male troop. ... *C. aethiops* tends to exhibit an age-graded-male to multimale configuration" (p. 871).

Sade (1980) has summarised the ecological factors limiting population size among wild primates as revealed by long-term observations and repeated population surveys. They point to humans as "the major factor in the decline of rhesus monkey populations" (p. 171), and Freese, Heltne, Castro and Whitesides (1981) reported similarly of the monkeys in South America: "Predation by humans was found to be the single most important factor affecting monkey densities" (p. 53). The quantity of available food and the quality of nutrients are, according to these workers, another major factor. Coelho, Coelho, Bramblett, Bramblett and Quick (1976) claimed that even if food resources are in superabundance, the population densities stabilise at a level lower than those allowed for by that food supply. Sade (1980) postulated that under these conditions a likely limiting factor would be the periodic outbreak of epidemic disease, which might be more severe under conditions of higher densities.

Wrangham (1980) crticised analyses of the evolution of social structures based on correlations of group size with ecological variables. Exceptions to

these correlations (see Crook, 1980) and an inability to explain species sex differences in migratory behaviour (see Clutton-Brock and Harvey, 1976) has led Wrangham to propose that an examination of the distribution of the individual rather than the group characteristics may be a more useful approach. In vervet troops migration both into and out of the troop occurs frequently. "The data suggest that it is a male phenomenon related to the availability of females" (Henzi, 1982: 1). This conclusion is in accordance with the observations reported by Lee (Wrangham, 1980). Wrangham described vervet troops as female-bonded societies. The females breed in their natal troops and consequently became bound to other females by close kinship ties. Sade (1980) found that kinship bonds were preserved, because fission of a group usually occurred some time after a mother died, and each sister with her own offspring began to act as an independent unit.

The social regulation of population density and age-sex distribution has recently received attention (Dittus, 1977, 1980; Sade, 1980; Wrangham, 1980, 1981). Wrangham (1980) investigated water competition in three free-ranging groups of vervet monkeys living in Kenya. According to Wrangham his study was "the first to show a relationship between the probability of death and dominance rank within a primate group" (p. 909). In the group where water was in short supply, the mortality rate was 38.5%, while in the other two where water was in superabundance there were no deaths. Wrangham found that during competition for water adult females and adult males obtained water by different methods. Females drank water from tree-holes in their normal home range, and were prevented from using water-holes by the territorial behaviour of a neighbouring group. Males invaded the territories of neighbouring groups. For the females, access to water was rank-related, and mortality was rank-related, implying that water stress was so severe that lower-ranking females were unable to maintain adequate physical condition. For males there was no evidence that competition occurred for access to tree-holes or water-holes. Wrangham hypothesised that the adaptive significance of female-bonded primate groups lay in providing coalitionary alliances in defence of resources critical for females. Deaths also occurred in the males but the reasons for this were not quite clear. In support of his results, Wrangham cited evidence for the following, from other researchers. First, that higher-ranking females have greater access to preferred resources and have higher reproductive rates,

and second that when inter-group interactions have led to the death of individuals in one of the groups, those who died were in the subordinate group. Wrangham (1980) asserted further that rank-related mortality would not necessarily be expected when the death-rate was low, since the different strategies of low and high-ranking animals may expose them to different kinds of risk. It could be argued, however, that death is an obvious phenomenon easily counted, but subtle rank-related physiological disturbances decreasing the individual's capacity to deal with the environment would be more difficult to detect in the absence of longevity figures. Dominance, subordination, aggressive and emotional episodes have been linked with specific physiological states; for example, it has been found that testosterone is higher in dominant males, and cortisol and prolactin are raised in more subordinate animals. Apparently subordination can prevent the luteinising hormone surge which is usually induced by giving oestrogen to female monkeys, offering an explanation for their reduced fertility (Bowman, Dilley and Keverne, 1978). Eberhart and Keverne (1979) further found that in males, plasma luteinising hormone and testosterone levels correlated positively with sexual behaviour and negatively with the receipt of aggression from male or female animal. Van Holst (1972) revealed that if *Tupaia belangeri* were exposed to persistent social stress, physiological changes occur "indicating persistent activation of the sympathetic nervous system" (p. 236). · He wrote that eventually renal failure leading to death may occur, and this may have far-reaching effects on the physical fitness of different individuals. Thus evidence for a relationship between physiological functioning and social status seems to be mounting.

Dittus (1977) examined the relationships between behavioural, ecological and demographic data of a wild population of macaques (toque monkeys) over a period of six and a half years. As with the vervets at Amboseli (Struhsaker, 1973, 1976), Dittus found that population size varied according to the food supply, that the mortality differed markedly according to age and sex, and that this pattern was not attributable to predation or disease alone. He determined that 81.5% of all threats occurred during foraging, that threatened individuals were prevented from feeding, and that their food was usurped in 36% of all threat interactions. Thus behavioural relationships during foraging influenced foraging efficiency in terms of amount of time spent foraging, feeding rates and quality of food consumed. By these

measures adult males fared best, then adult females, then juvenile males, and juvenile females fared worst. Dittus hypothesised that as a consequence of these behaviourally-imposed feeding efficiencies, young animals died at greater rates than adults, and infant and juvenile females died at greater rates than their male peers. Furthermore, he suggested that behaviourally-mediated access to other resources is likely to influence mortality in a similar manner.

During the mating season Dittus (1980) discovered that mortality in adult males was less than in subadult males who migrated more frequently, than adult females who do not migrate. This suggests that the rigours of migrating underlie the "extreme mortality in subadult males" (p. 282). "The effects of social behaviour (mainly aggressive and affiliative) and possibly its nature change in accordance with the age and sex distribution of the society, its density and available resources" (p. 318). He argued further that social behaviour, by maximising the reproductive success of some of its members, brings the society towards an equilibrium state ($R_o = 1$) with the resources and non-socially imposed mortality. Dunbar (1979), however, criticised Dittus "whose proofs of stationarity assume that the population is in fact stationary" (p. 85). He demonstrated that it takes no less than sixty-five years "for the variation in the rate of increase of each age class from year to year to be reduced to zero" (p. 73). Dunbar believed that much greater attention must be paid to the dynamic aspects of social systems, and he articulates dissatisfaction with the current study periods. These are far too short, he declared, for correlating features of the social organisation with factors such as gross or short-term ecological conditions, social or demographic processes. Furthermore, he maintained that to argue for species or population-specific characteristics on the basis of such short studies is to oversimplify an extremely complex situation.

Sade (1980) reinforced the idea of the importance of social factors for physiological functioning and, therefore, population regulation. He cited studies which demonstrated that social factors affect survival and maturation, influenced the synchronisation of reproductive cycles, and that stress is accompanied by physiological changes. Sade's research was organised around the characteristics of the life histories of males and females living in a colony at the Cayo Santiago, Puerto Rico, and established in 1938. Subgroups,

called genealogies, formed within the social units consisted primarily of animals related to one another through the female line. He discovered that higher-ranking genealogies had a considerably higher 'r' (intrinsic rate of increase) than the lower-ranking genealogies, and the females of the lower-ranking genealogies tended to have a lower life expectancy than those of the higher-ranking genealogies. This points to a connection between social behaviour, reproductive success and survival. Sade also argued that differences in rank among females may not be the result of, but may cause, genetic differentiation. Dunbar (1979) also looked at females and explained that the dominant females could prevent subordinate females conceiving "either by denying them access to the male(s), or by causing an increase in the frequency of an ovulatory cycle and/or premature abortion through harassment and stress" (p. 72). In gelada baboons, Dunbar and Dunbar (1977) found dominant females harassed subordinates, with the result that the latter took longer than the dominant females to become fertilised.

Snowdon (1983) also pointed to the importance of social factors for physiological function. He quoted Cheney, Lee and Seyfarth (1981) however, who found no correlation between rank and reproductive success in a study of free-ranging female vervet monkeys. Cheney, Lee and Seyfarth suggested that rank may be a reflection of different personality styles rather than an index of fitness as is commonly assumed. The contradictions between the observations of Cheney, Lee and Seyfarth and those of the previous researchers suggest that further rigorous studies are essential before the mechanisms underlying the regulation of troop structure will be elucidated. It seems that the regulatory control mechanisms would differ according to the availability of resources, the econiche, and the troop composition, at any particular time.

7.2.3   Spatial organisation.

Spatial organisation is a conspicuous feature of primate social behavior, but it has attracted relatively few systematic investigations.

Ehardt-Seward and Bramblett, 1980: 214.

Two fairly distinct aspects of animals' relations in space appear to

exist. Hediger (1955) was the first man to point out this distinction, and differentiated between territorial-behaviour and personal space. A territory may be defined as an area of ground which an animal, or a group of animals, will claim for its exclusive use, defending it against incursion by members of the same species. In terms of social structure, an animal is almost always dominant on its own territory, subordinate on another territory, and responds to threats by flight, usually back to its own home ground (Brindley, 1971).

Shirek Ellefson (1972) stated that there is a wide variation in how primate species distribute themselves in space. Some occupy exclusive territories (e.g. gibbons), some occupy overlapping home ranges (e.g. bonnet macaques), and others do either one or the other depending on the ecological niche (e.g. the vervet, C. aethiops). Generally vervets are regarded as 'territorial' (Wrangham, 1980; Henzi, 1982; personal observation), but Gartlan and Brain (1968) found that those vervets living on the lush Chobi Island in Lake Victoria had smaller troops with more males and were less territorially aggressive than those living in impoverished habitats. As described in the previous section, sex differences in territorial behaviour have also been observed (Wrangham, 1981).

Unlike territorial behaviour, personal space seems to be an almost universal aspect of spatial behaviour. According to Brindley (1971) personal space refers to the volume of space immediately surrounding an individual animal, whether it is stationary or moving, and all animals probably take account of this space in respect to other animals. He identified the following variations of personal space:-

- individual distance :   the distance characteristically separating members of the same species;

- flight distance :   the distance at which an animal will flee from a predator, termed FFD, Full-flight Distance, by Rosenblum, 1979;

- critical distance :   the distance at which an animal in a tight corner will turn from flight to attack;

- social distance :   the maximum distance for social contact among a group of animals; and

- rutting or male-female distance :   the distance between mated pairs in the breeding season.

The restrictions for entering spacing areas may apply to all conspecifics, or there may be varying degrees of exclusiveness. For example, a male may exclude only other males, admitting females or young or both; alternatively, there may be entry only by certain females, those with whom he is affiliated (McBride, 1971). Whatever the case, "again and again in observing a group of monkeys, whether in the field or in captivity, one is impressed by the more or less continual awareness of each members of the behaviour, the distance and the situation of the others" (Dolhinow, 1972: 265).

Animals probably use the ability to control space as a means of distributing various resources intraspecifically. McBride (1971) considered territoriality, home range patterns and dominance as important strategies for the control of space. Dominance is used within a group to exclude neighbours from a personal field. In this way animals exert priority of access to food, water, nest sites, shelter, toilet facilities and sometimes sex. Dominance distributes these priorities – the mechanism of space control. It is suggested that the idea that territorial behaviour and dominance may be behavioural mechanisms for achieving similar objectives seems strengthened by Barash's (1977) observations that under conditions of crowding many species revert from territorial behaviour to dominance structuring. McBride (1971) asserted that aggression is the most common behaviour used to control spacing – aggressive behaviour being accompanied by 'submission' or 'flight' behaviour. Flight removes subordinates from a particular space, while submissive behaviours enable neighbours to remain within a space without evoking aggressive responses. Leyhausen (1971) wrote that stronger, more aggressive animals keep a greater distance because of the avoidance action of others. This develops into an "individual distance differential ... space becomes a status symbol" (p. 23).

The dispersion pattern of primate groups almost certainly results from some form of mutual repulsion between the groups – at the same time, there must be a degree of mutual attraction among the group members, together with whatever repulsion is required to maintain spacing within the group. Aggression, therefore, is only one of the behavioural mechanisms for organising spacing. Marler (1968) postulated at least four categories of communication signals that serve to maintain patterns of spatial distribution: distance increasing, distance maintenance, distance reducing

and proximity maintenance.   Each species has a characteristic range of communicatory signals.   "Just as interesting as the lack of appeasers is the development of aggressive dominant signals among the guenons and the patas ...   arboreal guenons use fewer signals than the vervets" (Bolwig, 1978: 94).   Within the vervets Gartlan and Brain (1968) found that those living in impoverished areas used more signals than those living in richer habitats.

The individual spacing in a monkey troop varies with the species. Bolwig (1978) found that patas monkeys disperse more than baboons. Dolhinow (1972) pointed to the differential use of space by group members. "Some age-sex categories of animals tend to remain peripheral.   Subadult males, for example, tend to stay on the edge of the group, where they are least likely to come in contact with dominant adults (de Vore, 1962; Lindburg, 1967;   Jay, 1965).   If individuals do not get along well they may avoid one another and remain in different parts of the group" (p. 363). Bolwig (1978) cited Quiatt (1966) who "observed that for rhesus monkeys the smallest individual distances were between mothers and their youngest children and that related animals kept closer together than those unrelated" (p. 62).

In squirrel monkeys Burke, Kuehle and Dukelow (1981) found no differences in female-female and female-male distances in pairs when more than twenty-two observations were counted.   This result is in contrast to previous authors who maintain that there is a tendency for *Saimiri* adult single-sex grouping, and for females to group closer together when compared to male-male and male-female distances.   Weigel (1980) wrote that "various models of intragroup spatial structure have emerged, particularly for macaques and savannah baboons.   Predictions are that monkeys avoid aggressors, are attracted to others of similar dominance rank and age, and of like sex, and prefer kin over nonkin in proximity relationships" (p. 287). Weigel found that there was a clear preference for approaching kin in both pigtail and stumptail macaques, but the only other "prediction confirmed is an attraction to same-sexed group members by pigtail macaques" (p. 287). His post hoc analyses indicated that the developmental trends can be more clearly understood by examining proximal causes like dominance rank and activity level in addition to age.   The statistical analyses of Weigel's data

seem to have been rigorously performed yet the measures for understanding spatial relationships were based solely on behavioural interactions, that is rate of approach and number of aggressive acts exchanged. It would be useful to find out whether spatial measures, for example the spatial positions and distances of each animal in relation to each other and to their habitat, would yield the same results. Symmetrical relationships (e.g. walking together, sitting together) seem to have been omitted from the analysis – maybe some of the subjects like being together without active interchanges, and this has been considered in this thesis.

McBride (1971) theorised that most spacing behaviour can be described as variations of four main themes which underlie social organisation, that is: social phase, caste, roles, and the spatial patterns of all combinations of these three. Social phase refers to an organisation of behaviour for long periods of time (longer than a few days). Phases are often seasonal. For example, there is a social phase for the breeding season, and one for the non-breeding season. Subphases (the diurnal ordering of behaviour) occur within all social phases. Common subphases are movement, sleep, resting, body care, alarm and feeding. Each activity of the group is associated with a different structure in space.

McBride wrote further that the behaviour of animals is hierarchically organised at a number of levels, of which caste, role and interaction profoundly affect spacing between individuals. There are three types of caste – age, sex and seasonal – each represents a functional organisation of the behaviour of individuals, and a division of social labour within the society. Roles are determined by caste, and to some extent social rank, for example the alpha male of each caste may have a special role in each subphase. Interactions between animals serve a wide range of functions and are initiated by alerting responses as individuals move into each other's personal areas. All interactions have a spatial structure including orientation.

McBride concluded by commenting that the full range of spacing, that is territories, home ranges and hierarchies, separate systems for castes and phases, and a range of group structures all add up to a very complex spatial structure – nevertheless, "careful descriptions of structures will be necessary

before we can hope to understand social organisation" (p. 67).

McBride's advice does not seem to have been heeded. "Spatial organisation is a conspicuous feature of primate social behaviour, but it has attracted relatively few systematic observations", wrote Ehardt-Seward and Bramblett (1980: 214), echoing the observations of Mason (1968b) and of Fairbanks (1976). Mason maintained that "spatial relations within a group are technically more difficult to study quantitatively than is the spatial behaviour of entire groups, and it is probably for this reason that most attention has been given to the group phenomena of range and territory" (p. 200). A procedure facilitating the quantification and pictorial representation of spatial relations is suggested.

Ehardt-Seward and Bramblett (1980) studied "the structure of social space among a captive group of vervet monkeys" (p. 214), and developed a research model which is "descriptive in nature while allowing structured examination of predicted variations along parameters of age, gender, dominance status and uterine affinity" (p. 230). The results indicated that the first six months of life in vervet infants are characterised by a dramatic increase in the ratios of both uterine and non-uterine contact. In particular, contact with kin is more frequent than with nonkin group members for both genders. As the infant matures, the sustained closeness of the infant to the mother subjects him to those proximal relations usual to his mother. The juvenile and subadult years present overall decreases in uterine contact rates for both genders, and females exhibit higher rates of non-uterine contact than males. "At about 47 months of age as monkeys attain adulthood, females show higher rates of contact in general than the males. These results substantiate observations that distance decreases with age for females while males show increased dispersion" (p. 226). The authors hypothesised that in this captive group the kinship bond remained salient into adulthood, because even though the males were somewhat peripheralised and spatially distinct, their high nearness rates involving kin may reflect uterine ties. Prior to this study very little seems to have been recorded about *C. aethiops*. Struhsaker (1967c) noted that the greatest number of supplantations involved space, and the least number were over grooming roles. The adult male has been reported as sitting vigilantly nearby aunting circles (Lancaster, 1975), implying a larger personal space than any of the individuals in the groups described by

Basckin and Krige (1973) of mothers and infants with attendant subadults and juveniles.

In 1980, the author recorded differences in spatial organisation reflecting changes in the immediate environment. She found a significant decrease in interpersonal space when a vervet troop was faced with an unpredictable situation, that is when a free-ranging troop was captured and caged. Upon adaptation to the novel cage environment, interpersonal spaces increased once again. Spatial positions also changed, from remaining high above the ground when apparently frightened, to exploiting all spatial positions including the ground when the environment was familiar (Tollman, 1981). The spatial organisation is sensitive to all features of the environment, psychological and physical. Burke, Kuehle and Dukelow (1981), working with squirrel monkeys, found that interanimal distances decreased with decreasing temperature. Increased grooming, that is decreased interpersonal space, has been reported after aggressive encounters (e.g. Tollman, 1977). Reviewing the flexibility of spatial patterns, Crook (1978) declared that "we know now that the dispersion patterns of species' populations are in general more variable than are the behavioural elements of communication among their members" (p. 58).

The importance of studying the spatial structure for the understanding of the social organisation of different primate groups is highlighted by Fairbanks (1976). She found that "clique associations and social proximity relationships were found to be better predictors than dominance rank of the nature and frequency of behavioural interactions in the two colonies" (of baboons and squirrel monkeys) (p. 291). Kaplan and Zucker (1980) studied a free-ranging group of patas monkeys and found that dispersal was the major strategy utilised by these monkeys in the performance of intragroup social behaviour. Genealogical relationships and dominance phenomena (despite the presence of a linear stable dominance hierarchy among the adult females) were not of major importance for this species.

Finally, of interest to the present study, Leyhausen (1971) specified that an oscillatory dimension should be considered during research into the dynamic nature of individual distance. Since the overall motivational state of an animal varies with circadian, seasonal and other rhythms, and also because of interference by non-rhythmic factors, individual distance is not

rigid but 'pulsates'. He too concluded that the social interactions within a group are "far from being straightforward and easy to understand" (p. 23).

7.2.4   Aggression, dominance and hierarchy.

> Investigators are still far from a consensus on how to define and
> measure dominance.
>
> Bernstein, 1981: 426.

There seems to be considerable disagreement between authors attempting a definition of aggression – in fact, some authors purposely avoid the term as undefinable (e.g. Kummer, 1967; Vowles, 1970). Southwick (1972) stated: "Like many basic concepts, aggression is moderately easy to recognise, but hard to define" (p. 2). Further attempts to arrive at an operational definition have not succeeded and Leyhausen (1979) concluded: "The discussion of aggression in particular has proved unsuccessful and frustrating in the past because nearly every participant has insisted on defining aggression in his own way, and worse – has interpreted the contributions of others along his own lines. A reviewer was thus able to list over fifty definitions of 'aggression'" (p. 254).

Barnett (1981) deplored the confusion surrounding the term aggression, and rejected the more comprehensive term 'agonistic' because it entails different acts for different species. He has defined 'apotreptic' and 'epitreptic' behaviour. Apotreptic behaviour was defined as "conduct that tends to cause withdrawal by a conspecific. This term has the same meaning as threat" (p. 632). Epitreptic behaviour was "behaviour that tends to cause the approach of a conspecific" (p. 633).

Nowell and Heidrich (1978) favoured the term 'threat' and described two of its functions. Firstly, a threat serves to remind target animals of a previously established relationship, and secondly, displays the emotional state of the giver. Such communicatory mechanisms are vital because as Lancaster (1975) pointed out, the ability to predict the behaviour of others is basic to the evolution of complex social systems.

Wilson (1975) defined aggression as "an abridgement of the rights of

another, forcing him to surrender something he owns, or might otherwise have attained, either by a physical act, or the threat of action" (p. 242). He identified eight principal forms of aggression, each one expressed by a mixture of very different behaviour patterns, viz. territorial aggression, dominance aggression, sexual aggression, parental disciplinary aggression, weaning aggression, moral aggression, predatory and antipredatory aggression.

Intraspecific aggression among many species of wild animals (including the Old World monkeys) rarely results in the infliction of physical harm (Washburn and Hamburg, 1968; Nagel and Kummer, 1974). Ritualised displays, threats, submissive and appeasement gestures precede the actual fighting behaviour. Thus, if an individual monkey is protecting young, or attempting to gain access to food, sex, grooming, or social position, the acquisition of the goal is often achieved by threatening and not by physical aggression, which may lead to serious injury or death. This behaviour is adaptive because the monkey depends upon his social group for his survival. The curious phenomenon of infanticide noted in a few species (e.g. Hrdy, 1974) has not been reported for vervets, and a consideration of its function is beyond the scope of this thesis.

Wilson (1975) wrote: "The largest part of aggression among members of the same species can be regarded as a set of competitive techniques" (p. 273). Barash (1977) proposed that it "is the proximate mechanism of contest competition" (p. 210). Barash maintained that an individual should be aggressive "when such behaviour increases the individual's fitness" – it should "characterise situations in which contest competition is more efficient than scrambling. This is particularly true when resources are in short supply" (p. 212). He identified food, mates, and space as important resources leading to aggression, particularly if clumped, as well as the introduction of a strange individual, reflexive fighting (after pain) and the breakdown of social systems.

Vervet intratroop aggressive encounters were examined by Shapiro (1978). Working with a captive group consisting of one adult male, four adult females and seven younger ones of various age-sex categories, he found that successful involvement did not show consistent changes, and concluded that during long fights individuals concentrated on "avoiding defeats rather than pursuing

victories ... The strategy of lowering successful involvement may thus have profound consequences, both internal and external, for the well-being of the individual" (p. 596) – a pertinent observation for this thesis. McGuire (1974) studied *C. aethiops sabaeus* at St Kitts and wrote that "there was little agonistic or aggressive behaviour (p. 101). The author (Tollman, 1981) related intratroop aggression with the specific environmental circumstances. When cooperative behaviour was necessary for survival she found that intratroop agonism decreased, and when conditions were favourable intratroop agonism increased. This may account for the "mysterious anger of vervets in captivity" seen by Chernyshev (1978). Even if they were of "good disposition" (p. 597), his caged troop consisted of vervets that had been housed alone, had no familial bonds, and were thrown together in a very small cage. In Durban, females in both the free-ranging troops and the caged troop gave and received agonistic signals, and have been found to receive wounds (Henzi, 1982; Tollman, 1977). Alvarez (1975) identified a 'scapegoat' role – a very passive female receiving all kinds of attention from most subjects. The author (Tollman, 1977) also observed a 'scapegoat' who was the final recipient of redirected aggression – she was not a 'passive' female, however. Agonistic interactions and possible implications for physiological functioning are considered in this thesis.

Barash (1977) acknowledged the existence of differential social response thresholds between species, but did not seem to consider the individual differences within each species. Fry (1980) was concerned with the individual and presents evidence against group selection level interpretations. He proposed instead "that individual level selection and inclusive fitness theory explain better and provide a heuristically more useful way of examining aggressive behaviour" (p. 69). Are these two approaches mutually exclusive?

Barash (1977) pointed to the importance of a cost benefit analysis for individuals. Unfortunately, a measure of the costs has not yet been devised, even though some benefits may be easy to identify. The physiological consequences of aggression are noted: "a dramatic reduction in gonad size and hormonal output ... **psychological castration**" (p. 243), and also adrenal malfunction where "death may even result" (p. 244). Although Barash may have dramatised the situation, evidence of physiological changes accompanying

social interactions is mounting; for example, Bernstein, Rose, Gordon and Grady (1979) recorded drops in testosterone levels following repeated attack. Thermoregulatory responses to aggression are discussed in the thesis.

Deag (1977) suggested that the constraints which limit aggressiveness are avoiding injury to offspring; controlling individual distances because, if too large, individuals become vulnerable to predation; avoiding an escalation of fighting which may boomerang back to the initiator; and controlling energy expenditure.

Members of the same group of animals coexist within one territory and have to share the available resources. Since this leads to an active demand by two or more individuals for a common resource or requirement, priority for access will be decided on the outcome of a dominance aggression encounter. Dominance behaviour within the group usually leads to a set of sustained aggressive-submissive relations variously termed a dominance order, dominance hierarchy, or social hierarchy. A hierarchy, therefore, is the sequence of dominant and dominated individuals. McBride (1971) has emphasised the fact (often overlooked) that the dominance hierarchy is largely organised spacing behaviour. Once established, animals are free to devote their time and energy to the requirements necessary for survival of the group rather than fighting among each other. Dominance relations seem to act as the context determining direction and type of sharing (Estrada, 1977).

The simplest possible version of a hierarchy is despotism. More commonly though hierarchies contain multiple ranks in a more or less linear sequence. The networks are complicated by triangular or other circular elements (coalitions) but such arrangements seem *a priori* to be less stable than dominance or linear orders (Wilson, 1975). Wilson related the complexity of social networks to the physical development of the species. He wrote that the greater the size of the brain and the more flexible the behaviour, the more numerous are the number of hierarchies and therefore the determinants of rank, and the more nearly equal they are in influence. In some of the higher monkeys and apes we see the emergence of coalitions of peers, protectorates by dominant individuals, and strong maternal influence in the early establishment of rank.

It seems that aggression is a multifactorial behavioural expression strongly influenced by numerous external and internal variables. The evidence from behavioural studies still support Poirier's (1972) assumption that the aggression within any group is influenced by internal (e.g. genetic, hormonal) and external factors, as well as by learning, the particular social group, its socialisation modes, and the econiche. The Cercopithecoids, according to Nagel and Kummer (1974) are probably the most aggressive among the primates.

Controversy surrounds the definition of all the terms relating to dominance and hierarchy. Bernstein (1981) after a review of the 'plethora' of papers dealing with the problem, concluded that "investigators are still far from a consensus on how to define and measure dominance" (p. 426). Over twenty replies to his article have been included in an 'Open Peer Commentary' (1981), and the responses range from views which regard the concept as useless (Flannelly and Blanchard; Smuts) to indispensable (Plutchik). The confusion in this area seems to stem, in part, from the widely differing levels of analyses and interpretations among different research workers. As Bernstein (1978) pointed out, "we must remember Kummer's (1971) warning to separate conceptually (i) the form of the response or structure, (ii) the cause (immediate), (iii) function, (iv) ontogeny, and (v) evolution" (p. 153).

Deag (1977) reminded us that attempts to relate dominance and Darwinian fitness are difficult to interpret because a male's success in copulating during a short observation period bears an unknown relationship to its fertilisation success and to its lifetime production of young. Hinde (1978a) argued that dominance is a useful concept, and may refer either "to the pattern of imbalance of interactions within a dyadic relationship in so far as that pattern is consistent between dyads, or it may refer to an aspect of group structure, namely the extent to which the individuals can be ranked in terms of who bosses whom" (p. 27).

Bernstein (1981), in an attempt to distil the essence of these phenomena, concluded that agonistic dominance must be "distinguished from concepts of competitive exclusion, and from such things as being the most numerous taxon or achieving the highest biomass in a community" (p. 427). He

emphasised that agonistic dominance relationships are defined by the relationship itself, and not by the things that correlate with it. Thus dominance is not an absolute property of an individual but a relationship between individuals. Dominance is an outcome that has been influenced by multiple properties of individuals. "For example, if being the first to accumulate thirty seconds of drinking is in fact a valid measure of dominance, then any manipulation which altered who achieved the criterion first should alter dominance relationships". Thus, the relationship is situationally specific and temporally variable, and dominance explains rather than predicts. Now, "dominance would be universal in that in any test some individual would achieve the criterion first. Such a situation would seem to contribute little to the understanding of the principles of social organisation" (p. 427). Hinde and Datta (1981) challenged Bernstein's argument that does, they contended, for the most part competently summarise the conclusions to which most people's agonisings have led them. "But there is one nettle Dr Bernstein failed to grasp which we believe lies at the bottom of all the misunderstandings - the distinction between data and theory language" (p. 442). Hinde and Datta maintained that if dominance is to be useful in any explanatory sense its proper place is as an intervening variable. They pointed out that Bernstein and others have used dominance as both an independent and as a dependent variable which, they suspected, arises from the fact that the dynamics of relationships depend on positive feedback. Hinde and Datta disagreed with Bernstein on four more issues:-

1. Confining the argument to aggressive dominance - Hinde and Datta believed that its relation with authority and prestige ought to be considered, even if as Kummer (1968) noted they usually go together, but not invariably.

2. Failing to emphasise that dominance is only one of a number of sources of principles useful in the understanding of social structure.

3. Suggesting that position in a numerical hierarchy is crucial for directionality in dyadic relationships, but is largely irrelevant for most issues. Bernstein "could well be correct but he does not cite the evidence most likely to contravene it - namely, the evidence that monkeys themselves may discriminate according to relative rank (e.g. Cheney 1978a)" (p. 442).

4. Using the concept too loosely. This issue is taken up in the following section.

Bernstein correctly chastised researchers who regard a numerical rank as invariant. Changes in relationships between dominant and subordinate individuals have been recorded (e.g. Sade, 1972; Hausfater, 1975). Hausfater found that the changes could be demographically or agonistically-induced, that is changes occurred either when the composition of the group changed through animals dying, leaving or entering the group. Wade (1978) submitted that "social status will in fact probably be best understood as a dynamic, goal-directed process involving two or more animals at a time" (p. 130). Wade has criticised Rowell (1974) and Gartlan (1968) who have argued against the use of any concept of social dominance on the grounds that they "have assumed that the only feasible way to conceptualise it is as a rigid individual trait of a unitary motivational nature" (p. 130). Commenting upon the frequent failure of 'ranks' to correlate with important biological factors such as genealogies, weight, grooming, etc., Bernstein asked: "what can we predict with any accuracy based on each individual's numerical rank in a dominance hierarchy?" (p. 428). Yet, "there is a growing body of evidence showing that animals do differentiate the relative ranks of other group members", wrote Chalmers (1979: 168), reinforcing Hinde and Datta's criticism of Bernstein's article, so it seems we cannot discard the idea.

In his article, Bernstein (quoting Hinde, 1978) stressed the distinction between dominance relationships which exist between two animals and a dominance rank hierarchy which requires transitivity. Unfortunately no pure dominance rank hierarchy may exist, as evidence of the importance of affiliative behaviours for gaining access to resources mounts.

There exist two different mutually exclusive ideas about the mechanisms that form and maintain hierarchies (Chalmers, 1979). The first suggests that there are special qualities of dominance and subordinacy, while the second argument put forward by Rowell (1974) suggests that dominance and submissive qualities do not exist – rather, the circumstances will favour one animal over the other allowing it to gain first access to a resource and eventually become dominant. In both instances, the individuals will cease to compete because their memories will remind them who gets first access to the resource. Rowell also suggested that clear-cut linear hierarchies were the product of captivity and are maintained by the behaviour of the low-ranking individuals. Observations on vervets (Struhsaker, 1967b, 1967c;

Tollman, 1977), macaques (Deag, 1977), and baboons (Hausfater, 1975, in Chalmers, 1979), however, reveal that hierarchies do exist in the wild. Lomnicki asserted that dominance hierarchies "seem to be much more common among animals than previously supposed and recently have been found even among *Anthozoan coelenterates*" (1982: 159). Furthermore, Deag (1977) and Wade (1978) found that these natural hierarchies are maintained by the joint action of dominant and subordinate animals, so disagree with Rowell's hypothesis regarding the maintenance of the hierarchy.

Chapais and Schulman (1980) have developed an evolutionary model of female dominance relations in primates based on individual selection, kin selection, reproductive value, and evolutionarily stable strategies. For any dyadic dominance relationship between Females A and B the measure of inclusive fitness used is a function of the reproductive value of A and B, the coefficient of relatedness, the effect of rank on reproductive success and the component effects of rank on personal fitness and inclusive fitness. The authors confirmed their hypotheses on macaques and concluded that "based on the assumption that females optimise their inclusive fitness, the predictions derived from the models are, on the whole, remarkably consistent with what is known about the behaviour of macaques" (p. 85).

Bernstein, however, highlighted another important mechanism to promote fitness – social strategies. "Selection would then be for the social skills leading to successful alliances in troop defence" (1976: 459). Anderson and Mason (1978) compared two captive groups of macaques, one socially deprived, the other not, and found that the experienced monkeys were able to influence the behaviour of higher status members by including second and third parties in their interactions. They concluded that "higher orders of social cognition are dependent on early social experience" (p. 289).

"The study of dominance is essentially the study of correlations ... it is by no means always the case that such correlations are close or immediately apparent" – thus wrote Chalmers (1979: 184). He added that neither aggressiveness, physique or size necessarily correlate with dominance. Age is important for some species (e.g. Hausfater, 1975), while the rank of a rhesus male was found to be directly correlated with its age, and with the length of time that had elapsed since it had joined the group (Drickamer and Vessey, 1973).

Adapting successfully ultimately implies reproducing successfully.
Bernstein (1976) asserted that "many theoreticians have postulated selective
mechanisms operating on the genetic attributes which contribute to high
dominance rank.   Alpha males were hypothesised to increase their genetic
fitness by successfully competing with other males for access to ovulating
females.   Evidence to these speculations has been mixed" (p. 459).
Studies examining correlations between rank and reproductive success are
equivocal.   The results seem to suggest that high-ranking males may also
leave more progeny than low-ranking males (e.g. Stephenson, 1975, in
Chalmers, 1979), yet Eaton (1974), working on caged Japanese macaques, as
Stephenson did, found no correlation between adult male rank and the
frequency with which adult males ejaculated, nor between an adult male's
rank and the frequency with which it initiated copulation.   Takahata (1982)
also found no positive correlation between rank and mating success in adult
Japanese monkeys.   A detailed examination of the different measures used
to measure mating success is indicated.

The degree of correlation between hierarchies when assessed on the
basis of different behaviours is contradictory, but it seems that in some
situations the correlation between research assessments is poor.   Consequently
when referring to a hierarchy or the ranks of individuals within a hierarchy
it is necessary to specify the method by which the hierarchy has been
assessed (Deag, 1977;   Chalmers, 1979;   McGuire, Raleigh and Johnson, 1983).

McGuire, Raleigh and Johnson (1983) have traced the historical
development of ideas on social dominance, and have suggested the following
four reasons for the lack of agreement among investigators regarding the
definition and theory of dominance:-
1.   The different meanings, methodological and theoretical implications of
      the various terms used to denote dominance, for example social rank,
      asymmetrical relationship or social roles.
2.   Studies of captive groups may not generalise to free-ranging groups.
3.   The adaptive benefits of dominance have not been established.
4.   Unitary causes of social dominance are now seldom considered.

Investigators are now attempting "to interrelate dominance and the
themes of resource access and control, adaptive benefits, social reciprocity,
kin relationships and reproductive success" (p. 91).   Views regarding female

dominance relationships must take into account that agonistic behaviour and social rank in offspring has been found to show a close relationship with maternal rank, kinship and birth order (e.g. Sade, 1972; Cheney, 1977; Seyfarth, 1976, 1977; Fairbanks, 1980; Dolhinow, McKenna and Von der Haar Laws, 1978; Dunbar, 1980).

Rosenblum and Lowe (1971) have suggested that familiarity is a critical variable in the determination of affiliative relationships, while Kummer (1979) considered that a number of variables such as sex and availability to assist may impact affiliation. However, according to McGuire (1983) for vervets the importance of affiliative relationships may be minimal when social status differences are considered because new dominant males do not seem to show partiality towards previously preferred affiliative partners.

Evidence of physiological correlates with dominance points to the interrelatedness of physiological, social and behavioural functioning, the central concern of this thesis.

Adequate nutrition is essential for optimal physiological functioning. Post, Hausfater and McCuskey (1980) found that high-ranking individuals generally had longer feeding bout durations than lower ranking individuals, and were less likely to have their feeding bouts aggressively interrupted. The animals whose feeding bouts were most frequently interrupted showed the lowest mean duration bout. Dittus (1980) criticised studies of dominance which do not involve resource competition. "The importance of rank to feeding ecology, however, is demonstrated by the fact that dominant-subordinate relationships are defined frequently and most reliably on the basis of priority of access to food or other contested items among the Cercopithecinae" (p. 279).

Further measures of dominance have included the frequency and direction of attack, threat, avoidance, grooming, non-sexual mounting and attention (Torres de Assumpcao and Deag, 1979). Studies of reproduction indicate that the physiological correlates of reproductive behaviour are influenced by social dominance. Snowdon (1983) cited studies of monogamous primates, that is marmosets and cotton-top tamarins, where the subordinate females display ovulatory suppression. In lemmings, Buhl, Hasler, Tyler, Goldberg and Banks (1978) found long-term effects of rank on

plasma testosterone concentration and spermatogenesis. The situation does not seem as clear-cut with higher primates, because Eaton and Resko (1974) found that plasma testosterone levels did not correlate with dominance rank or aggressive behaviour in male Japanese macaques, yet Mendoza, Coe, Lowe and Levine (1979) found that the dominant male had the highest level of plasma testosterone and the y male exhibited the lowest level of plasma testosterone in groups of three adult male squirrel monkeys. Neither testosterone nor cortisol levels prior to group formation however could be used to predict the subsequent dominance status of the males. The influence of dominance on plasma cortisol was not observed until females were introduced, and at this time the dominant males showed the highest level of cortisol and the y males the lowest. In contrast to testosterone, cortisol levels generally increased for all animals when successive phases of group formation occurred. "Cortisol has been documented to be a sensitive measure of the individual's state of arousal (Hennessy and Levine, in Press)" (p. 228). Chamove and Bowman (1978) examined corticosteroid elevations during social stress, and provided evidence that it is related to behaviour suggestive of fear and not aggression, and is dependent upon "dominance rank, the level of dominance competition, and previous dominance history" (p. 43). McGuire, Raleigh and Johnson (1983) have also described biochemical concomitants of dominance.

Jones (1981) has presented a theoretical formulation, classification and assessment of the evolution and socioecology of dominance in primate groups. She held that dominance hierarchies have evolved by individual selection from an evolutionary compromise between intraspecific competition for resources and for mates. "The hypothesis is put forward that when competition in 'stable' habitats leads to 'niche breadth' a species is preadapted to life in heterogeneous environments, and the consequent selection for fecundity" (p. 70). Jones suggested that "a continuum may exist from less to greater patchiness in the distribution of resources, less to greater variability in the abundance of resources, smaller to greater "niche breadth" ("phenotypic plasticity") and less to greater omnivority" (p. 80). She maintained that vervets display a rare type of status system, where females are dominant to males, and which has only been identified in seven primate species with multi-male organisation. She proposed that similarities between the vervet (*C. aethiops*) and the blue monkey (*C. mitis*) suggests that selection for survivorship and "niche breadth" in 'stable' habitats may have resulted in

the evolution of this status pattern and preadaptation to 'unstable' conditions. Males may have adopted subordinance to females as a strategy to maximise survival in stable forests, a trait that would enhance female fecundity and their own reproductive success in variable habitats. An apparent inability of the male to deal with an unpredictable situation and the females' flexibility and protectiveness towards the male has been noted by the author (Tollman, 1981). It would seem that the conception of a single linear hierarchy for vervet males and females does not account for the range of social hierarchies reported. Lancaster (1975) suggested that vervet females have a linear hierarchy separate from that of the males. Basckin and Krige (1973) saw no linear dominance and suggested that "dominance in vervets may be a multi-dimensional phenomenon in that dominance may apply to specific classes of situation and to specific times" (p. 295), while Struhsaker (1967c) noted that adult males were the highest ranking animals in two troops at Amboseli. McGuire (1974) found that the vervets of St Kitts "were conspicuous for their lack of obvious hierarchy, at least if the behaviour of the Amboseli vervet is taken as a basis for comparison" (p. 107). Bramblett, Bramblett, Bishop and Coelho Jr (1982) wrote that "status hierarchies are universal among cercopithecines studied so far" (p. 42), and they back their statement with reports of status hierarchies in both wild troops (e.g. Struhsaker, 1967c; Gartlan, 1968; Seyfarth, 1980) and captive troops (e.g. Rowell, 1972; Fairbanks, 1980). . Bramblett, Bramblett, Bishop and Coelho Jr, after a twelve-year study of captive vervets found no gender difference in rank was demonstrable, and suggest that the apparent gender difference in rank among wild-living vervets may be a consequence of male intergroup mobility. These researchers further established that relative rank was quite stable for the vervet adults of both sexes, although males were more variable than females, and there was a strong matriline effect on all captive-born animals' rank position. They emphasised the relative importance of social learning in the establishment and maintenance of dominance relationships.

McGuire, Raleigh and Johnson (1983) have identified the following issues as impeding our understanding of dominance:-

1.   The uses of theory. "Generally, the necessary work of setting forth and testing specific hypotheses has not been done although some exceptions exist (see, for examples, Kummer, 1974; Fairbanks, 1980; Bernstein and Gordon, 1980)" (p. 91).

2.   Criteria for across-species generalisations, and the relative importance
       of dominance relationships in different species.

3.   Form-function relationships – behaviours similar in form may have
       different functions and consequences, and vice versa.

4.   The inclusion of environmental variables in data interpretation and the
       use of functional categories.

Dominance was one of the first axes of social organisation to be described
for nonhuman primates, probably because it is relatively easy to observe.
However, "it is important to remember that dominance is only one principle
of social organisation and even for the most dominance-orientated species,
it is only one aspect of social life" (Lancaster, 1975: 19).   Indeed,
McGuire (1983) has come to the conclusion that being a nondominant animal
does not appear to be so costly or so free of benefits as to preclude an
animal's remaining in his group.

7.2.5   Social roles.

> Because the role concept can be useful in understanding social structure
> even when it is not helpful in understanding the determinants of the
> behaviour of the incumbents it can be of use in studies of non-human
> species.
>
> Hinde, 1978: 36.

It seems that the concepts of role and dominance are sometimes
confused in the literature, and it was therefore considered pertinent that
the concept of 'role' should be examined in this literature review.

Chalmers (1979) deplored the existence of different uses of the term
'role' because they "not only cause confusion, but reduce the usefulness of
role as a concept that can be used in the analysis of social behaviour" (p.
215).   He maintained that two ideas are central to the concept – namely
that a role refers to a collection of behaviours that fulfil a specific function
within the group, and that the collection of adaptive behaviours that
constitute a role can be recognised regardless of the individual who performs
them.

Hinde (1978a) has suggested that the terms 'dominance' and 'role'
become jumbled because both are used to describe patterns of inter-individual

relationships. Unfortunately, both terms have been derived from everyday speech and so have developed multiple meanings. In an explanatory article Hinde identified the role concept with respect to two problems: "(a) that of the determinants of behaviour in the individual, and (b) that of the way in which individual behaviour contributes to the structure of relationships, groups or societies" (p. 34). This would seem to be in agreement with Chalmers' (1979) criticisms of authors such as Fedigan, who use the term simply to denote the behaviours that are characteristic of a particular age-sex class without regard to the adaptiveness of these behaviours.

Hinde has identified three salient points in the use of the concept 'role':-

1. 'Role' is used in relation to behaviour that is associated with a position or status in the group.
2. 'Role' refers to behaviour that has effects on others and is characterised in terms which ultimately have reference to those effects and not to effects on the incumbent.
3. 'Role' is used in relation to behaviour that is normally shown by the diverse incumbents of the role, not to their individual idiosyncrasies.

In considering role as a determinant of social action, Hinde contended that the role concept is useful only if applied to the subset of determinants that constitute the goals of the subject "defined in respect to real or imagined effects of his behaviour on others". Nonhumans would have no verbal precepts to guide them, and therefore the ways in which the role concept can be applied to man and monkey may differ. He disagreed with Reynolds who "defines monkey roles as 'statistically probable behaviours' in a given interactional and ecological setting. Used in this way 'role' is equivalent to behaviour and thus a redundant concept" (p. 34). Hinde pointed to the importance of interactions in terms of the goals that are set in relation to the society, "biological factors continuously affect social ones, and social ones biological" (p. 34).

The role concept may be useful in analysing the determinants of the behaviour of individuals who hold a particular position in the society, or it may be useful in describing how the behaviour of individuals in certain positions in a society contributes to its structure - that is to the consequences of behaviour. The determinants and the consequences need

not be related and, warned Hinde, must not be confused.   Hinde also pointed out that roles as determinants of social action may be important for understanding the principles underlying the structure of a group even when the relative goals are never attained.   This means that role as determinant may be relative to either 'surface' or 'deep structure'.   By contrast 'role' as social consequence is usually concerned with actual events and refers only to "surface structure and not to the underlying principles" (p. 36).

The flexibility found in primate social structures has consequences for all the facets of social functioning.   Not all primate species organisations have the same roles, and the roles played by males and females vary from species to species among the primates (Dolhinow, 1972;   Lancaster, 1976).

Fairbanks, McGuire and Page (1978) maintained that role should refer to a social position occupied by one or more individuals, not to an age–sex class characteristic, and should be a property of group structure independent of the individuals who are filling the role at any given point in time. These researchers identified six behaviour clusters through factor analysis of the individual profiles of eighteen vervet monkeys *(C. aethiops sabaeus)* living at St Kitts.   They judged three of the clusters to represent the social roles of Control Male, Control Female, and Subordinate, and the other three as describing the behaviours associated with the developmental stages of yearling.   In view of Hinde's and Chalmers' criteria described above, it is suggested that Fairbanks, McGuire and Page's roles require further clarification, for example, in terms of Chalmers' requirement of ultimate causation, and the behavioural clusters therefore may need further examination.

Snowdon, in the **Annual Review of Psychology,** (1983), suggested that "animals of different ranks played different roles" (p. 83).   Although this may hold for some roles, others (e.g. mothering) cut across ranks.   The statement may reflect a confusion of terms: "to avoid confusion in the use of each of these concepts (dominance and role) it is essential to define precisely the manner in which it is being used" (Hinde, 1978: 27).

7.2.6   The adult female.

The adult female may be regarded as a focus of group organisation in that
they interact at multiple levels with all other animals.

Bernstein and Sharpe, 1966: 100.

The evolutionary role of the female is to raise as many infants as
possible to maturity (Lancaster, 1975).   Implicit in this statement are
requirements for efficient mothering, sexual selection for a mate whose
genes are well adapted for her particular ecological niche, and a social
environment providing protection and optimal opportunities for learning all
the skills necessary for survival.   In 1979, Lancaster wrote: "new data
have important implications for the understanding of the role of sexual
behaviour in integrating primate societies" (p. 53).   Vervet male intertroop
transfers (Henzi and Lucas, 1980) give credence to her statement that
"females form the stable, organised core of a longterm social group, and
males compose a more or less shifting population within a neighbourhood"
(p. 70).   The author (Tollman, 1981) found that when a vervet troop was
drastically disturbed by caging and the adult male's behaviour disintegrated,
the adult females' flexibility and capacity to fulfil a wide spectrum of
roles ensured the retention of all behaviours necessary for the everyday
functioning of the troop.

Krebs and Davies (1981) believed that "the fundamental difference
between male and female is the size of the gametes" (p. 134).   Barash
(1979) succinctly supported: "Sperm are cheap.   Eggs are expensive" (p.
48).   Thus, according to these researchers, males put most of their
reproductive effort into mating, and females put theirs into parenting.
For males, then, females are a key resource but for females, food is a key
resource.   Following this reasoning, Wrangham (1980) hypothesised that
two classes of multifemale primate groups have evolved in response to
varying ecological characteristics, a female-bonded (FB) group and a non
female-bonded (non-FB) group.   FB groups, of which vervets are typical,
are based on cooperative relationships among females.   These groups
exploit high quality food patches which are available in limited numbers, so
the female troop members cooperate to supplant outsiders - individuals
or troops.   FB females persist in travelling and feeding together despite
increased intratroop aggression over food, and uneven distribution of food

because of a relatively stable linear hierarchy (Lancaster, 1975). Unlike males, females have not been seen to transfer to other groups (Gartlan and Brain, 1968; Henzi, 1982) so the gains must outweigh these costs (Wrangham, 1980). In contrast, the relationships in non-FB troops are loose - food sources are of lower quality, relatively evenly distributed, not easily defended, and female intertroop transfers occur. Vervet females also participate actively with males in intertroop encounters, although females with infants often hang back (Lancaster, 1979; Tollman, 1977). Female vervets are found to be tolerant of strange adult males that move between troops. Nevertheless Lancaster (1975) observed that in species like the vervet where dimorphism is 'minor' there may be very little difference in the aggressive potential between males and females.

Cooperative living extends beyond foraging. Adult vervet females will readily form coalitions against individual males, in dominance encounters, if they frighten an infant, or try to monopolise a concentrated or prized food source. Lancaster (1975) postulated that genealogical cores probably form the nucleus of such coalitions. She found that these coalitions were formed irrespective of status, so that even females from the lowest genealogies would chase a male that had made one of their infants scream. Males who had recently joined the group were more vulnerable to such attacks than males belonging to high-ranking lineages but no males were immune. Although these female coalitions never seem to affect the rank of the male concerned, "his ability to bully subordinates is curbed" (p. 30).

Close kinship ties exist among vervet females because they breed in their natal troops (Struhsaker, 1967c). As Henzi (1982) pointed out, the females go to great lengths to preserve the integrity of a group with longterm bonds. They can maintain group cohesion and still benefit from the influx of new genes by excluding strange females, and attracting strange males directly through oestrus (Lancaster, 1979), or soliciting them, or indirectly through ignoring them. Seyfarth (1976) has developed a model of rank-related access and attractiveness for predicting the distribution of grooming over time. Fairbanks (1980) confirmed the model's predictions on *C. aethiops sabaeus* but pointed out that the same outcome could be predicted by an alternate model based on kinship. It seems that in the formation of subgroups, members from the same matriline tend to have an affinity for one another. In vervets, sleeping subgroups and grooming

relationships have been shown to be formed, at least in part, with reference to the mother-infant relation (Struhsaker, 1967c and Sade, 1965, respectively). This matrifocal unit forms the nucleus of the troop, because "ultimately the bonds that attract these individuals to each other are based upon their commonly-held focus of attention and emotion, a mother or even a grandmother" (Lancaster, 1979: 27). The adult females provide the group with stability and continuity through time (Tollman, 1977). The mother-infant dyad appears to exert a particular attraction (Krige and Lucas, 1975; Seyfarth, 1976).

Bernstein (1971), in his investigation of the activity profiles in six different taxa of captive monkey groups, found that the female patterns were generally the inverse of the male patterns – the females were more active and spent more time participating in social interactions than the males, and also performed more than they received. Field data analyses (Wilson, 1975) revealed that the adult female vervet received more friendly approaches and led in group movements more than any other age-sex category. She was rivalled only by the subadult females in friendly approaches to others. In most species adult females seem to groom more than the other age-sex categories (e.g. see review article Tokunaga and Mitchell, 1977). McKenna (1978) added that females not only groomed more, but their grooming networks were more extensive – a finding consistent with the vervets being studied (Tollman, 1977). Further data confirmed that both juvenile and adult males receive more grooming than they give, while both juvenile and adult females groom and are groomed more than their male counterparts (Tokunaga and Mitchell, 1977; Tollman, 1977; Raleigh, Flannery and Ervin, 1979).

Cheney, Lee and Seyfarth (1981) looked at rank and reproductive success among free-ranging female vervet monkeys. They concluded that there was no correlation between rank and success, because high-ranking animals survived no better than low-ranking animals. Death among low-ranking animals was primarily due to illness probably through food shortages, while deaths among high-ranking animals were due to predation. These researchers suggested that different animals within the same group confront different selective pressures. Certainly each environment presents with different pressures, because each environment is unique. In caged troops, for example, predators do not exist and therefore success in the cage probably reflects

rank. However, Darwinian fitness refers to ability of offspring to survive and reproduce, so can we move beyond speculation before longitudinal data is collected to measure this? During water shortages, Wrangham (1981) found animals of high rank survived better than animals of low rank. It is argued that physical fitness will improve individual performance, and consequently mothering may be more effective, and individual survival enhanced. Thus, high rank may exert a subtle ripple effect: priority of access to resources and, therefore, enhanced physiological functioning.

Cheney, Lee and Seyfarth (1981) suggested that females of different rank play different roles. High-ranking vervets gave more alarm calls and were more aggressive in intergroup encounters, while low-ranking females interacted in a friendly way with strange groups. In her caged troop, the author (1977) found that the low-ranking female actually initiated intertroop aggressive encounters, and a high-ranking female was the first to become friendly with a peripheral male. Cheney, Lee and Seyfarth suggested that rank may be a reflection of different personality styles rather than an index of fitness. Is it possible that behavioural styles do not reflect rank but personality, so that aggressive animals could be high- or low-ranking?

7.2.7   Group integrative mechanisms.

Bonding between particular individuals or subgroups in primate societies occurs when there are special advantages to keeping individuals together.

Lancaster, 1975: 31.

An examination of the mechanisms promoting group unity seems an important requirement for any investigation attempting to understand all the factors involved in maintaining the equilibrium of socially-living individuals. Gartlan and Brain (1968) considered that the following invariant factors promoted social cohesion in vervets:-

1. Defence against a common enemy. Unity is most necessary when the survival of the group is threatened – and all troop members work together when dealing with predators. Territorial encounters also elicit the cooperation of all vervet age-sex categories (except infants).

2. The comparatively late development of the infant. This tends to make the infant-mother bond strong and enduring. In addition, the presence

of an infant in a group has a very strong cohesive influence, since all females are attracted towards infants and attempt to get close to them. Wild vervet groups usually contain some infants, and so a constant cohesive effect is present.

3. Sleeping subgroups. Vervets habitually sleep in small clusters with their arms around each other for warmth. Any cool or cold nights will therefore serve to promote social cohesion. Struhsaker (1967c) assumed that sleeping subgroups were formed as camouflage against predators. Since predation is a constant threat, social bonds will continually be reinforced through clustering.

4. Sexual behaviour. Literature on this subject is controversial and contradictory. Gartlan and Brain maintained that if vervet sexual behaviour does act as an integrative mechanism, it is a much less potent force in vervets than in baboons because of the low frequency and possible seasonality of mating, and since females do not pass from male to male during oestrus. Rowell (1972) pointed out, however, that if the cohesive function of sexual interaction is denied we are left with the task of explaining why monkeys and apes are receptive proportionately more of the time than are other mammals.

Lancaster (1979), in examining new data on sexual behaviour, has concluded that it "is clearly a very important way of expressing and maintaining special affectionate relationships in nonhuman primates" (p. 58). She points to four important generalisations that come from the data (much from vervet behaviour):-

1. "Old World monkeys and apes do not engage in sexual activity only around the period of ovulation" (p. 73). As early as 1972, Rowell reported that captive vervets appeared to be in continuous oestrus, copulating throughout the menstrual cycle.

2. Lack of evidence that female behaviour and social status in nonhuman primates are largely under the control of hormonal cycles.

3. Lack of evidence for major sex role differences in regard to important aspects of social behaviour in selecting mating partners, in seeking consummatory responses and in forming sexual attachments, and that the roles are not rigidly sex-specific.

4. Dominance and reproductive success seem to correlate most strongly with full social maturity and length of tenure in the group rather than

one of several effective strategies for passing on genes to the next generation.

Bernstein (1971) found that "the green monkeys are distinct among the Old World monkeys studied because of their extremely low sexual response rates, the high percentage of contact aggression compared to non-contact aggression, and their low grooming scores" (p. 25). Field studies in the Natal area have supported Bernstein's conclusions. Basckin and Krige (1973) reported that no sexual behaviour was noticed during their study between October 1972 and March 1973, while Lucas (1980, pers. comm.) saw relatively little mating behaviour over the ten years he worked at Karkloof, Natal. Gartlan (1968) reported that a long refractory period followed each vervet copulation, and this may account for the low frequency rates recorded. Visibility limitations would also occur if mating was a nocturnal activity. In the cage little mating activity has been observed, except while the troop were adapting to the caged environment, when it was hypothesised to be a social mechanism to produce cohesiveness during stress. Despite the lack of observable sexual activity infants are born each year. Rowell and Richards (1979) have classified the vervets as a fast-mating quick-breeding species.

Further aspects which promote solidatiry need consideration.

Wilson (1975) has emphasised the importance of altruism for the survival of a species. "How can altruism, which by definition reduces personal fitness, possibly evolve by natural selection? The answer is kinship; if the genes causing the altruism are shared by two organisms because of common descent, and if the altruistic act by one organism increases the joint contribution of these genes to the next generation, the propensity to altruism will spread through the pool" (p. 3). The affinity that members from the same matriline tend to have for one another has been discussed.

Individual monkeys have also been shown to be attracted towards the same age groups and the same sex groups. Infants and juveniles gravitate towards play groups (Chance and Jolly, 1970; Bernstein, 1971; Rowell, 1972; Lancaster, 1975). The social group itself draws the individual – monkeys that have been isolated have been shown to seek the company of other monkeys. Responses of individuals to mildly disturbing situations

were found to be reduced by the presence of their companions (Hall, 1963). Harlow and Suomi (1971) found that the most critical and valid measures of social recovery by monkeys reared in isolation were those of social contact and play. At the human level Stumpfer (1970) recorded a significant positive interrelationship between fear and affiliative tendencies. Thus the social group seems to exert a force drawing the individual toward it, and the strength of the force is related to environmental circumstances. Snowdon (1983) referred to the reconciliation of male chimpanzees (described by de Waal and van Roosmalen, 1979) who embraced, touched, hugged and kissed each other after agonistic interactions. Reconciliation, wrote Snowdon, may serve a socially homeostatic function restoring the cohesion of a group after an agonistic interaction.

According to Gartlan (1966) the basic maintenance activities of the group such as running, walking, feeding, chasing and grooming are coordinated through 'socially infectious behaviour' or 'social facilitation'.

7.2.8   Grooming.

> Indeed the possibility exists that particular behaviors such as grooming have multiple meanings.
>
> McKenna, 1978: 506.

In all the groups he studied Bernstein (1971) found that the social response which accounted for the greatest percentage of time that individuals were in contact with one another was social grooming. Grooming behaviour has been recorded for all species of Cercopithecidae (Sparks, 1967) and therefore must be very important. Grooming appears to have several functions, and to be influenced by both internal and external factors. Hypotheses regarding the survival functions can be divided into two groups: 'clean and eat' and 'social bonding and tension reduction'. "Both of these hypotheses are incomplete", according to Goosen (1981: 110).

Studies demonstrating that socially-living males have fewer lice and ticks in their pelage than solitary males, and that host-specific lice have adapted to the grooming dexterity of their host, indicates that grooming does result in the removal of ectoparasites such as ticks and lice (McKenna, 1978; Goosen, 1981). Goosen maintained that removal or recovery of debris or

vermin is of only minor significance, it is not of urgent interest, but McKenna observed that recent investigators call for more attention to the disease-controlling functions of grooming, particularly since grooming must have originally functioned as a parasite-controlling mechanism and not as an accommodation to group living. McKenna declared that he can neither verify nor refute this contention, but referred to his own observations that during social grooming langurs tend to groom inaccessible regions of the body rather than accessible regions. He suggests that in the light of Curtin's discovery that during the wet season solitary male langurs suffer leech infestations on parts of their bodies inaccessible for self-grooming, it seems the hygienic argument must not be underemphasised, and could even be urgent.

The social importance of grooming is generally acknowledged. "Grooming is undoubtedly one of the major ways in which social bonds are expressed and maintained", wrote Lancaster (1976: 2). Baxter and Fedigan (1979) agree, and have identified an incest taboo mechanism operating which leads to a distinction between grooming in long-term affiliative bonding and consort partner selection in macaques. Goosen was critical because "the concepts of social bond or low tension are defined such that they cannot explain why grooming varies with the type of situation in which animals meet" (p. 110). He described postulates by various authors, such as: "grooming serves to strengthen social bonds" ... "maintaining and renewing peaceful solutions" ... "regulating certain aspects of social life" ... "a result rather than a cause of a strong social bond" ... "the above hypotheses, however, are not readily testable" (p. 111). Goosen, in considering that grooming is elicited by proximity in a variety of social situations, is often time-consuming, possibly reduces aggression toward the partner, and may have different effects, theorised that by grooming, both partners indicate that they are not preparing for hostilities against each other. If, at the same time, the situation involves a third party over a survival resource, "it is likely that the grooming partners reduce the risk of confusing partner and opponent in such a critical situation" (p. 116).

Chalmers (1979) highlighted the importance of reevaluating grooming data interpretations by quoting Simpson's research with chimpanzees.

He found that rank correlations differed with frequential and durational measures. According to the frequential data, Male A and Male B groomed each other an equivalent amount, yet low-ranking partners groomed high-ranking partners for longer than the partner would groom him. The findings of Kaplan and Zucker (1980) pointed to the importance of low-ranking monkeys as the focus of affiliative behaviour in patas monkeys because a positive correlation was discovered between low rank and amount of grooming received. McKenna (1978), in deriving general principles from age-sex grooming frequencies, emphasised intraspecific individual differences: "there is much variation within age and sex classes which deserves attention" (p. 504). It seems that each study needs to be thoroughly assessed in order to ascertain whether species differences are real or artefacts of experimental procedure.

Physiological involvement in the incidence of grooming has been implicated. For example, Seyfarth (1976) found that his females were most attractive to others during lactation, even though females of high rank in whatever condition are more attractive than females of low rank.

Grooming as a tension-reduction mechanism is of particular interest. It has been postulated by many authors (e.g. see review Goosen, 1981; Rhine and Linville, 1973; Tokunaga and Mitchell, 1977), yet this conclusion seems to have been intuitively derived and not through hypothesis testing. McKenna (1978) investigated the relationship between grooming and aggression and found that "while aggression preceded tension-reducing grooming at statistically significant rates, aggression did not follow grooming at rates different from what would be expected by chance" (p. 506). The author has found a significant correlation between an increase in grooming and vervet intertroop encounters (Tollman, 1981). She also found a marked increase in intratroop grooming during stress.

Grooming appears to have evolved to serve a multiplicity of functions, and is therefore displayed in varying amounts in a variety of circumstances. It would seem important, therefore, that any analysis of grooming must take account of the subject's physiological condition, and the social and ecological context. These ideas are explored further in the chapters which follow.

7.3   PROCEDURE.

7.3.1   Data collection.

Social functioning was always recorded with behaviour.   Detailed information of each subject's social activity, therefore, was included during the collection of the randomised blocks of five-minute focal time samples of behaviour, monitored in conjunction with body temperature, and described in detail in section 6.3.1.   The recording schedule was presented in Table 5.1.   In addition, troop scans were conducted before and after each study.

A dominance ranking for the three troop-living vervets, as judged by the author, was confirmed in a separate set of observations in which the subjects were ordered in terms of first access to food, sun (there was only one sunny spot in the cage in the early morning) and shelter (one shelter was enclosed on three sides, and appeared to be the favourite).   This hierarchical order was confirmed by blind and independent assessments of two other researchers.

7.3.2   Data processing.

Please turn to section 6.3.2 for a full description of the procedures followed in transcribing and organising all the information that had been captured visually, and on audiotape.   Social behaviours in this study were not confined to interactions but also included 'coaction', symmetrical events in which two or more conspecifics appeared to act together, for example climb together, sit together, or walk together.

The Sociogram :

In order to obtain a visual representation of the way the individual communicates with the rest of the troop members, the following interaction matrices have been designed.   The sociogram takes account of the spatial relationships allowing each animal to advance towards a particular conspecific, or retreat into a personal space.   These sociograms are versatile and are suitable for friendly or for agonistic interactions.   Only

the labelling needs to be changed.

Radii in each semicircle are calibrated into fifteen equal divisions. Along each radius a link is set up between the target animal and a member of the troop (as shown in the diagram). When this has been done, interaction frequencies are scored and filled in.

Friendly interactions :

When 'friendly' behaviour is observed the animal may be seen initiating, receiving, or combining in a friendly interaction and a specific semicircle provides for the symmetrical (coaction) and asymmetrical behaviours. In the former case, the score is indicated by allowing the midpoint of the score to be the midpoint of the appropriate semicircle. The animals are arranged along the outer circumference, the various troop members occupying positions in the upper half of the outer semicircle, and the target member on the opposite ends of the axes, along the lower half of the inner semicircle.

Agonistic interactions :

During agonistic encounters the aggressor and aggressee were usually identified. Provision is made for the representation of the specific animals involved to advance, retreat or avoid. In this figure, troop members are ranged along the circumference of the inner semicircle and the target subject is at the centre. This allows for each animal to have its own personal space, so that both initiating and avoiding can be plotted.

In this study, the social behaviour of each of the subjects as described by their interactions with their troop conspecifics is displayed in Figures 7.1 and 7.2 respectively.

Appendix 7 describes the categorisation of behaviours recorded on the activity matrix, for use with the sociogram.

7.4   RESULTS.

7.4.1   The dominance hierarchy.

The troop-living subjects were ranked according to the criteria outlined in Table 7.1

TABLE   7.1

PRIORITY OF ACCESS TO RESOURCES IN TROOP-LIVING SUBJECTS.

	NUMBER OF TIMES FIRST SUBJECT			TOTAL NUMBER OF EPISODES
	3	4	5	N
Food	28	2	0	30
Sun	27	3	0	30
Shelter	30	20	6	56
Total Frequency	85	25	6	116

For the above resources, subject 3 had priority of access to resources significantly more than subject 4 (X^2 = 16.36, p < .001), and subject 4 gained first access significantly more than subject 5 (X^2 = 5.82, p < .02). Therefore hierarchical ranking was: subject 3 highest, then subject 4, then subject 5.

7.4.2   Social interactions.

Social interactions have been categorised as 'social friendly' or 'social agonistic'.   Subcategories are:-

Social friendly :   Initiator, receiver, coaction.

Social agonistic :   Initiator, receiver, avoiding, being avoided.

Figure 7.1 and Figure 7.2 provide a visual display of the social behaviour of each of the subjects living within the troop.

the interaction frequencies during the first block of rigorously randomised simultaneous recordings of T_b, behavioural and social functioning.   An interesting observation first noted by Tollman (1977) was that although the adult male interacted more with the dominant female, he interacted with all the females at some time over the day.   He also usually went to sleep at night huddling the dominant female – prime time?

Significant individual differences in social behaviour were revealed when the interaction frequencies were evaluated with a Chi-Square test. The following description is based on the interaction frequencies of each subject with all troop members (see Table 7.2 and Table 7.3).

Total interactions :
There was a significant difference in the total number of interactions exhibited by the three troop-living subjects (X^2 = 32.54, p <.001).   S3, the highest ranking subject, was seen to interact more, and S5, the lowest ranking vervet, to interact less than their respective conspecifics.

Friendly interactions :
There was a significant difference between subjects (X^2 = 32.24, p <.001).
S3 : Initiated and received more friendly interactions.   She coacted more than S4, but an equivalent amount to S5.
S4 : Initiated and received less friendly overtures than S3, and coacted less than S3 or S5.
S5 : Initiated and received less friendly overtures than S3.   However, coaction was more frequent than S4, and equivalent to S3.

Agonistic interactions :
A significant difference in agonistic interchanges was displayed (X^2 = 11.6, p <.01).
S3 : Initiated agonistic interactions to the same extent as S5 but more than S4.   Was target of agonism less than S5.   S3 avoided conspecifics less than and was avoided more than S5.
S4 : Initiated agonistic encounters less than S3 or S5, and was a target less than S5.
S5 : Opposite avoidance trends to S3: avoided significantly more and was avoided significantly less.   She initiated agonistic interactions as frequently as S3, but was the butt of agoni....

FIGURE 7.1 SOCIOGRAMS DEPICTING FRIENDLY INTERACTIONS OF
TROOP-LIVING SUBJECTS : 2 APRIL 1979 - 4 MAY 1979.

CODING: S3 S4 S5 : Target subjects; F : An older female; M : Adult male;

TABLE 7.2

FRIENDLY INTERACTION FREQUENTIAL SCORES.

date .... April 2 through May 4, 1979

1. Target subject as initiator :

time sample .... $N = 75 \times 25$ elements

Receiver

Initiator	3	4	5	o→	♀	Subad.	Juv.	Jun.	N
3		6	0	15	3	8	25	45	102
4	14		0	11	5	8	17	1	56
5	4	0		8	10	4	10	18	54

2. Target subject as receiver :

Initiator

Receiver	3	4	5	o→	♀	Subad.	Juv.	Jun.	N
3		11	2	5	0	3	15	10	46
4	4		0	6	0	5	8	4	27
5	1	0		1	6	2	6	11	27

3. Coaction :

	3	4	5	o→	♀	Subad.	Juv.	Jun.	N
3		7	0	12	2	6	22	44	93
4	3		1	7	5	9	10	17	52
5	2	0		4	7	6	14	55	88

Note: Detailed interaction matrices have been bound into Appendix B and
lodged in the Department of Psychology. University of Natal, Durban
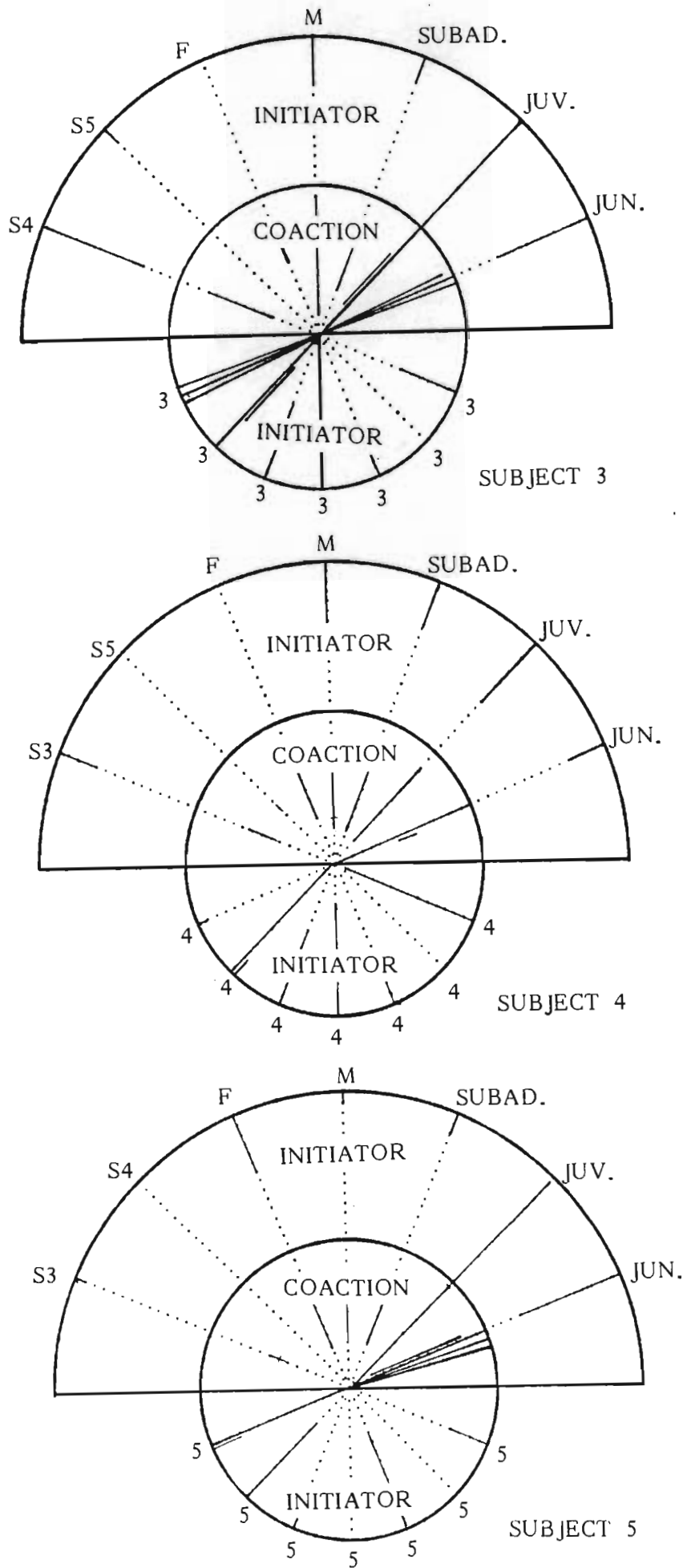
FIGURE   7.2   SOCIOGRAMS DEPICTING AGONISTIC INTERACTIONS OF
TROOP–LIVING SUBJECTS : 2 APRIL 1979 – 4 MAY 1979.

CODING: S3 S4 S5 : Target subjects;   F : An older female;   M : Adult male;
SUBAD. : Subadults;   JUV. : Juveniles;   JUN. : Juniors

TABLE 7.3

AGONISTIC INTERACTION FREQUENTIAL SCORES.

date .... April 2 through May 4, 1979

time sample .... N = 75 x 15 elements

1. Target subject as initiator :

	Receiver 3	4	5	o→	♀	Subad.	Juv.	Jun.	N
Initiator 3		0	3	0	3	0	5	3	14
Initiator 4	0		0	0	1	0	0	0	1
Initiator 5	0	6		0	0	0	3	3	12

2. Target subject as receiver :

	Initiator 3	4	5	o→	♀	Subad.	Juv.	Jun.	N
Receiver 3		0	1	2	0	0	0	0	3
Receiver 4	1		2	1	0	0	2	0	6
Receiver 5	1	2		1	3	4	1	3	15

3. Target subject avoiding conspecific :

	Being Avoided 3	4	5	o→	♀	Subad.	Juv.	Jun.	N
Avoiding 3		0	1	0	1	0	0	0	2
Avoiding 4	7		0	0	2	0	0	0	9
Avoiding 5	9	0		1	0	4	1	2	17

4. Target subject being avoided :

	Avoiding 3	4	5	o→	♀	Subad.	Juv.	Jun.	N
Being Avoided 3		1	4	0	8	2	2	1	18
Being Avoided 4	0		1	0	2	1	3	2	9
Being Avoided 5	0	0		0	1	0	0	1	2

7.5   DISCUSSION.

Cercopithecus aethiops are social animals, and live within a social context.   If these monkeys are separated from their conspecifics, and forced to live alone in single cages, they are deprived of this area of functioning.   Social behaviour was shown, in Chapter Six, to be a part of the behavioural spectrum, to be just as important as individual behaviour, and to occur concurrently with it.   This chapter, which focusses upon the behaviour of the troop-living subjects, highlights once again the unique qualities possessed by each individual, only this time in relation to social behaviour.   It strengthens the call of researchers, for example McKenna (1978), of much individual variation which needs attention.

Consistent with expectations based on the review of the literature (section 7.2.4), a dominance hierarchy was clearly evident in this caged troop in terms of general impressions, and statistical procedures monitoring access to food, sun, shelter and interaction with the adult male.   Subject 3 was the dominant vervet, then subject 4, and subject 5 was ranked lowest on the hierarchy (section 7.4.1).   The complexities of dominance hierarchies are acknowledged, and the problems attending such a conception are noted in the literature review.   The presence of a dominance hierarchy in this experimental troop conflicted with the observations of Basckin and Krige who reported that "no linear dominance was determined" in two free-ranging troops living within the same metropolitan area as the caged troop. They continued: "However, our observations suggest that dominance in vervets may be a multidimensional phenomenon, in that dominance may apply to specific classes of situation ... and to specific times" (1973: 294). The results of this observation tended to support their contention.   If dominance had been estimated on the basis of accompanying the male, who was seen to vary his company throughout the day, conclusions may have differed according to the time of day the observations were made.

Comparisons between cage and field are difficult.   Since the idea of a linear rank constant in all circumstances is a simplification surely not entertained by any experienced researcher, detection of hierarchical rankings within a free-ranging troop in their natural habitat is complicated. For example, resources are usually scattered, not confined to single clumps,

visibility of animals at all times of the day is not usually possible, and individual animals are difficult to identify.   In addition, free-ranging troops have to find resources, there is the possible presence of predators and, generally, the greater unpredictability of events and wider range of tasks which attend a non-protected environment.   A spectrum of abilities not required in the cage are tapped, and so the multidimensionality of dominance becomes extended.   Furthermore, in any situation where a resource is evenly distributed and freely available, no hierarchy need develop.   The advice that dominance is only one of a number of principles useful in the understanding of the complexities of social structure seems pertinent (Hinde, 1981; Lancaster, 1975).   The information gained from the sociograms (Figure 7.1 and Figure 7.2) points to the complexity of social behaviour.   There are many facets to the terms 'friendly' and 'agonistic' and these needed to be explored in an attempt to understand how each subject functioned within the troop's social organisation.

Consistent with the MANOVA results of Chapter Six, the data from the interaction matrices point to significant differences in sociability. Subject 3, the dominant vervet, engaged in more interactions than the other two, and subject 4 engaged in less. However, when the type of interaction was probed, it was found that the difference lay in the exhibition of friendly interactions.   Subject 3's agonistic exchange frequencies were comparable to the other two subjects.   For these subjects, subject 5 was involved in more agonistic interchanges than subject 4.   Subject 4, it seems, was as friendly as subject 5, but less agonistic.

The scenario took on a further dimension when the situation was examined even more closely – perhaps a warning to researchers that no matter how robust a statistical analysis may be, it can reflect nothing more than the specific result for those questions for which it was developed.

Subject 3 initiated, received and combined in more friendly interactions than the other two.   Subject 4 and subject 5 initiated and received social advances approximately equivalently, but subject 5 coacted with the other troop members as frequently as subject 3 – and more than subject 4.

The sociogram of friendly interactions (Figure 7.1) illustrated that the youngest members of the troop were responsible for subject 5's high coaction score. Yet the other females had offspring of comparable ages. Subject 5 frequently huddled a young member of the troop (unfortunately unmarked, so it was not known whether this junior was her own, nor whether it was the same individual every time). A ventero-ventral position was adopted such that an approaching conspecific would be confronted with a view of a young vervet monkey, partially masking subject 5. The author holds that this behavioural pattern employs the infant as a buffer between the subject and her conspecifics, and may be a strategy to counteract harassment and/or aggressive attack. It is believed that a similar phenomenon was manifest during her study of the mechanisms a vervet troop employed during adaptation to an unfamiliar environment: the dome in the territory of an unknown wild troop (Tollman, 1977, 1981). During that study, the troop huddled at first in an invariant conformation (see Figure 7.3). "The adult male was barely visible as he crouched behind, while the female infant units were in the centre of the front line, and therefore the most prominent troop members to any observer. Since different responses would be evolved by the sight of a leader male and the sight of a female infant unit, it is postulated that this troop formation may have been a submissive display to inhibit the attacking behaviour of possible territorial adversaries. This hypothesis could be tested by noting whether the response of a dominant male to strange female-infant pairs, and strange dominant males, is different" (Tollman, 1981: 48).

It is also suggested that huddling has become a multi-purpose strategy. Its function as a thermoregulatory mechanism is discussed in Chapter Eight.

Agonistic responses were seen far less frequently than friendly responses (compare Figures 7.1 and 7.2). Subject 4 initiated less agonism than her two conspecifics, and was also a target for agonism less frequently than subject 5. Subjects 3 and 5 apparently initiated agonistic interchanges with comparable frequency, but subject 3 was an agonistic target less frequently than subject 5. Total participation in avoidance behaviour was equivalent for all three subjects – but, once again, opposite trends for subjects 3 and 5, in that subject 3 avoided other troop members less than subject 5, and was avoided more.

All troop members huddled (see inset below)
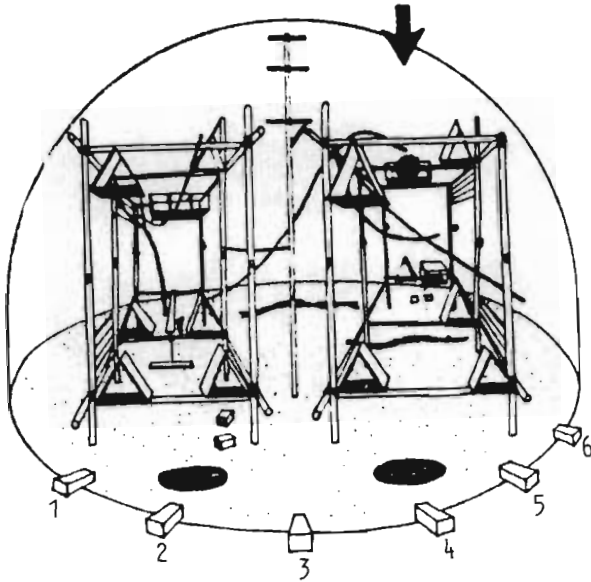
ON CAGING

(Coincident with territorial encounter)
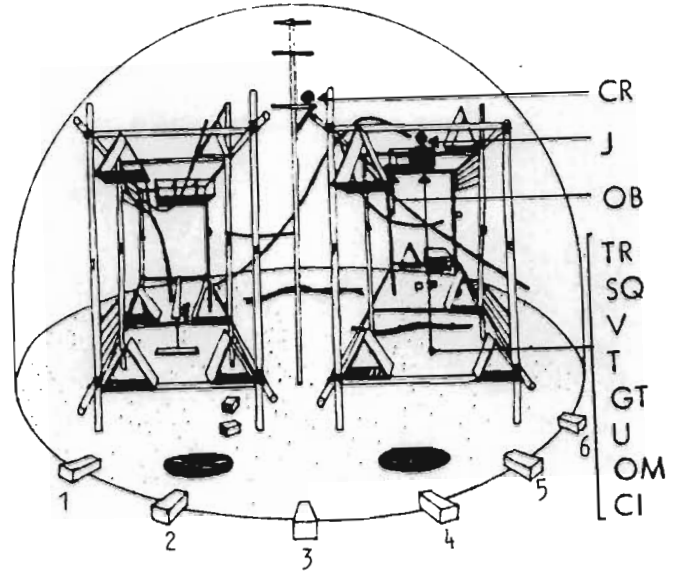
AFTER 2ND DAY
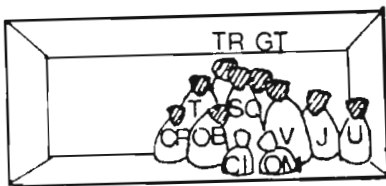
Inset

Day 1
Formation
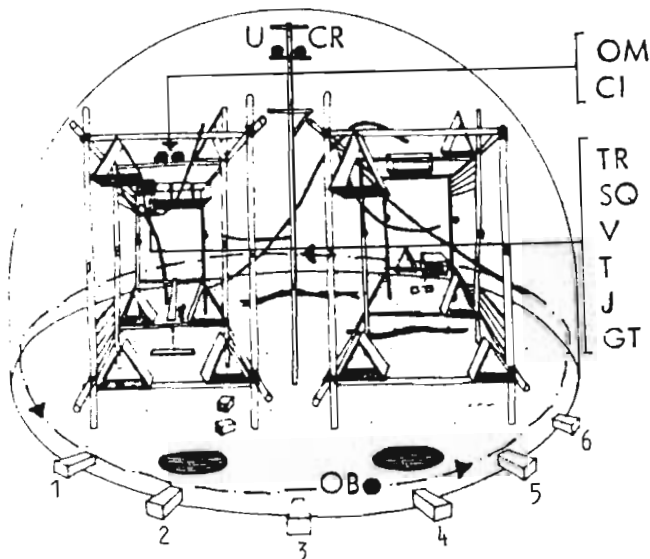
AFTER 4TH DAY
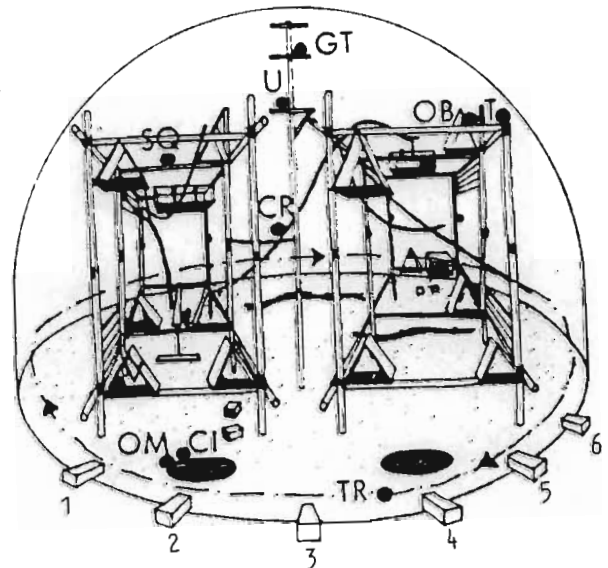
AFTER 11TH DAY

FIGURE 7.3

DIAGRAMMATIC REPRESENTATION OF DAYTIME CHANGES IN TROOP SPATIAL CONFORMATION, DURING ADAPTATION.

Mature vervets: TR adult male; OB, SQ, V, ⊥, J adult females.

These results correspond with observations recorded by other researchers (see literature review). For example, Bolwig (1978) suggested that vervet monkeys, as with other groups studied, "were not equally aggressive and did not distribute their aggression evenly" (p. 78); McKenna (1978) found individual differences in the grooming rates of different female langurs, and Dolhinow (1979) also emphasised individual differences in primate interactions. Horrocks and Hunte worked with *Cercopithecus aethiops sabaeus* (1983), and found the frequency of aggression by adult females against juveniles was correlated with maternal rank.

Nash and Chamove (1981) have been concerned with separating the effects of dominance and the effects of individual differences (personality) upon behaviour. It would seem that this task may only become feasible when studies like the present one have been repeated many times. Shunting the same individual from one group to another in relatively short spaces of time and then to infer that the behaviours elicited are the effects of the dominance status upon that individual may be suspect. Such a procedure may lend itself to a controlled situation which can then be elegantly analysed statistically, but it is possible that the trauma of removing individuals from their natal troop, and then from group to group, would cloud the issue and the results obtained merely reflect the coping strategies of particular individuals, and not the effect of rank.

In summary, the dominant subject engaged in significantly more friendly interactions than her conspecifics. In contrast, she and the subordinate female participated in equivalent amounts of agonistic interchanges, only the subordinate female was the butt of the exchanges significantly more than the dominant animal. In addition, the subordinate female was harassed significantly more than her dominant counterpart, who was avoided significantly more, thus enabling the dominant female to 'do her own thing' while the subordinate female was continually stopped from doing so. Subject 4, of intermediate rank, seemed to avoid agonistic interchanges as she initiated significantly less agonism than her two conspecifics.

The sociogram for agonism revealed how all age-sex categories in the troop threatened subject 5, and she had to retreat into her personal space, while for subject 3 the troop members retreated. The consequences of subordinate animals being the recipients of agonism as revealed by this

study are also in accord with the literature survey. Dunbar and Dunbar
(1977) found dominant females harassed subordinates. Dittus (1980) found
that subordinates were prevented from eating, confirmed by Pool, Hausfater
and McCuskey (1980), who found that high-ranking individuals generally had
longer feeding bout durations than lower-ranking individuals, and were less
likely to have their feeding bouts aggressively interrupted. McBride (1971)
emphasised the importance of aggression for controlling spacing, and
Leyhausen (1971) asserted that space became a 'status symbol' (p. 23)
because the avoidance action of others allowed stronger, more aggressive
animals to develop greater individual distances. It seemed that subject 3
was able to manipulate her personal space – increasing individual distances
when competition for resources was necessary, but decreasing them when
appropriate (e.g. for grooming and huddling).

Despite the disadvantages to subordinates outlined above, the subordinate
female appeared to be an integral part of the troop. She conformed to the
rhythmic activity pattern, and was submerged within the changing spatial
conformations that generally appeared to cut across age-sex categories.
Observations, the spatial distribution charts, and the interaction patterns
pointed to a rhythm in spatial organisation which mirrored the social
organisation. This link would appear to be so strong that Weigel (1980)
hypothesised various models of intergroup spatial structure for macaques and
savannah baboons on the basis of behavioural interactions (see section 7.2.3).
During the midday period (level 3) activity was reduced, social interactions
increased and consequently interpersonal spaces decreased. Similarly, at
night, all the subjects huddled in groups as they slept in the shelters. Thus
the spatial organisation alternated between an increase and a decrease in
interpersonal distances: dispersal in the early morning periods (level 1 and
level 2) with emphasis on solitary activities, followed by clustering around
midday (level 3). Dispersal once again during the afternoon (level 4 and
level 5) followed by clustering as the troop huddled in sleeping groups at
night. The socio-ecological adaptiveness of a 'pulsating' regime for these
diurnal primates is discussed in Chapter Two.

It was noted that the 'dominant' vervets, that is subject 3, the adult
male and the subadults were not generally targets for aggressive displays.
An interesting observation was that subject 5 did display aggression towards
subject 3 and subject 4. Does this suggest a low threshold for aggression?

This phenomenon could be seen to be consistent with the author's finding in an earlier study of intertroop aggression that it was the adult female lowest on the caged hierarchy that consistently threatened an outside troop, even precipitating intertroop territorial displays. The author postulated then that her 'level of aggression' was high, and suggested it was a case of 'redirected aggression' (unpublished M.Sc. Thesis, 1977; the vervet concerned was not a part of this study).

Thus subjects 3, 4 and 5 exhibited very different social behaviour. The author is tempted to hypothesise that subject 3 and subject 4 had different 'personalities', one sociable, the other non-sociable, but it was not this quality which led to their positions on the troop hierarchy: rather, it was the type of social interaction involved, and the response it generated.

7.6   CONCLUDING COMMENT.

This study reveals the complex nature of individual differences in social behaviour.

In an attempt to approximate 'naturally' occurring conditions, the three adult female vervets selected for particular study still lived within their natal troop (which had been captured and caged). In this situation, the social responses were shown to be as important as the non-social responses which together made up the behavioural repertoire. All the subjects were in phase with the troop's rhythmic fluctuations between social and non-social activity, reflected as a pulsating spatial organisation which alternated between clustering and dispersing.

An analysis of the social responses revealed that individual variations were as prominent for social functioning as for behavioural and thermoregulatory functioning. Resources were not evenly distributed, and priority of access occurred on the basis of a dominance hierarchy. In interaction with the troop, the dominant subject was found to interact significantly more with her troop conspecifics than either of the other two females. Further analyses revealed that it was the frequency of friendly and not frequency of agonistic interactions that accounted for this difference.

For agonistic interchanges the reciprocal influences between the subject and her troop conspecifics were significantly different. The dominant animal was threatened significantly less, and avoided significantly more, than the lowest-ranking individual, although there was no difference in the frequency with which these subjects initiated agonistic episodes. The middle-ranking subject, on the other hand, was involved in a smaller number of agonistic exchanges, because she initiated significantly less episodes.

Do these individual differences in social functioning relate to the individual differences in behavioural and thermoregulatory function? This issue will be addressed in Chapter Eight.

PLATE   5.0

THE   SOCIAL   SITUATION.

5.1 Vervets live in a
     social environment.

5.2 'MESSY EATING',
     A SOCIAL ADAPTIVE
     MECHANISM ?
     Infant feeds from food
     dropped by adult.

5.3 A Dominance Hierarchy:
     Individual differences in
     access to resources.

CHAPTER   EIGHT

BEHAVIOUR,   THERMOREGULATION
AND   THE   SOCIAL   GROUP.

8.1   INTRODUCTION.

In the 1983 **Annual Review of Psychology**, Snowdon reported: "It is not
the case that the effect of physiology on behaviour is a unidirectional
influence.   There is now considerable evidence that physiology is affected
by the social behaviour of animals" (p. 81).   A model which holds that for
group-living individuals physiological and behavioural functioning has evolved
within a social context would support the logic of Snowdon's dictum.
Washburn and McCown asserted that "the analysis of any system of animal
behaviour must include an understanding of the biology of the actors in that
system" (1978: 287).   It is suggested that an understanding of the social
system may be equally important.

In this chapter links between thermoregulatory, behavioural and social
functioning are explored.   The literature review points to the dearth of
studies integrating these three facets of functioning, even though a systems
approach is not new to theory (Miller, 1980).   Satinoff's (1982) ideas on
the evolution of thermoregulatory responses are examined, and parallels with
Luria's Theory of the Functional Organisation of the Brain (1980) and
Salzen's (1979) comprehensive interactive approach to individual functioning
have been considered.   This is followed by speculations about the usefulness
of group living.

In primates, internal body temperature is considered to be relatively
invariant, in contrast to the relative variability of behavioural and social
functioning: "... at any given time the body temperature is carefully
defended against any fluctuation" (Kalat, 1984: 237).   Yet subject differences
were exhibited in the extent to which the internal temperature oscillated
around the mean.   Their individual and social behaviour was investigated in
the light of these thermoregulatory differences.   It has been argued that
the difference between the individuals that lived in isolation and those that
lived in a troop lay in the additional range of strategies that the conspecifics
offered for effective thermoregulation, which is vital for survival.

the troop a linear regression model was used to correlate internal temperature changes with behavioural variations and significant parallels were revealed. T_b differences in the troop-living vervet subjects were also examined, and the data has indicated that the individual exhibiting the greatest T_b variation was subjected to more disruptive influences than her two conspecifics, both at an individual and at a social level.

8.2   LITERATURE   REVIEW.

8.2.1   Behaviour, thermoregulation and the social group.

Despite a literature search* for investigations which explore the links between thermoregulation, and individual and social behavioural function, only one paper dealing with thermoregulation and social status was found, and that on a poikilotherm, the green lizard, *Lacerta viridis*.   The paucity of literature may be due, in part, to the considerable time investment required for a biological rhythm to be detected, which has to be coupled with the time-consuming exercise of intensive monitoring of each individual's ongoing behavioural and social functioning, and a consideration of the troop's activities.

Saint-Girons (1977), in a four-year study, found that adult males and dominant female green lizards moved more frequently than submissive females;   dominant females tended to sunbathe for a longer time (to increase internal temperature), climbed bushes less frequently, and produced a greater yearly egg production than subordinate females.   This would suggest that in Darwinian terms dominant female green lizards are fitter than their subordinate counterparts.

8.2.2   The theories of Satinoff, Luria and Salzen.

A brief consideration of the comprehensive approaches of Satinoff, Luria and Salzen seems pertinent.   These psychologists (among others) have emphasised the complexity and multilevel functioning involved in the mechanisms which lead to the overt behavioural responses of each individual

system, and it is to the complexity of this system, of which individual behaviour forms a part, that the author wishes to draw attention.

Satinoff (1982) maintained that most thermoregulatory responses were originally used for other purposes. The following points summarise her argument for the evolution of thermoregulation:-

1. Many changes are needed to evolve from an ectotherm like a lizard into a well-regulating endotherm like a mammal. These include changes in degree and efficiency, e.g. lizards and dogs both pant. Some, like chemical thermogenesis, are unique to mammals.

2. Evolution takes a long time, so each response took millions of years to become efficient for thermoregulatory purposes, and were constrained by other responses evolving for other purposes.

3. These responses did not evolve concurrently, and most if not all were originally used for other purposes.

4. Given the tremendous variety of thermoregulatory mechanisms, that no species has all of them, that many if not all are also used for nonthermal purposes, there is no reason to suppose there should be a single site of thermal integration in the central nervous system.

Satinoff advanced the following four assumptions inherent in her approach, which has striking parallels with Luria's (1980) Theory of the Functional Organisation of the Brain. She presumed that the following propositions would hold both for complex behaviour and for its neural organisation.

1. All complex patterns are built up out of simple components or elements.

2. The components, evolved for use by a particular system, were opportunistically taken over by other systems if the need arose and the conditions allowed.

3. Any component, at any level, can be broken down into smaller subcomponents.

4. Any stimulus that affects a (sub)component of one system will affect that (sub)component in any other system of which it is a part.

Satinoff regards point 4 as 'the most important' (p. 225), and it is suggested, corresponds to the principle of 'double dissociation' which, according to Luria (1980) is integral for the reliable detection of brain damage. He, too, looks at the multilevel functioning of the nervous system

so that any local pathological focus arising in the cerebral cortex disturbs the successful performance of those psychological processes sharing a common factor, while others are left intact. Satinoff has applied her model of neural organisation to sexual behaviour, and demonstrated similarities between thermal and sexual behavioural patterns. The identification of variables that will affect subcomponents of behaviour at many levels of organisation is integral to this model. For example, removal of the olfactory bulbs in mice results in deficits of social interactions; these mice do not mate, fight, or care for their young (Rowe and Edwards, 1971, in Satinoff, 1978). Huddling is a social behaviour, and it is also used in temperature regulation. Since the social interactions of bulbectomised mice are drastically affected, predictably these mice will not huddle in the cold, even though the solitary forms of thermoregulation such as heat seeking and overeating are not affected by the operation (Satinoff, 1982). Thus, a multilevel approach is indicated if the underlying mechanisms of behaviour are to be elucidated.

Salzen (1979) also addressed himself to the complicated interactions between physiological, psychological and social functioning. He pointed to the importance of the social environment in the life of the individual. "Early social experience ensures that the species partner becomes the source of maximum security, allowing social interactions for physiological homeostatic needs and for later reproductive functions. Thus it might well be true to say that social attachment gives a sense of security - for life" (p. 622). Salzen identified three 'distinct functional and evolutionary' vertebrate behavioural systems: Physiological homeostasis, sensory homeostasis and reproductive mechanisms. For each of these he also described associated emotions in man. He proposed that thermoregulation, respiration, and skin-care, together with ingestive, eliminative and perhaps part of care-soliciting behaviour are mechanisms concerned with maintaining the physiological homeostasis of the individual. He believed that reproductive behaviours depend on hormonal states and are concerned with maintaining the species, while sensory homeostatic behaviour is the basic security motivation system. The latter behaviours are shelter-seeking; care-soliciting in part; allelomimetic or protective; and investigative; and all depend on changes in the environment for their occurrence. They "serve to maintain the individual in its safe environment by restoring the familiar environment, since any change is potentially to the organism's detriment if

the familiar existing environment is supporting normal bodily functions" (p. 598). The sensory homeostatic system takes precedence over the others which will only operate if the security system is in a set ready state. The associated emotional classes for the physiological homeostatic system, the system of focus for this thesis, are Comfort-Discomfort, Hedonism-Asceticism, Appetites-Aversions. Salzen proposed that emotion and emotional behaviour are social signals reflecting thwarting and conflict, and that pleasant emotions signal the cessation of thwarting. He presented a scheme (based on a classification by Morris, 1956) which analysed the primary somatic and autonomic responses to thwarting and conflict, as well as secondary behavioural responses. Morris believes that any of the responses could be developed as signals through evolutionary selective processes if they influence the social partner to assist in removing the thwarting stimulus.

Autonomic thermoregulatory responses such as sweating and pilomotor activity are categorised as being primary responses. Satinoff (1982) also regarded sweating as an emotional response, and one over which thermal sensations have no control. Humans sweat on their palms and the soles of their feet when they are emotionally stressed, and when they are exercising, but not in response to heat. She explained the evolution of the sweating response by citing studies of Adelman, Taylor and Hegliend (1975) which suggested a major function of footpad sweating in animals is to prevent slippage between the foot and the substrate when running or climbing. They speculated that sweating may occur in response to stress in order to prepare an animal to flee from the situation. Hinde challenged Salzen about the usefulness of his comprehensive theory, claiming that: "In general, in behaviour studies, the generality of a statement is likely to be inversely related to its precision" (1979: 642). In reply, Salzen argued that the value of an ethologically based theory such as the one he has proposed is that such "synthesising theories of foundational systems and mechanisms are a necessary guide for the meaningful data collection and analysis of the detailed microstructures of interactions and of more limited problems" (p. 649). Satinoff (1982), in evaluating her own approach, maintained that the value of any approach ultimately lies in its ability to generate new, unexpected findings. Their models would seem to satisfy these criteria, and provide a holistic and comprehensive framework for generating hypotheses, and interpresting research results.

8.2.3 Functions of the group.

> Why does an individual put up with the time-consuming, frustrating and
> often harmful ado of group life rather than live in unhindered, but
> perhaps dangerous and uninformed solitude?
>
> Kummer, 1979: 381.

The vervet monkey, like all other animals, must eat and drink, maintain homeostasis, avoid predators, find shelter, and use safe breeding places in order to survive and reproduce. Although for many animals these are matters for the solitary individual to solve, for the higher primates these major problems of existence are solved in a social context.

Kummer (1971b) has pointed out that primates do not exchange resources but exchange information about them. He wrote that mutual assistance is negligible in primates, in that each group member has to feed, drink, flee and climb for himself. Nevertheless, before primates can react to resources and dangers these must be located, and this can be done more efficiently in groups. Rowell (1979) agreed that "a case can be made for the primate group as an educational institution in which learned information about feeding in an exceedingly complex environment can be shared to general advantage" (p. 6).

Struhsaker (1967c) maintained that protection from predators is a primary feature of vervet social groups. Increased efficiency in detection of predators, a better chance of surviving an attack, and the distracting or confusing effect caused by the flight of several vervets as opposed to one or a few, are all advantages of group living. Rowell (1979) agreed: "Protection from predation seems to me the most probable advantage of group living, although very little is known about predation in primates" (p. 6). Human predation needs to be given more consideration. Additional adaptive features of the social group outlined by Struhsaker were maintenance of physical well-being by the removal of ectoparasites through social grooming, the development of social behaviour in the infant, and the perpetration of learned patterns of behaviour. Rowell (1972) added conditioning of the medium, breeding synchrony and genetic variability as advantages of group living. 'Conditioning of the medium' involves behaviour such as freeing regular pathways through the trees from dead

branches, as well as Gartlan and Brain's observations of the reforestation of Lolui Island by seed dropping through vervet feeding and defaecation. The author (Tollman and Simpson, 1975) has demonstrated that the apparently 'messy' feeding pattern of *Cercopithecus aethiops* facilitates and may ensure the distribution of food among all troop members.

Breeding synchrony refers to a postulate by Rowell (1972) that the sight, sound or smell of conspecific breeding activity may elicit mating behaviour thereby increasing the number of offspring, as well as ensuring that the young are born when food is most plentiful. Rowell speculated that exclusive breeding in small groups probably increases the genetic variability of the species so that it is more likely to be able to meet environmental changes with an appropriate pre-adaptation. She admitted that recent long-term studies have shown more movement of individuals between troops than expected – and this has now been confirmed (e.g. Wrangham, 1980; Henzi, 1982). Thus the intertroop movements of subadult and young adult vervet males helps provide genetic variability.

In line with the present mood of enquiry, Kummer (1979) contended that discussions of the adaptive values of primate social systems are too often restricted to the level of entire groups, and so he presented a "tentative conceptual scheme" for finding an answer to the question: "what does a primate gain from establishing social relationships?" (p. 394). Kummer examined interactions classified into two functional categories: beneficent and disruptive (maleficent), by Clutton-Brock and Harvey (1976), because they are seen as a means of building or preventing a particular aspect of a relationship, and a relationship is seen as an investment which in some way, sooner or later, benefits the interactor. Kummer's discussions are limited to two individuals, and he focussed on the acts of only one animal, regarding the second as a social resource. Although triadic relationships have been demonstrated, Kummer maintained that their analysis depends on a clear understanding of the component dyads. Kummer proposed that a companion can influence production (altering the inventory or quality of A's environment); information; motion (leading A to or away from a resource/predator); motivation (e.g. caution, arouse or reduce tendency to explore); and nutrition (metabolic intervention through chewing and digesting food, nursing him, killing him, etc.). This model

provided a framework which could include the maintenance of physiological homeostasis. The benefits to the individual for mating successfully, the mother-infant bond, the father, and kinship ties are further issues considered by Kummer.

The paradoxical nature of altruistic behaviour led Trivers (1971) to put forward the theory of reciprocal altruism, hypothesising ultimate advantage to the individual. Kinship theory, as supported by sociobiologist Wilson (1975), implies not only immediate but also ultimate advantages to the individual. Clutton-Brock and Harvey (1976), in citing six different situations where kin selection helps to explain a variety of cooperative relationships, pointed to an analytic hurdle: social relationships and degree of kinship need not indicate kin selection have been involved. For example, proximity and grooming have been found to be more pronounced between relatives than between unrelated animals. Chamove (1979) agreed: "most social animals prefer that species or specific animal with which it was reared" (p. 265). The mechanisms that promote and enhance social living need further clarification.

Maynard Smith (1982) suggested that two main concepts have dominated the study of the evolution of social behaviour 'during the past fifteen years'. The first "arising primarily from the work of John Crook is that social systems should be seen as ecological adaptations" (p. 1). The second, stemming mainly from W.D. Hamilton, is that the evolution of behaviour is influenced by the fact that the genes of relatives may be identical. Maynard Smith added a third, mutualism, already pointed to by Kummer – two animals may cooperate because it pays both of them to do so. Thus he concluded that "the immediate future of sociobiology will be concerned with the joint effects of mutualism and of kin selection on the evolution of societies subject to particular ecological constraints" (1982: 2).

Kummer (1979, following Hausfater, 1975) has aptly stated that: "The more complex a social structure, the more a monkey needs adaptive strategies for his career within that structure" (p. 383).

8.3 PROCEDURE.

The procedures employed to investigate thermoregulation, behavioural and social functioning have been described in Chapters Five, Six and Seven respectively.

8.4 RESULTS.

The data for body temperature, behaviour and social functioning have been analysed in Chapters Five, Six and Seven respectively and will be considered in relation to one another in the discussion which follows.

The correlation between internal temperature on the statistically derived behavioural factors were also explored through a Multiple Regression Analysis and are described in Table 8.1

8.5 DISCUSSION.

Homeostasis is defined by Kalat (1984) as a "tendency to maintain some variable, such as temperature, within a fixed range" (p. 501). He stressed Satinoff's leading role in calling increased attention to the role of behavioural mechanisms for temperature regulation. She has demonstrated that behavioural responses are not only more effective than autonomic responses, but may be crucial for maintaining a constant body temperature (see literature review, Chapter Five). It would seem pertinent, therefore, to focus upon thermoregulation and its dynamic interrelationship with behaviour in an attempt to begin to understand reciprocal influences that physiological, behavioural and social functioning may have upon one another.

Despite the apparent importance of a stable body temperature, a detailed, in-depth, quasi-longitudinal study of the body temperature of five vervet monkeys revealed individual differences in the standard deviations from the mean. Furthermore, the statistical analyses indicated that the subjects belonged to two different populations. When the social conditions of these two populations was examined, it was found that the individuals in one population were part of a troop, and in the other population the

TABLE 8.1

MULTIPLE REGRESSION OF TEMPERATURE ON THE

DERIVED BEHAVIOURAL FACTORS 1 AND 2.

DURATIONAL DATA

Overall F test

Multiple R = .213 R² = .045 Standard error = .229	Analysis of variance	DF	Sum of Squares	Mean Square
	Regression	2	.556	.278
	Residual	222	11.689	.053
F = 5.739	P <.017			

Variables in the Equation

Variable	β	t	
DUR 1	–.160	–2.441	P <.015
DUR 2	–.143	–2.174	P <.031

FREQUENTIAL DATA

Overall F test

Multiple R = .225 R² = .051 Standard error = .229	Analysis of variance	DF	Sum of Squares	Mean Square
	Regression	2	.62	.310
	Residual	222	11.624	.052
F = 5.928	P <.003			

Variables in the Equation

Variable	β	t	
Freq 1	–.187	–2.861	P <.005
Freq 2	–.124	–1.892	P <.06

NOTE:

1.   The multiple regressions are significant.   It is interesting that both the durational and the frequential data give a consistent picture, i.e. that factor 1 (Solitary-Interactive) and factor 2 (Coactive) significantly predict temperature changes.

2.   The weights for factors 1 and 2 differ slightly in importance – with 1 being more important than 2.

3.   The β weights are negative for both factors indicating a reciprocal relationship – as factors 1 and 2 scores increase, signal frequency decreases i.e. temperature increases as the scores for behavioural factor 1 and/or behavioural factor 2 increase.

4.   The multiple R^S are both significant but very small 0.22, indicating that a large proportion of temperature variance is still unexplained on the assumption of a linear regression function.   A complication arose from the fact that between subject differences were eliminated using deviation scores on the temperature variable.   This would have had the effect of reducing individual differences in temperature and possibly reducing correlations between temperature and the predictor variables, resulting in a reduced multiple

individuals were living in isolation (see Chapter Five). The oscillation of temperature around the mean was less for the individuals living in the troop than for the subjects living alone. At the behavioural level, the analyses disclosed that social behaviour occurs together with individual behaviour, and is equally important. Thus an integral and prominent aspect of functioning was removed from the subjects that were individually caged. It is argued that conspecifics are a resource for thermoregulation. This resource was denied to the subjects living alone, and so they exhibited larger deviations from the T_b means. Such an idea appears compatible with the three concepts that Maynard Smith has put forward as dominating "the study of the evolution of behaviour during the past fifteen years" (1982: 1). It is consistent with Maynard Smith's (and Kummer's) contention of 'mutualism', each individual being a resource for the other, it does not contradict kinship theories which look to the preferences and likelihood of interacting, and also supports Crook's conception of the importance of sociability and the evolution of social systems as ecological adaptations. This hypothesis, it is believed, extends the present answers to Kummer's challenging question: "why does an individual put up with the time-consuming, frustrating and often harmful ado of group life rather than live in unhindered, but perhaps dangerous and uninformed solitude?" (1979: 381).

Two social behaviours, huddling and grooming, have been examined as thermoregulatory mechanisms which are employed to counteract thermal disruption triggered by psychological or physical stimuli. These behaviours were considered in relation to the two behavioural factors which bear a significant relationship to an increase in body temperature. Factor 1 consisted of a group of individual behaviour patterns, and factor 2 of a cluster of symmetrical social behaviours (see Figure 6.1). The detection of two factors, one social and one non-social, which will elicit the same physiological responses, supports the contention that a social group provides additional strategies for thermoregulation.

The multifunctionality of huddling and grooming responses is acknowledged. Indeed, Satinoff (1982) has pointed out that most thermoregulatory responses were originally used for other purposes, while Schwartz and Rosenblum point to secretions, for example the nasolacrimal secretion of rodents, that function in thermoregulation and in communication (1984 pers. comm. - in press).

Satinoff believed that "in nature, the major method of thermoregulatory behaviour in social animals is huddling" (1980: 193). McGuire, Raleigh and Johnson have worked with *C. aethiops sabaeus* and they found that "frequency of huddling varies as a function of temperature" (1983: 103). Throughout this project the vervets huddled at night and when it was cold and raining, supporting the postulate that huddling is a social strategy for maintaining thermal equilibrium. Decreases in the ambient temperature were accompanied by increases in huddling, and all the monkeys huddled at night. It seems that huddling is a social mechanism which generates warmth and counteracts a $T_a - T_b$* temperature gradient imbalance when the atmospheric temperature T_a drops at night. Such a behavioural strategy is important because the customary heat generating responses of movement cannot be used during the immobile sleeping state.

Psychological events may also disturb the $T_a - T_b$ gradient. There seems to be extensive evidence demonstrating that stress and apprehension will cause an increase in internal temperature (e.g. see literature review, section 5.2.1), and these findings have been confirmed for the Cercopithecidae (Bush, Custer, Smeller and Bush, 1977). The increase in temperature is usually transient. Keele and Neil (1971) described an initial shivering response to an increase in internal temperature, leading to a 'cold' sensation, and this may, it is suggested, motivate a huddling response to counteract excessive heat loss.

When the experimental troop for this study was first captured and caged, the caged situation was unfamiliar and the environmental conditions unpredictable. Further, the caged monkeys were subjected to vigorous territorial displays by the local troop whose territory had been invaded (Tollman, 1981). At this time, a behavioural change in the form of a significant increase in huddling took place which was independent of atmospheric temperature (see Graph 8.1). It seems reasonable to suggest that the caged monkeys were in a state of apprehension and fear, their internal temperatures had risen, and so they huddled to compensate for a $T_a - T_b$ gradient disturbance (see literature review, sections 5.2.1 and 5.2.3). Social huddling is a strategy, therefore, that would have multiple

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* T_a = atmospheric temperature

T_b = body temperature

survival advantages ranging from the provision of greater protection against predators to an increased level of vigilance due to the presence of many eyes, as well as a thermoregulatory device. It is argued that physiological and behavioural factors are interconnected, and since they take place within a social context, the same social mechanism has evolved to regulate these two diverse, yet interrelated functions.

If the major method of thermoregulatory behaviour for vervets is huddling, as is asserted by Satinoff, then this social mechanism is denied to vervets that live alone in separate cages. It is not surprising therefore that the internal temperature oscillation around the mean is greater for vervets living alone than in a troop.

Grooming behaviour is a prominent aspect of social behaviour, and several different functions have been attributed to this behaviour pattern (see literature review, section 7.2.8). It is suggested that thermoregulation may have to be added to the list.

A multiple regression analysis has displayed a significant correspondence between an increase in temperature and an increase in the behavioural responses clustered together in Derived Factor 1, Solitary-Interactive (see Results, Table 8.1). This result can be readily explained when we examine the behavioural elements which clustered within this bipolar factor (see Figure 7.1). The durational data led to the following behavioural grouping for factor 1:

+ve : sitting, travelling perimeter, standing, walking, running, climbing, vigilant, eating.

-ve : coalition, groomed, grooming.

The frequential data resulted in the following behavioural cluster in factor 1:

+ve : walking, sitting, standing, eating, investigating, avoided, climbing, vigilant, jumping, running.

-ve : groomed, coalition, grooming.

Travelling perimeter (or boundary pacing), walking, climbing, jumping and running are behaviours concerned with physical exertion, and are known to lead to a temperature increase. Added to this group of activities is

eating, which has also been shown to lead to a temperature increase, so would augment the overall temperature increase for this factor. Standing and sitting behaviour, investigating, vigilance and being avoided generally accompanied the other behaviours in this factor, but when they did they were of short duration. This may explain why sitting behaviour was also clustered in factor 3, Durational, and in factor 4, Frequential, where the emphasis was on individual sedentary behaviours. Presumably sitting in this context would have been of much longer duration.

It is also of interest that concentration on this factor was in the morning, when the endogenous T_b rhythm had been shown to increase.

Factor 1 was a bipolar factor - so the social behaviours coalition, grooming and groomed were in opposition to the individual behaviours, grooming having a particularly heavy negative weighting with the durational data (see Figure 6.1). It is argued that if an increase in the non-social individual behaviours was accompanied by an increase in temperature then these social behaviours would have accompanied a decrease in temperature, and this may throw some light on the function of grooming. "Hypotheses concerning the survival function can be divided into two groups: 'clean and eat hypotheses' and 'social bonding and tension reduction ones' ... both types of hypotheses are incomplete ... Hypotheses of the second group are incomplete because they are too broad; the concepts of social bond or low tension are defined such that they cannot explain why grooming varies with the type of situation in which animals meet" (Goosen, 1981: 110). In discussing the Social Bonding and Tension Reduction Hypotheses, Goosen asserted: "The above hypotheses, however, are not readily testable" (p. 111). 'Stress' has been shown to cause an increase in temperature - if social grooming accompanies a decrease in temperature, is this not evidence that social grooming is a mechanism for reducing tension?

Derived factor 2 and body temperature also increased together. This was a social factor, 'coaction', comprising, in order of importance, climbing SF,* vigilant SF, walking SF, huddling, sitting SF, for the durational data, and climbing SF, walking SF, vigilant SF, huddling, sitting SF, coalition for the frequential data (please refer to Figure 6.1). It is suggested that a social mechanism is being used here to prevent heat loss. The 'active'

behaviours in factor 1 are coupled with eating, the 'active' behaviours in derived factor 2 with huddling, both heat-generating strategies, one non-social, the other social. It has been pointed out (see analysis of factors) that certain activies, for example, walking, sitting, climbing, can be done alone or together with other animals, implying that vervets may have a choice between performing heat-generating behaviours which have grouped into factor 1, or into factor 2. It seems, therefore, that a strategy for increasing internal temperature is necessary for optimal functioning and the vervets have a choice as to which one they use. It is proposed that social living has enabled additional thermoregulatory strategies to evolve. This would be adaptive, because not only do the vervets now have a choice, but if there are more strategies available for maintaining thermal homeostasis, the vervet is more likely to function efficiently and, in times of danger, to survive.

The troop-living subjects, with social bonds intact, also exhibited individual variations in the extent to which their internal temperature fluctuated. This despite the fact that the body temperature in this population remained significantly steadier than in the population of segregated subjects (Chapter Five). Shifting from their internal temperature to the social situation, the presence of a dominance hierarchy was evident (Chapter Seven). When temperature functioning and social status were synthesised, it was found that the dominant vervet, S3, displayed the least internal temperature variation, and the least dominant vervet exhibited the largest fluctuation in body temperature. The body temperature oscillation of vervet 4, the subject of middle status, was intermediate between the other two subjects. Thus, as status increased, so temperature variation decreased.

These results are consistent with the only study discovered which relates these two variables. Saint Girons (1977) found that dominant female green lizards showed more efficient thermoregulatory behaviour than submissive female green lizards. The environmental advantages that accrued to the dominant female in this study would appear to be comparable to those attending the dominant female green lizards. Subject 3, too, had most protection from the vagaries of the weather, including the atmospheric temperature changes. She gained first access to sunny spots when the

weather was cold, to the shady areas when it was hot, and to the enclosed shelter when it was stormy, windy, and at night. When these resources were in short supply (e.g. in the very early morning only one sunny spot was available) they were not available to the subordinate subject. The subordinate subject was, therefore, less able to compensate for changes in T_a - T_b gradient, which, it is suggested, may have led to greater fluctuations in her internal temperature.

The hypothesis that dominance and fitness are related has been discussed in the literature review (Chapter Seven). Likewise Wrangham's (1980) declaration that he was the first to show, in vervet monkeys, a relationship between the probability of death and dominance rank. Wrangham pointed out that the higher-ranking females in his study in Kenya had greater access to preferred resources, higher reproductive rates, and lower death rates (section 7.2.2). The literature review also described Dittus' (1977, 1980) demonstration that a social mechanism can regulate population density. Behaviourally-mediated access to resources, he wrote, as is achieved through the establishment of a dominance hierarchy, would lead to earlier death of a subordinate, so influencing mortality rates. Further pertinent issues in the literature review (section 7.2.2) included Dunbar and Dunbar's (1977) observation that harassment and stress of subordinates can lead to ovulation suppression, and Sade's discovery that higher-ranking genealogies had considerably higher 'r' (intrinsic rate of increase). Interference with thermoregulatory strategies would inhibit the maintenance of a steady body temperature. Van Holst's (1972) evidence of the far-reaching effects on the physical fitness of different individuals was aptly illustrated by his demonstration that if *Tupaia belangeri* are exposed to persistent social stress, physiological changes occur indicating persistent activation of the nervous system, and eventually renal failure leading to death may occur. Evidence for the physiological consequences of aggression (e.g. Barash, 1977, and Bernstein, 1979), and differences in hormonal levels between dominant and subordinate monkeys are also cited in the literature review (e.g. Bowman, Dilley and Keverne, 1978; Eberhardt and Keverne, 1979; Chamove and Bowman, 1976, 1978; McGuire, Raleigh and Johnson, 1983). Following this line of reasoning, animals of different social status experience different physical and social stimuli, which differentially influence their physiological status, including the thermoregulatory responses. So it has been found in this research project. It is submitted

that since the body requires a constant body temperature for optimal functioning, the less the temperature deviates from the mean the more efficient are the thermoregulatory strategies. In this project, the internal temperature of the dominant female was the most constant, oscillating least around the mean, and the most subordinate female's body temperature deviated the most. This made sense when the dominant female's individual and social functioning was examined. She had exclusive access or priority of access to all resources, social and non-social, so could execute immediate and appropriate responses to maintain homeostasis. She was also subjected to less harassment than her female counterparts, and participated in more tension-reduction behaviour.

The behaviour of the troop-living vervets was consistent with the literature. As illustrated in Figure 7.2 and Table 7.2, subject 5, the subordinate vervet, was the receiver of significantly more aggressive attacks than her dominant conspecific. Since aggression has been shown to elevate body temperature, each of these attacks may have precipitated a transient deviation of the body temperature.

The following comparison of the eating behaviour of the three socially-living subjects further illustrates the consequences of harassment, even though a univariate ANOVA revealed no significant difference. An examination of the data, however, provided an insight into the reasons for interobserver agreement on rank, when feeding behaviour was one of the parameters used for assessing the female hierarchy. Subject 3, the dominant subject, was consistently seen to be eating first, often together with the dominant male. Subject 4 would eat after subject 3's feeding seemed well established, but subject 5, the most subordinate subject, would only start eating after most of the other troop members were eating or finished, and she rarely approached the food source – she relied almost exclusively on food discarded by the other animals. The ANOVA did not provide for this order effect. In addition, a comparison of durational and frequential means indicated that S5 had the lowest durational score, yet the highest frequency score (see Table 6.11). For the other two animals, S4 had a higher durational and similar frequency score to S3. This meant that S5 was seen to eat much more frequently than her conspecifics, and for far shorter periods coinciding with observations that she was frequently threatened during eating, causing her to drop her food, and retreat. A similar observation has been recorded by

Post, Hausfater and McCuskey (1980 – see section 7.2.4). It is suggested that this erratic feeding behaviour may have generated internal temperature fluctuations, since eating is known to lead to a short-term elevation in body temperature. Thus it appeared that vervet 3 ate until she was satisfied. Subject 4, on the other hand, had to rely more on leftovers and discarded food. These were smaller portions so she had to move and find food more frequently. Subject 5, however, was forced to eat according to the most irregular schedule.

The differences in body temperature fluctuations are clarified further by studying the sociograms (Figures 7.1 and 7.2). The troop members directed significantly less aggression toward the dominant subject (S3) than the subordinate subject (S5), and there was a direct relationship between status and avoidance. The higher the status, the more she was avoided. Nevertheless S3, the dominant subject, participated in significantly more friendly interactions (predominantly grooming) than the other subjects. A role for grooming in reducing temperature elevations has been discussed and is strengthened by the observation of researchers. For example, McKenna (1978) and de Waal and Yoshihara (1983) reported an increase of grooming behaviour after aggressive episodes. The author (Tollman, 1981) found a significant increase in grooming following agonistic encounters in the vervet troop under study (see Graph 8.2). De Waal and Yoshihara have put forward a suggestion that post-conflict contacts serve to maintain social bonds. They suggest a "dominance-subordinance model which includes **attraction** between individuals as a central factor" (p. 239), and the author is tempted to suggest a corollary: and for the purpose of restoring physiological and psychological homeostasis. It would appear to be in the interests, particularly of the dominant individual, to maintain the 'status quo', and in the interests of all 'disturbed' troop members to re-establish their equilibrium. Seyfarth (1976) has found evidence for a physiological involvement in grooming activity – that is, that females are most attractive to others during lactation.

There were significant subject differences for both the durational and the frequential grooming data. Subject 3 was, overall, the most social of the subjects, and she groomed the most. Subject 4 was the opposite – non-social and groomed least, while subject 5 was intermediate between the two. An examination of the differences in grooming activity over the day

GROUP MECHANISMS ELICITED WHEN COPING WITH AN UNFAMILIAR SITUATION

ACTIVITIES CONCERNED WITH PHYSICAL CONTACT
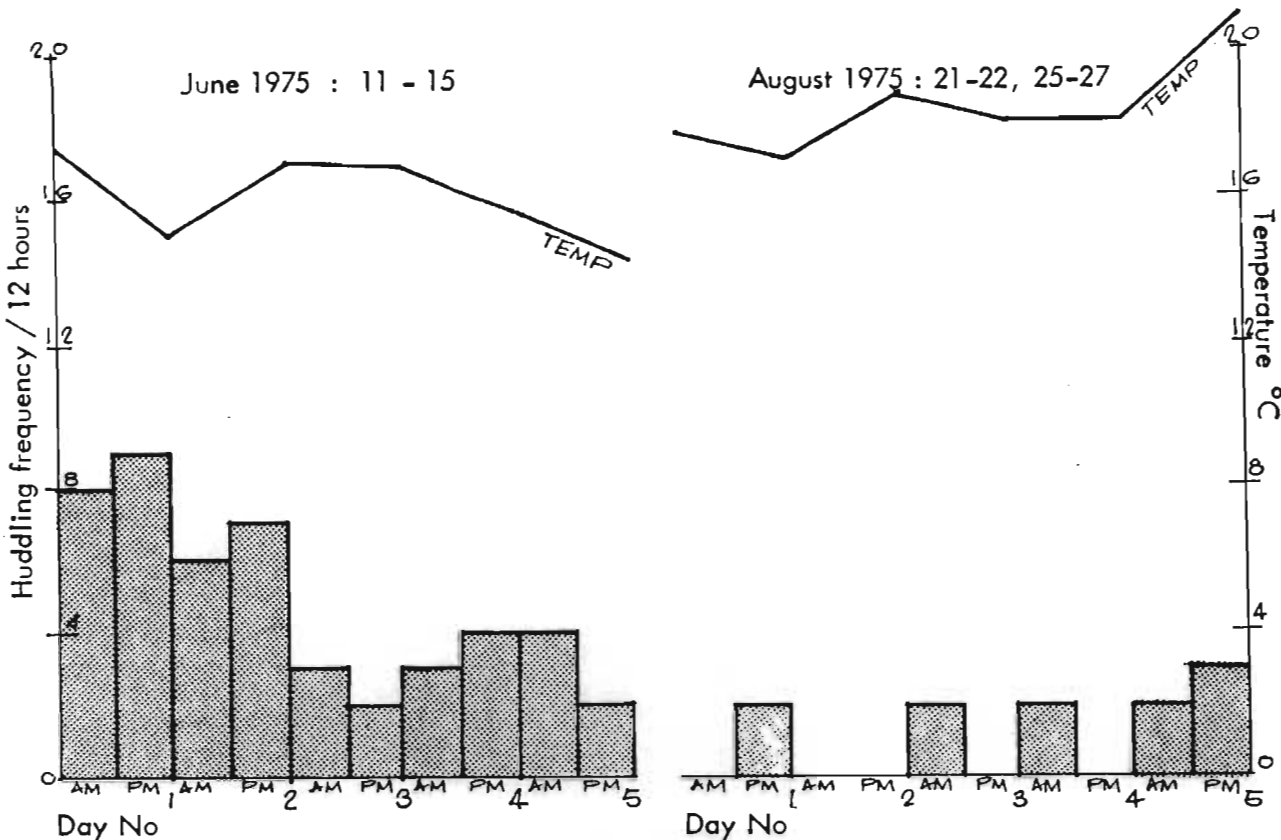
Note: (i) Significant difference in huddling : p <.002 (sign test).
(ii) No apparent relationship between huddling and atmospheric temperature.

GRAPH 8.1

VERVET HUDDLING BEHAVIOUR UPON CAGING AND AFTER
ADAPTATION TO CAGE   (after Tollman, 1981: 46).

Date : June 1975

KEY ——————— Mean No. of grooming individuals / time sampling
round (11 x 5 minutes)
– – – – – – Total No. of territorial fights / day.

Rs : 0.95   Significant correlation : p <,01
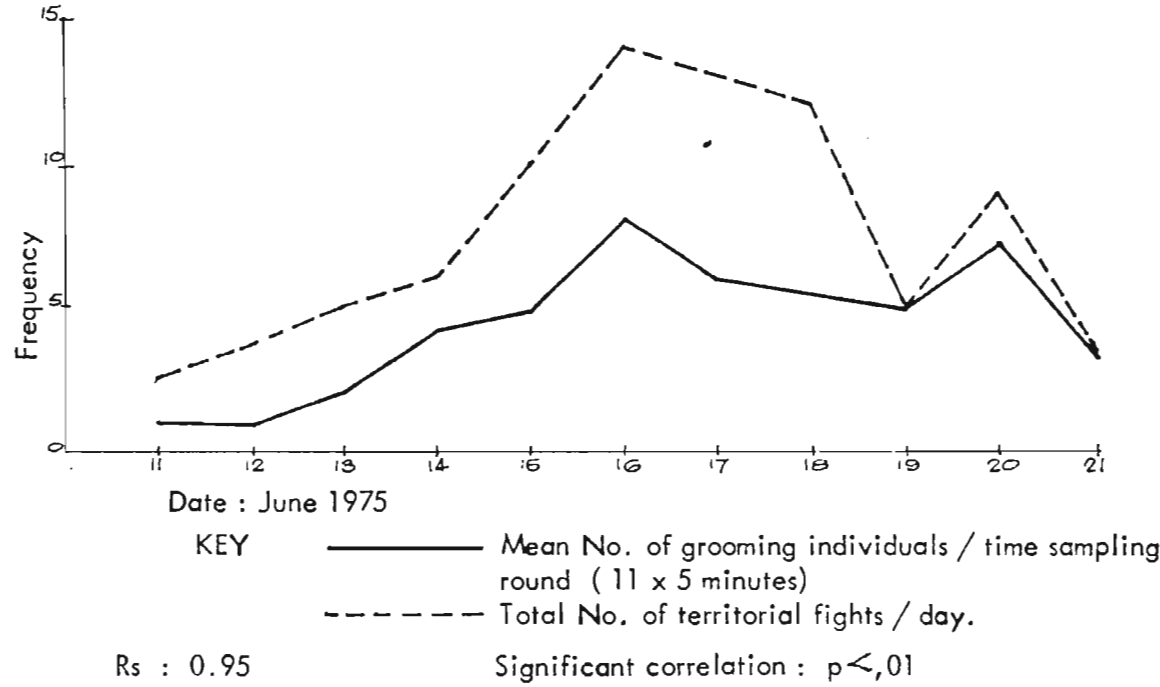
GRAPH 8.2

SIGNIFICANT CORRELATION BETWEEN GROOMING

led to some interesting observations. Subject 3 maintained a high level of grooming both in terms of duration and frequency throughout the day. Toward evening, her frequential grooming increased sharply suggesting more frequent but shorter grooming episodes. It was subject 4 who seemed to display a trend different to the other two. Despite her low level of durational and frequential means, her grooming activity increased so steeply at night that frequentially the level was the same as subject 5, while durationally it was the highest. Was this an adaptive behavioural mechanism which operated to maintain physiological homeostasis, despite a non-social 'type' of personality? She may have needed her conspecifics at night for huddling, to counteract the drop in atmospheric temperature. This relatively 'non-social' subject also displayed a durational peak in grooming at level 3 (over midday), a rest period – when 'active' thermoregulatory behaviour of movement was at a minimum.

Body temperature in subject 4, in parallel with dominance status, was intermediate between subjects 3 and 5. It is suggested that even though she did not interact as frequently as S3, her temperature was more stable than S5 because she initiated significantly less agonistic interactions than subject 3 or subject 5, and was socially active at appropriate times. Thus we encounter individual differences in all facets of functioning and, if the range of available strategies for effective activity are to be explored, studies, it would seem, must focus upon individual modes of operating. As Rowell pointed out: "A population cannot be uniform if natural selection is to act. There is a range of forms which are viable at a given time" (1979: 3).

Van Schaik (1983) focussed upon a longstanding question: "Why are diurnal primates living in groups?" (p. 120). He maintained that three different answers have been suggested for the evolution of group living: predation pressure; feeding advantages; "most authors, however, whilst accepting that predation pressure is an important factor, presume various advantages to feeding in a group". He tested the first and second views which, he believed, are mutually exclusive. He concluded that his results "provide strong support for the predation-feeding competition theory and are clearly unfavourable for the theory postulating feeding advantages to group living. Such feeding advantages may, however, gain prominence under some

conditions" (1983: 141). Some acknowledgement of the idiosyncratic nature of each social structure operating within an everchanging econiche.

Vervet monkeys are social animals, and successfully inhabit diverse environments (see Chapter Two). Their adaptiveness has been attributed to their flexibility which, it would seem, must encompass a wide range of available responses in order to deal with the demands of varying circumstances. Irrespective of which of the three alternatives triggered group-living as a viable strategy for survival, this way of life has been sustained and so, it is believed, physiological and behavioural functioning has evolved with a social context, and become interdependent. It is theorised that the addition of group mechanisms to the behavioural repertoire enhances physiological functioning by extending the range of available strategies to maintain homeostasis. Furthermore, these mechanisms are available to all troop members, dominant or subordinate.

In her research, the author has presented evidence to support the idea of group living as promoting feeding and protection from predators, and other external pressures as well (see Chapter Three, and Tollman, 1975, 1981). In the latter case, a free-ranging troop of vervets was caged in the open, in the range of an unknown wild troop. The investigation indicated that "the success of the vervet may, in part, be due to the versatility of the troop's social organisation, where the social structure varies with environmental characteristics". It is suggested that group living provides increased support not only against predators, but against environmental hazards, physical and psychological: "... the troop became consolidated as a single, united entity, to deal with an unpredictable situation" (Tollman, 1981: 51).

This research thesis has drawn attention to an interplay between thermoregulatory, behavioural and social functioning. Individual differences in thermoregulation could be explained by differences in the behavioural and social data, and the results appear to point to a direct relationship between the efficiency of thermoregulation and the favourableness of the social condition.

8.6 CONCLUDING COMMENT.

> ... studies should link what we see primates do with what sociobiologists
> think they should do for reproductive survival.
>
> Kummer, 1979: 394.

Kalat (1984) declared that "at any given time, the body temperature is carefully defended against any fluctuation" (p. 237). Protecting the integrity of body temperature, therefore, would surely contribute to the survival of the individual.

A synthesis of all the data collected in this research thesis indicated that thermoregulation, behaviour and the social condition do vary together in a manner unique to each individual.

In terms of internal temperature fluctuations, the vervet subjects living in isolation were a significantly different population to those living within a troop – the deviation from the mean being reduced in all three of the troop-living subjects.

Two behavioural factors bore a significant relationship to a change in temperature – the one factor consisted of a cluster of individually executed behaviours, the other of a group of social behaviours. This result, together with the indication that social huddling and grooming behaviour influence body temperature, provided the troop-living vervets with additional strategies for thermoregulation, and has been interpreted as providing a possible explanation for the observed T_b differences between the individually and the socially-living vervets.

Within the troop, individual differences in temperature fluctuation were also apparent, and these seemed to relate to status. The higher the status, the less the internal temperature oscillated around the mean. Behaviourally, priority of access to resources, and socially, the high level of friendly interaction of the dominant female, the agonistic avoidance behaviour of the intermediate female, and the harassment of the subordinate female, supported these findings. Despite these differences, however,

these individuals appeared to be submerged within the social system in times of disturbance, and with the activity cycle, which appeared to be in phase with environmental circumstances. Thus, during the midday heat, the active solitary behaviours were reduced and all troop members rested, and they all huddled with conspecifics as they slept at night. For vervets, therefore, it seems physiologically advantageous to live within a social group – and even better to enjoy a high status within that group. The group, by providing social mechanisms for achieving homeostasis, would seem to be enhancing physical fitness, and so contributing to the survival of the individual to reproduce.

PLATE   6.0

BEHAVIOUR,   THERMOREGULATION
AND   THE   SOCIAL   GROUP.

6.1 Grooming following fighting.
     A social strategy to
     facilitate thermoregulation?

6.2 Female and infant huddling.
     Evolutionary coadaptation
     postulated for huddling
     and grooming.

6.3 Huddling in fear. Warmth
     generated may counteract
     physiological stress response
     and promote homeostasis.

CHAPTER NINE

AN EVALUATION OF THE RESEARCH

The study of behaviour encompasses all of the movements and sensations by which animals and man mediate their relationships with their external environments – physical, biotic and social. No scientific field is more complex, and none is more central to human problems and aspirations.

Alexander, 1975: 77.

9.1 INTRODUCTION.

In reviewing the methodology of this thesis, and the reconciliation of the thesis concept with the procedures employed – the logic of the procedure can be evaluated.

The theme of this dissertation revolved around the fact that primates live in social groups, and so physiological and behavioural functioning must have evolved within a social context. The major focus was upon interactions between body temperature, behaviour and the social condition in *Cercopithecus aethiops pygerythrus*. Fundamental prerequisites for such a study are sensitisation of the researcher to the behaviour of vervet monkeys, the construction of an ethogram, and the provision of an environmental situation which will permit body temperature to be recorded from a subject which is undisturbed, free moving and a member of an ongoing social structure. Intensive examining of individual subjects becomes a requirement, because each situation is unique.

The thesis was crystallised over five years of vervet observation and theorising. As Hutt and Hutt so aptly pointed out: "... to avoid premature (and irrelevant) experimental manipulations it must be known what behaviour there is to be modified" (1970: 413). It was the lengthy period of study and cogitation that led to the design of wide-ranging, intensive and repeated probes into thermoregulatory, behavioural and social functioning as they occurred together within one individual. In order to understand any one of the parameters, it was contended, it is necessary to take the other two into account because of their interrelatedness.

An investigation into such a theory required an in-depth case study approach, with special attention to each level of functioning, in an environment that preserved ongoing spontaneous functioning. As this was an original study it seemed appropriate to retain as broad a perspective as possible. It was argued that this approach would serve a two-fold purpose — it would test the theory, thereby assessing the usefulness of its framework, and also generate specific hypotheses for confirmation by further researchers.

Five individual vervets were examined as dynamic systems functioning at three interdependent levels, which varied together to preserve homeostasis. The rhythmic nature of the phenomena under scrutiny demanded regular, rigorously randomised monitoring over the days and over the weeks. "In several ways rhythmic research is heroic" (Rusak, 1981: 184).

9.2 METHODOLOGY.

The research took place in two stages. During the first stage the theory was developed, and in the second stage in-depth investigations of the relationships between body temperature, behavioural and social factors in individual vervet monkeys were conducted to find out whether the hypotheses generated in the first stage were supported.

The studies which gave birth to the research objectives in Chapter Four have been outlined in Chapter Three. The procedures used are described in detail, assessed, and improvements suggested in an unpublished M.Sc. thesis (1977) and the publications cited in the references.

The projects included investigations into the behaviour of two local free-ranging troops, and the target troop (pre and post capture), as well as the erection and establishment of the caged troop of vervets. The advantages of working within the natural habitat of the vervet monkey are emphasised. Important environmental cues such as climate and the day-night cycle did not have to be manipulated, and a natural troop with social bonds intact, could be caged.

In the second stage, 150 repeats of concurrent measures of behavioural, body temperature and social functioning were collected. Thus each subject became its own control. The time samples were randomised across subjects and across five levels (periods) of the day, to control for any underlying rhythmic fluctuations in functioning. Following two pilot runs (not recorded in the thesis), two adult vervets, each living alone in a single cage, were monitored concurrently according to the randomised schedule and comparisons with the troop's behaviour were made when necessary. Following this, three female adult vervet monkeys who were part of the caged troop, and whose behaviour before implantation had been extensively monitored, were also investigated according to the same schedule. The atmospheric temperature was noted with every time sample. It is suggested that it was because the collection of data was well controlled that the regularities in functioning were detected.

9.2.1 Behavioural and social data.

An attempt was made to gather as much behavioural information as possible. However, as Bernstein (1971) reported in his study: "Despite excellent visibility from the observation point, an investigation scanning a group spread over the area of one of the compounds often failed to notice brief responses involving one or two animals" (p. 79). It seemed that a combination of troop scans, randomly assigned focal five-minute time samples of each subject, movement outlines on a cage plan, videotape, and general descriptions as described in the procedure, captured much contextual and specific behavioural data. The relatively long focal time sample (five minutes) was thought to be necessary in order to obtain sequences of behaviour, and to try and understand the precursors of responses, and the social situation. Weigel (1980) emphasised Altman's contention (1974) that focal animal sampling minimised biases in estimating the frequency and the rates of occurrences of behaviour.

A major difficulty in this investigation was organising the vast amount of information that had been collected. Three different types of data recording sheets were designed to facilitate categorising and quantifying the information, detecting behavioural trends and interaction patterns, and exposing spatial organisation. These charts, termed the activity matrices,

the interaction matrices and the spatial distribution and movement charts, have been described in the procedure. A sociogram was also developed. It is suggested that the construction of charts similar to these may be useful for any behavioural study.

The activity matrices provide a technique whereby frequencies, duration, sequence and patterning of one or any number of a comprehensive list of activities can be readily extracted for analysis, and solitary, intratroop, and intertroop social activities can be contrasted. The comparative activity matrices permit comparisons between the subjects for all the parameters described. A glossary defining the behaviours listed in the ethogram was also compiled in an attempt to avoid semantic confusion. The distinction between agonistic and friendly behaviour is occasionally blurred, and this was the major difficulty encountered when compiling and scoring the charts; for example, is 'avoiding' a friendly or an agonistic behaviour pattern? It prevents a fight, but does not promote social interaction. The ethogram (which Lehner (1979) described as a catalogue which closely resembles the complete repertoire of behaviour) was adjusted according to recommendations made in the author's M.Sc. thesis, and yet modifications were still found necessary. For example, mating behaviour was not noted during the present study even though it was pertinent to the previous study when an increase during a 'crisis' became apparent, that is, when first captured and caged. Thus it appears that each research situation is unique, and the flexibility to modify existing formats should be displayed (see Appendix 3). Event-recorders and checklists should be treated circumspectly, because they presuppose that the categories are clearly defined and comprehensive. It would seem that a model activity matrix which could form the basis for vervet behavioural studies could be constructed if several research workers combined to ensure a comprehensive list of the major behaviour patterns, and to test intersubjective reliability for interpreting the activities. The vast amount of behavioural information collected was unwieldy until the behaviours were grouped into factors. The rationale for the analysis was discussed in Chapter Six. Two sets of factors were formed, and it is proposed that a comparison between these two types of factors, one based upon the grouping of behaviours according to the researcher's assumptions, and the second derived statistically with no *a priori* hypotheses as to their nature or number, is a useful procedure for testing hypotheses. It should be remembered, however, that factors derived statistically reveal

which behaviours group together, but not why. Thus the groupings can merely be used as a guide to explaining underlying mechanisms. Nevertheless, they may point to behavioural combinations not previously considered.

Bekoff (1972) wrote that the initial step in any behavioural study should be the establishment of ethograms and sociograms of the animals under study. Her view is supported by many workers. Chance (1967) pointed to the importance of assessing attention structure which "underlies or plays a part in all the social relationships by which an animal relates itself to others in a group" (p. 7), while Rowell (1971), describing her study of caged groups of *Cercopithecus* monkeys, related that "a picture of social structure was built up by asking the basic question of who did what to whom" (p. 625). The interaction matrices of grids used in this study were simple to construct and could be filled in and scored quickly and easily. The charts permit an examination of who interacted with whom, how often, and the type of interaction. Quantification of the number of interactions, and elucidation of the type of interaction at any phase of the study becomes relatively simple, and computer programming, if required, is straightforward. The interaction matrix is recommended as a practical tool for elucidating the social structure of any group. The sociogram provided a technique whereby visual examination for interaction patterns was possible. This may circumvent unnecessary computational work, by displaying whether relationships do or don't exist and how strong they are.

Spatial behaviour appears to have been neglected in many studies of social organisation even though spatial behaviour is a central aspect of social organisation (Brindley, 1971). Mason (1968b) maintained that spatial relations within a group are technically more difficult to study quantitatively than the spatial behaviour of entire groups, and for this reason most attention has been given to the group phenomena of range and territoriality. This difficulty would probably be reduced if the movement patterns of individual troop members were traced on previously dimensioned maps of the study area, and/or the troop's distribution in space plotted. The spatial distribution and movement charts used in this study seemed to cater for diagrammatic and quantitative information on intratroop spatial relationships without difficulty. It would have to be modified for use under field conditions, but this does not seem impossible.

Conflicting research results have led to an increasing emphasis on the quantification of data in observational studies of behaviour in recent years. Dunbar (1976) evaluated the effects of using different parameters to quantify social relationships in gelada baboons, and he found that the strategy used to estimate overall social relationships in that species is relatively immaterial, so long as the data are ordinally scaled (p <0.001). However, in many cases, the correlations were far from perfect, and he proposed that every different parameter answers a slightly different question. In this research project, interaction frequencies were used to estimate the troop social interaction profiles. Since the observation times were equal, the frequencies could be compared directly (Altmann, 1974). The activity matrices, however, provide for both duration and frequency. Of the use of these two measures, Dunbar (1976) wrote: "In an absolute sense, neither can be considered better than the other, since each examines a different aspect of the situation ... it may often be valuable, however, to record both kinds of data" (p. 91). Rhine and Flanigan (1978) and Rhine and Linville (1980) concur. They addressed the issue using stumptailed macaques and concluded: "No evidence exists demonstrating that any of several widely-used techniques for measuring social behaviour is more valid than others; therefore, there is no scientific justification for raising any of these measures as a standard against which the truth of others can be legitimately compared" (1980: 121). Even if behavioural strategies do vary in terms of the economics of time, surely a crucial issue is the actual time spent gathering the information. The complementary nature of these two measures was well illustrated when 'eating' behaviour was studied. It was found that the dominant female living in the troop exhibited higher durational, lower frequential feeding bouts than the subordinate female, who ate more frequently for shorter periods. This had implications for the study. The dominant vervet could eat when she wanted to, and until she was finished, but the subordinate female was harassed, so would drop her food and continue to eat later. This phenomenon may have an important consequence for internal temperature fluctuations since food intake is accompanied by an increase in body temperature, so erratic, frequent food ingestion periods may be accompanied by frequent bursts of temperature deviations.

Two related difficulties encountered in this study which need consideration are intersubjective reliability and replication. Atz (1967)

identified extraction of parts to measure, count and compare from the
continuum of the animal's total behaviour as perhaps the most difficult
task in behavioural studies.   While the problem seemed partially resolved
by compiling a glossary and the design of relatively straightforward
measuring techniques, it was felt that the attempt to capture the evanescent
behaviour patterns upon videotape was limited, mainly because the field
encompassed by the videotape is so small when compared with the total
scene requiring capturing.   Photographs recording specific events were
beneficial, but need to be used in conjunction with videotape.   It is also
proposed that this initial work may form a baseline for future studies, and
all the sixty-five activities that have been extensively categorised, numbered
and timed, and computerised, should be stored.   This would enable
investigation of many behavioural interactions, and clusterings, and would
allow future research workers to extract any information they may require,
with ease.

A salient aspect of any research investigation is an assessment of its
external and internal validity.   Rowell (1972) wrote that each successive
level of approach – field, artificial colony and cage – exchanges a
further distance from naturalness in return for increases in convenience and
in the control the observer has over what particular information he will be
able to obtain.   In this investigation it is proposed that the internal
validity was high.   Statistical conclusions based upon 150 randomised
repeated measures seemed robust.   Thus, for the five vervets investigated
in depth, the conclusions appear valid – there were significant individual
differences, and idiosyncratic combinations between behavioural,
thermoregulatory and social functioning.   External validity was more
difficult to assess.   An attempt was made to retain all the conditions seen
in the wild, except for troop movements over long distances.   It was noted
that the free-ranging activity cycle had been retained.   An important
prospective study remaining to be done is to trace the troop's behavioural
changes in the cage over time.   Will all the behaviour manifested by the
vervet troop after several years only be relevant to caged vervets?   The
considerable advantages of the caged setup itself, of intact social bonds,
and of working within the natural habitat have been discussed.   A corollary
for the question is: to what extent is the behaviour of any troop of vervets
only appropriate to their own specific ecological conditions?

9.2.2   Thermoregulatory data.

The use of biotelemetry to obtain body temperature data as described in Chapter Five did not seem to produce any major difficulties in the execution of the research.   The procedure had not been used in Natal, so had to be developed.   A grant enabled temperature sensitive transmitters to be purchased from the U.S.A.*

For this particular research project, it did not seem necessary to convert the body temperature as measured by the signal frequencies emitted from the receiver into body temperature as measured by degrees centigrade. This was a comparative study and relied on changes in body temperature. Thus, since the instrument used recorded signal frequencies, it seemed a more appropriate measure and it was never intended to make any absolute statements regarding body temperature.   Reite, Short, Seiler and Pauley (1981) also discussed their variables only in terms of change (% from a baseline).   Furthermore, completely accurate conversions of signal frequency to °C were difficult because it was impossible to count fractions of one beat.   The author did attempt to obtain an idea of the relationship between internal body temperature as measured in signal frequencies and °Centigrade, and this was used to standardise between subject signal frequency comparisons (Chapter Four).   Unfortunately, the only apparatus available at the time were waterbaths in the Department of Biological Sciences, which did not appear to be accurate enough for absolute judgments.   It would be useful, in future research projects, to obtain a temperature conversion figure because they do convey extra information.   Accurate electronic procedures for measuring temperature have been developed.   The stability of the minimitter signal was subsequently confirmed by our Department of Electrical Engineering (see section 5.3.6.   The full text of the report has been bound with the raw temperature data, and lodged in the Department of Psychology, University of Natal, Durban).

A contentious decision was whether to 'fix' the temperature sensitive minimitter, to the subcutaneous layer of the peritoneal cavity, or whether to allow it to freefloat, merely inserting the transmitter into the peritoneal cavity.   Even though the former approach has been used with apparent

success (van Holst (1981) pers. comm.; Martin (1980) pers. comm.; Reite, Pauley, Kaufman, Stynes and Marker, 1974), the latter procedure was adopted. The surgeons advising the author were convinced that any attachment in an active animal which frequently jumps, runs and climbs would lead to adhesions. Subcutaneous attachment reflects the surface body temperature which is influenced by the atmospheric temperature, more closely than a sensor which is inside the peritoneal cavity. Mackay wrote that "temperatures above the fatty layer are quite labile" (1970: 159). The minimitters in this research, it has been shown, may become attached by being enclosed by mesenteric tissue. Apart from these considerations the distribution of bloodflow is known to change from time to time, so anchoring the sensor would not necessarily give a more 'representative' temperature. The clinching argument, however, is that the temperatures did, in fact, show regularities and if minimitters move around the peritoneum in response to social variables, then the result would be even more amazing and worthy of study.

9.3   CONSTRAINTS AND DIFFICULTIES.

The purpose of this research thesis was to generate a theory and formulate hypotheses which would provide a framework for future research, and then to test the theory. In order to do this, a comprehensive, tri-level study of a small sample of subjects was conducted. Data collection was detailed and highly structured so that it could be extensively analysed and subjected to statistical analyses, that is, large numbers of repeated measures (N = 150) of concurrent body temperature and behavioural and social parameters (65x) per individual. Each subject became its own control. It now remains for the author and future research workers, however, to verify and extend the hypotheses generated in this project, and on different troops, when an intimate knowledge of their social structure is known. Kazdin has asserted that: "Single subject research designs have been a source of continued controversy. For years, and even today in some quarters, it has been debated whether these designs are at all useful relative to traditional large-scale between group research. The now extensive experimental and applied literature that has generated findings via single subject research would seem to make this debate of historical interest" (1978: XIV). Hutt and Hutt have also explained that "far from

being gratuitous, detailed observations of behaviour in a psychological experiment may throw light directly on the mechanisms activated by a particular set of environmental variables" (1970: 20). This seems compatible with Hinde's (1978b) assertion that understanding requires coming to terms not merely with the 'surface structure', but with the 'deep structure', the principles in terms of which the observed patterning can be understood. It is hoped that this research project may assist in throwing light upon such mechanisms. Calls for more attention to individual differences have been discussed (e.g. section 6.2.3). It is wondered whether the underlying mechanisms for preserving homeostasis in a dynamic multilevel system in interaction with an everchanging environment can be discovered if the variations of the theme are not investigated. As Rusak (1981) and Slater (1981) pointed out, individual differences are obscured when statistical testing is used to extract an average animal, and may not even reflect the functioning of any single animal. It is argued that the strategy used is appropriate for research progression. An attempt to test many subjects in different environments immediately after formulation of the theory is uneconomical in terms of time and expense and may actually be impossible. Certainly the situation would be difficult to replicate. It requires money, technical aid and a relatively large time investment to set up such an environment and the number of free-ranging troops available for study and capture to preserve bonds is limited. Yet Hinde (1978b) asserted that interactions within a primate group can be understood only in terms of the long-term relationships between the individuals concerned. The appropriateness of the vervet as a model for study has been discussed in section 2.2.3.

Thus the difficulties encountered in this research project included:-
- **Time limit :** The "low yield for the time and effort spent" (Hutt and Hutt, 1970: 196) on an observational study. This seems to act as a deterrent to many researchers. However, Hutt and Hutt pointed out that regrettably if we are to find out how people and animals actually behave there seems to be no substitute for detailed and painstaking observations. They point to ethologists who in contrast to psychologists "apparently have never felt the need to spare themselves the drudgery" (p. 9). They present an excellent account of why observation is essential in their book, **Direct observation and measurement of behaviour.** This problem was compounded by the necessity to take into account the rhythmic changes in body

temperature and, possibly, behaviour – so that monitoring had to be rigorously randomised over the days and over the weeks. The difficulties in studying rhythmicity are considered in section 5.2.2.

– **Lack of money and technical help** : The ready cooperation of the University, the staff and our technicians is gratefully acknowledged. However, these resources were limited. Our conditions were such that the author, with help from her supervisor, had personally to carry out and organise every facet of the experiment, from raising money to the construction of the cage, to getting it designed and supervising the construction, to catching and caging the free-ranging troop and transporting them to the University. Similarly, finding out about the minimitters, raising money to purchase them, actually getting them from the U.S.A., and developing a procedure for insertion, was her responsibility.

– **Availability of research subjects** : An emphasis in this study was to study a natural troop with social bonds intact, in contrast to one which has had monkeys from diverse sources thrown together. The procedure referred to in the previous paragraph would have to be repeated from the beginning in order to get another troop. In addition, there are not many free-ranging troops available for capturing and caging, and the necessity and usefulness in doing so has to be carefully ascertained. If the troop is in a cage, it is no longer free-ranging.

– **Ovulation** : The problem of ovulation was taken into account. Fortunately the rhythmicity of the temperature results were consistent with the findings of Bauman (1981), Horvath and Drinkwater (1982), and see section 5.2.1: that the daily activities override and obscure the temperature changes that may take place during ovulation. It is, however, recommended in future studies to take automatic readings in the early morning before the vervets wake up. This would help to find a baseline, and also generate useful data relating to ovulation, gestation, and the possible influences upon behaviour.

– **The receiver** could only pick up internal temperature from three different animals at one time (i.e. it contained only three different channels). This was not too serious in this project, which concentrated on individual systems.

Hutt and Hutt asserted that:

> Ethologists proceed from naturalistic observations; they are interested
> in questions of WHY and HOW animals do what they do. Methods serve
> these ends and therefore are not of primary consideration. Psychologists
> are much more concerned with methodology, usually dictated by theoretical
> tenets or the requirements of statistical propriety. Consequently, what
> ethologists find out is interesting and significant even if methodologically
> circumspect, whereas what psychologists find out is technically exemplary
> even if its validity and significance are sometimes obscure.

1970: 20.

This thesis has attempted to bridge that gap.

9.4 SUGGESTIONS FOR FUTURE RESEARCH.

Satinoff (1982) maintained that the value of any research approach
ultimately lies in its ability to generate new unexpected findings. It is
suggested that the possibility of social control over physiological functioning
presents some novel possibilities. Apart from extending the theme of social
status (in its broadest sense) and temperature to other free-ranging and
wild troops, there is the theme of temperature control generally, for example
work on reptiles. Originally, it was believed that there was no control of
body temperature in poikilotherms, then behavioural control was demonstrated,
and now there is the possibility of social control, to be explored in all ages
and sexes.

Next, further correlations with physiological (preferably temperature)
variables and social ones (e.g. testicular temperature) could be considered.
Even some observational material on adduction of testes, and running
positions, as measures of thermoregulation. Another possibility is research
into the social control of temperature in children - clothes worn,
gooseflesh, even shivering and sweating may be on the way to physiological
variables. It may even be possible to use a quick-response thermistor to
get a correlation of any of these measures with mouth, forehead (etc.)
temperature.

It is tempting to speculate that the theme of this thesis could usefully
be applied to studies attempting to elucidate the complexities attending *Homo
sapiens* in dynamic interaction with the environment. Legally, punishment

by solitary confinement may disrupt effective thermoregulation – that is, as in this study with vervets, social deprivation may eliminate a range of socially based thermoregulatory mechanisms and undermine the efficiency with which body temperature stability is maintained. A ripple effect would lead to a disturbance in physiological homeostasis.

Medically, the influence of social factors upon physiological functioning may need closer scrutiny. Studies of social status and thermoregulation could be extended to studies relating social status or change in status, to temperature, and vulnerability to infection, which may even relate to psychosomatic diseases. This would be consistent with Miller's call for the adoption of general living systems theory for psychiatry because it "seeks to eliminate the firm disciplinary boundaries that obscure the orderly relationships among parts of the real world and overlooks their shared characteristic" (1980: 98). Accordingly, when Lomov at the prestigious **First Joint Seminar in Psychology and the Neurosciences** between the National Academies of Sciences of the U.S.A. and the U.S.S.R. defined behavioural mechanisms in functional systems theory as "a hierarchy of systems that include molecular physiological and psychological levels" (1980: 8), it is believed his definition was found wanting. He omitted to include a social level.

9.5   CONCLUDING   COMMENT.

In adopting an ethological approach to the study of the behaviour of *Cercopithecus aethiops pygerythrus*, the dynamic interaction between individual and environment became increasingly apparent. It seemed, eventually, that a complete understanding of behaviour had to take cognisance of all the attendant variables and the impact that one has upon the other. While a 'total' study may be an unrealistic enterprise for any single researcher, it is suggested that a study at any one level of enquiry needs to be complemented by studies at the other levels, and neither is more important than the others.

Focussing upon individual subjects also gave rise to an awareness of marked individual differences, even within the same age-sex category of the same troop. Thus, in the same way that stereotypic perceptions of populations such as the Russians, the Americans, and the South Africans are formed by strangers to these communities, so, too, is it with vervets. Increasing familiarity with the troop brought increasing awareness of individual differences. It would seem that the conclusions based on this research project supported these hypotheses.

CHAPTER TEN

SUMMARY AND CONCLUSIONS

The formulation of this thesis – that physiological and behavioural functioning has evolved within a social context and are, therefore, interrelated, arose from independent studies of the behaviour of locally indigenous vervet monkeys. For example, when the survival of a free-ranging troop of vervets was apparently threatened by caging inside the range of an unknown wild troop, behavioural mechanisms were elicited which enhanced the troop's social cohesion, and decreased the activities disrupting bonding. Interpersonal distances diminished, physical contact and social facilitation increased and intratroop agonism decreased. However, it was noted that caging precipitated physiological changes as well in the direction of increased arousal – faeces were liquid and smelly, the whites of the eyes became prominent and hair stood on end. It seemed that the behavioural strategies evolved, such as a significant increase in physical contact, may not only promote social cooperation, but may also serve as regulatory mechanisms to sustain physiological homeostasis. The interplay between social, biological and behavioural parameters was also noted in the feeding pattern of the vervet. The wasteful habit of breaking and dropping food, the author had demonstrated, may serve a positive social function. It facilitates the distribution of food from a localised source, and enables infants to obtain food particles of a size that they can manipulate and handle. The dynamic interaction between behaviour and environment was observed when the caged vervets began to moisten their bread before eating it – this change in behavioural response was not noted in the free-ranging troops, so it appeared to be a modification generated by the continual presence of two shallow pools of water in the cage.

Biotelemetry was coupled with an ethological approach in order to test the theory that body temperature (a physiological measure), and behavioural and social functioning vary together interdependently. Intensive studies of each of these variables as they occurred together were conducted on five freely-moving and undisturbed adult vervet monkeys. Two (a male and a female) lived in isolation in single cages, and the other three (all

females) were part of a caged troop.

All the subjects exhibited a similar daily T_b rhythm, displaying significant T_b differences at different times of the day. Approximating the human cycle, T_b in the vervets also rose to a peak between early morning and sometime after midday, and then dropped, supporting the idea that the vervet may be an appropriate model for studying T_b. Despite the presence of an endogenous rhythm, however, the extent to which the body temperature deviated around the mean was different in each subject. A statistical computation of the body temperature variations separated the subjects into two different populations which, it was discovered, corresponded to their social condition. One population consisted of the subjects living alone, the other population of subjects living in a group. Body temperature fluctuated more in the isolated subjects than in any of the socially-living subjects.

Behaviour, like body temperature, was characterised by significant individual variations superimposed upon an underlying rhythm. The behavioural repertoire of the socially-living subjects was explored by subjecting the data from each of sixty-five behavioural components to a principal axes factor analysis. The factors that emerged separated the social behaviours from the individual behaviours, but indicated that these two forms of behaviour were equally important, and occurred together. Since vervet infants are born into and evolve within a social group, it is not surprising that social behaviour was found to be an integral aspect of their behaviour, and this was denied to the subjects living in isolation.

The factor analysis pointed to three different categories of social behaviour, and of individual behaviour. The social variants were identified as **interactive, coaction** and **organisational;** the individual variants as **solitary, territorial,** and **eating and border patrol,** and each served a different function. The division of behaviours were consistent for the frequential and durational data, and agreed with and extended arbitrary behavioural divisions via observation. Interactive behaviours consisted predominantly of grooming, were asymmetric, and required cooperation. This may be an important mechanism in the maintenance of social and physiological homeostasis by reinforcing social bonds, reducing tension and promoting cleanliness. No such mechanism would have been available to the isolated subjects. The

organisational factor was made up of behaviours which, it seemed, could be rituals to preserve order. Coaction consisted of symmetrically executed behaviours, which could be performed alone, and were grouped in a complementary individual category, which was labelled 'solitary'. It was surmised that these corresponding factors may imply a choice for the individual, by allowing for social or non-social preferences. The remaining two individual categories focussed, it seemed, upon the acquisition and maintenance of resources – territory, food and boundary checking.

Statistical analyses revealed marked individual differences in behaviour, emphasising sociability as a prominent variable in individual differences. No differentiation in agonistic involvement was apparent, however, the differences being confined to friendly interactions. Despite these individual differences, the behaviour of the troop-living subjects in parallel with their free-ranging conspecifics, was organised into an overall activity cycle of alternating sequences of rest and socialising over noon and night, and active non-social activities during the mornings and afternoons. Spatial behaviour mirrored the cyclical rhythm of the social organisation. Thus the pulsating sequences of social engagement and disengagement coincided with spatial conformations of clustering and dispersal and these, it was suggested, seemed to be in phase with the limitations of the vervet monkey's physiological status, and the characteristics of their econiche. Thus, for example, these monkeys with diurnal vision slept at night.

A study of each subject in interaction with the troop further emphasised subject differences. The troop's social organisation was structured so that a dominance hierarchy existed for the three adult females of the study. The dominant female had priority of access to resources, and it was she that was behaviourally the most social of the subjects. The intermediate female of the hierarchy was, behaviourally, the most solitary subject, while the female that was lowest on the hierarchy displayed behaviour that was intermediate between her two counterparts. The other members of the troop threatened the most subordinate subject significantly more and avoided her significantly less than the dominant female. The middle-ranking subject reduced her participation in agonistic altercations altogether by initiating significantly less episodes.

The body temperature, behavioural and social data supported one another, and provided insights into possible connections between these three levels of functioning. The effects that the different social conditions may have exerted upon body temperature were explained when the behavioural repertoire specific to each social situation was explored.

Two behavioural factors correlated significantly with a rise in body temperature: one, consisting of individual behaviours, and the other consisting of a complementary set of behaviours which were performed with conspecifics. The socially-living subjects, therefore, could participate in two behavioural situations which accompanied a T_b increase, but the isolated subjects only one. The socially-living subjects also had access to social grooming, an activity which it was revealed may correspond to a decrease in temperature – and is not related to an increase. Social huddling is a further social behaviour which modulates T_b. Thus social living provided for a range of situations in which body temperature could be elevated or reduced, leading, it is proposed, to more effective thermoregulation. Body temperature in the socially-living subjects was, consequently, more stable than in the isolated subjects.

Within the troop individual differences in the extent to which body temperature deviated from the mean was related to status. The higher the status, the less the internal temperature oscillated around the mean. These results were supported behaviourally and socially. The dominant female had first access to resources, so could thermoregulate most efficiently. For example, she sat in the only sunny patch of the early morning when it was cold, and had priority of access to shady spots when it was hot. She could choose the food she wanted to eat, and perform any activity without hindrance. Socially she was involved in most grooming interactions. She was avoided more than her counterparts, and was the butt for fewer agonistic advances. She seemed able to control her personal space. In contrast, the animal of lowest status had least access to resources, was avoided least, and was harassed the most. The intermediate subject avoided agonistic interchanges altogether. If, as has been shown in other species, stress is accompanied by an increase in temperature and, as suggested in this thesis, grooming is a tension-reduction mechanism which may reduce internal temperature, differences in agonistic behaviour also supported the internal temperature analysis,

that is, that the oscillation around the mean is greatest with the least dominant subject and least with the most dominant conspecific.

The maintenance of a constant body temperature is essential for ongoing physiological functioning. The effectiveness of thermoregulatory functioning, therefore, would contribute to the fitness and to the survival of the individual. It is theorised that animals living in a social situation have access to a wider range of thermoregulatory mechanisms than individuals living in isolation, while within the group the individual of higher status employs thermoregulatory strategies more effectively than the individual of lower status. There does not appear to be any previous documentation of such a phenomenon.

GLOSSARY OF BEHAVIOURAL TERMS TABULATED IN THE ACTIVITY MATRIX.

agonistic	any interaction tending to increase the distance between conspecific individuals or groups, and which may lead to the infliction of physical harm on one or more of the participants (after Sussman and Richard, 1974).
attacking	physical assault, or an attempt at a physical assault, even if physical contact does not occur.
avoiding	(1) Moving out of the path of an oncoming animal. (2) Quitting on approach, e.g. for grooming.
biting	cut into, or nip, with the teeth. This was not noted during this study, although evidence of fresh wounds was seen.
boundary pacing	travelling around perimeter of cage.
chasing	pursuing – may or may not be agonistic – usually seen during play.
chewing	movement of the jaws, lips closed or slightly parted. It seems to be a fear response possibly derived from a yawn. Frequently observed among caged adults before adaptation.
climbing	go up, or down.
coalition	cooperation between two or more monkeys for peaceful or agonistic purposes.
eating	masticating and/or swallowing food.
following	go after.
grabbing	snatching either (1) an object (2) a part of the anatomy of a conspecific.
grooming	the process of cleaning and picking through the fur and skin (after Lancaster, 1975). Hypothesised to be a multi-purpose mechanism.
auto	grooming self (a non-social activity).
allo	grooming other (social activity).
huddling	nestling close together, with bodies touching.
ignoring	looking away, taking no notice of friendly or agonistic gesture. (soliciting grooming or threatening response).
interfering	intervening
investigating	examining
joining	come together

licking	pass tongue over to taste, moisten or clean (self or other).
lying down	being prostrate.
presenting	displaying or 'offering' body (usually an apparent invitation for grooming or sexual activity).
pushing	shoving.
redirecting aggression	threatening or attacking an unsuspecting uninvolved conspecific – in response to an attack or a threat.
resting	relaxing, lying down.
running	advancing at very rapid pace.
scratching	rubbing, usually nails (tabulated as distinct from grooming, may serve similar function).
sexual	behaviour involving genitalia.
sitting	stationary position in which body supported by ischial callosites.
sniffing	(1) individual activity – draw up air audibly through nose. (2) social activity – smell a conspecific.
social	any activity involving more than one animal.
solitary (non-social, individual)	any behaviour apparently performed without reference to another individual.
standing	stationary, all limbs extended.
submission	an appeasement gesture – giving in to another.
supplanting	displacing – taking the place of another.
threatening	a signal preceding and, if effective, superseding actual fighting.
touching	physical contact between two or more animals.
traversing perimeter	see boundary pacing; terms have been used interchangeably.
vigilant	watchful.
walking	advancing leisurely.
yawning	opening mouth and exposing teeth. Open mouth position sustained approximately 3-5 seconds. Threat.

NOTE:

– ed	subject was recipient of behavioural response.
– ing	subject exhibited the behavioural response.
SA	social agonistic behaviour.
SF	social friendly behaviour.

APPENDIX 1
APPARATUS AND MEDICATION

1.1 BIOTELEMETRY

Instruments purchased from:
The Minimitter Company Inc., P.O. Box 3386, Sunriver, Oregon 97702.

- **Minimitter :** Model: L-M
  Batteries: Lithium 1000mah. Battery life: 4-5 months.
  Temperature range: 10-45°
  Transmission range: 6-150 metres.
  Transmission frequencies: 27,555; 27,565; 27,575; 27,585; 27,605; 27,615 MHz respectively.
  Capsule coating: paraffin/elvax.

- **Receiver :** Model CH : 3 channel
  Receive crystals.

1.2 RECORDING INSTRUMENTS

- **Tape deck :** Akai Model 4000D 4 track reel to reel (for simultaneous recordings of body temperature and behavioural observations. An electric clock fed 60-second time pulses onto track 1).

- **Cassette recorder :** Phillips.

- **Videorecorder :** Sony AV-3420CE. Portable black and white with

- **Video camera :** National WY-85.

- **Camera :** Minolta fitted with zoom lens - Tele Rokkor - PF 1:18 f = 135mm - 35mm film.

- An Omega digital stopwatch was used for checking the timing of temperature signals and observational samples.

1.3 SURGERY

- **Medication :** Parenteral Administration:
  Anaesthetic: Ketalar 10ml ampoule 100mgm /ml (Parke-Davis)
  Muscle Relaxant: Valium 2ml ampoule 10mgm/2ml (Roche)
  Antibiotic: Streptopen 250,000 units
  Procaine Penicillin G (0.25gm) dihydrostreptomycin base (as sulphate) per ml.
  Glaxo-Allenbury (SA)(Pty) Limited.
  Topical Administration:
  Antiseptic/Antibiotic: 1. Germotol
  Alcohol 70% equal parts for local application.
  2. Surgispray 110gm (Novo Industries) post surgery. Each can contained:
  Neomycin sulphate as base 525mg
  Polymixin B sulphate 150,000 units
  Zinc Bacitracin 37,500 units.
  Wound moisturiser: Physiological saline.
  Minimitter steriliser: Hibitane concentrate .5%. 100ml bottle (I.C.I.)

- **Surgical instruments :** Forceps: artery; Forceps: toothed; Retractor; Scalpel; Scissors; Mayo; Tweezers.

- **Sutures :** Internal - sterile absorbable surgical sutures. 00 surgical gut medium chromic (90cm) with .318 circle reverse cutting atraumatic needle.
  External - 00 silk (45cm) with 1/2 circle reverse cutting atraumatic needle.

APPENDIX 2

BODY TEMPERATURES : INDIVIDUAL STRAIGHT LINE PLOTS
ILLUSTRATING WEEKLY DAY-LEVEL MEANS OVER A FIVE-WEEK PERIOD.

(Plots are complementary to three-dimensional plots of Graph 5.1)

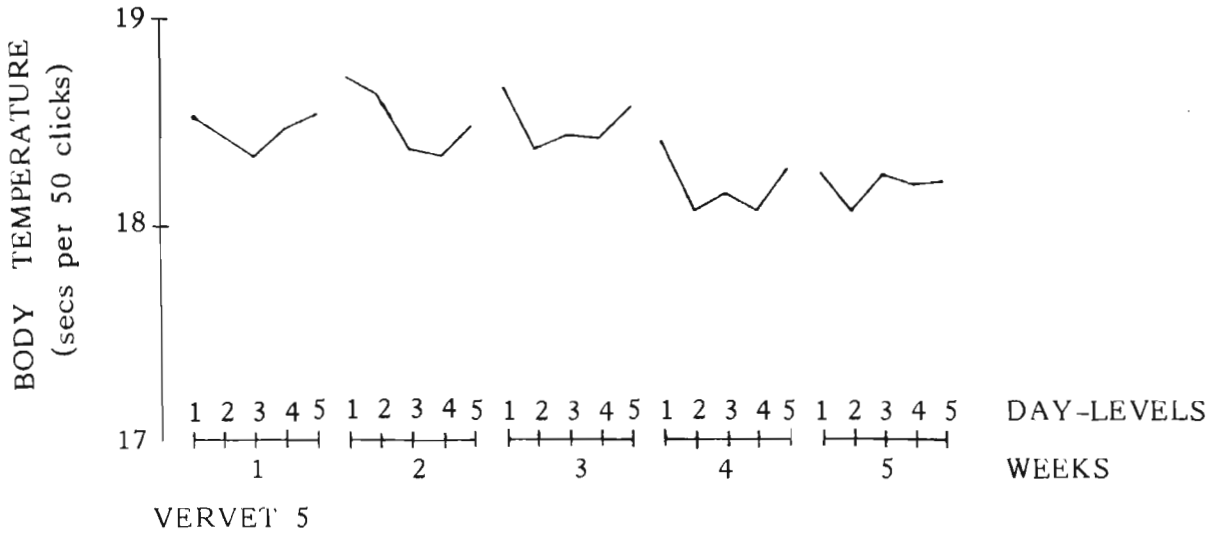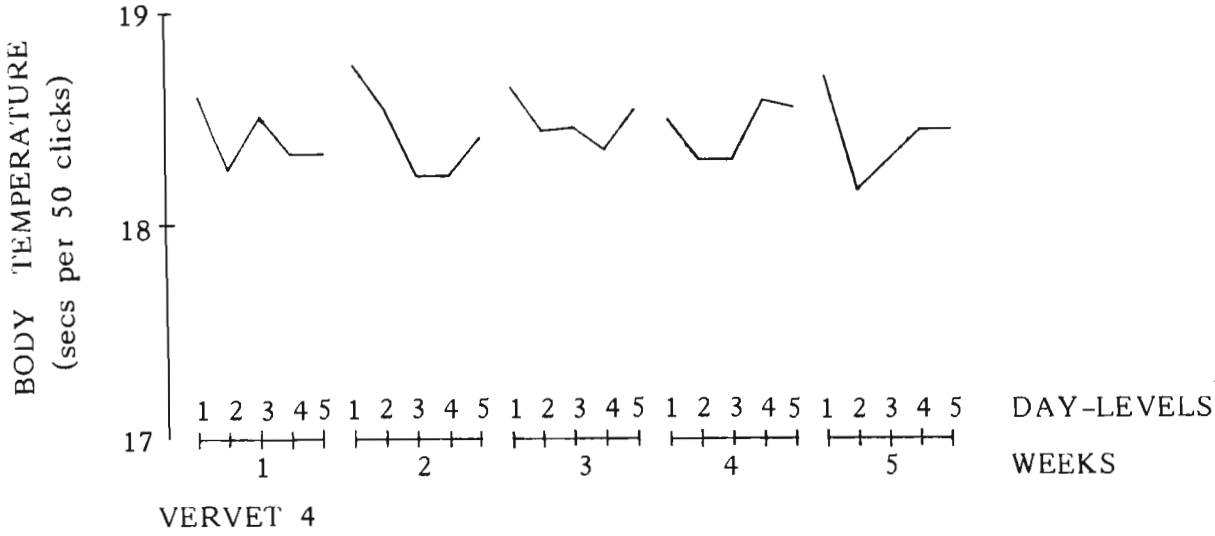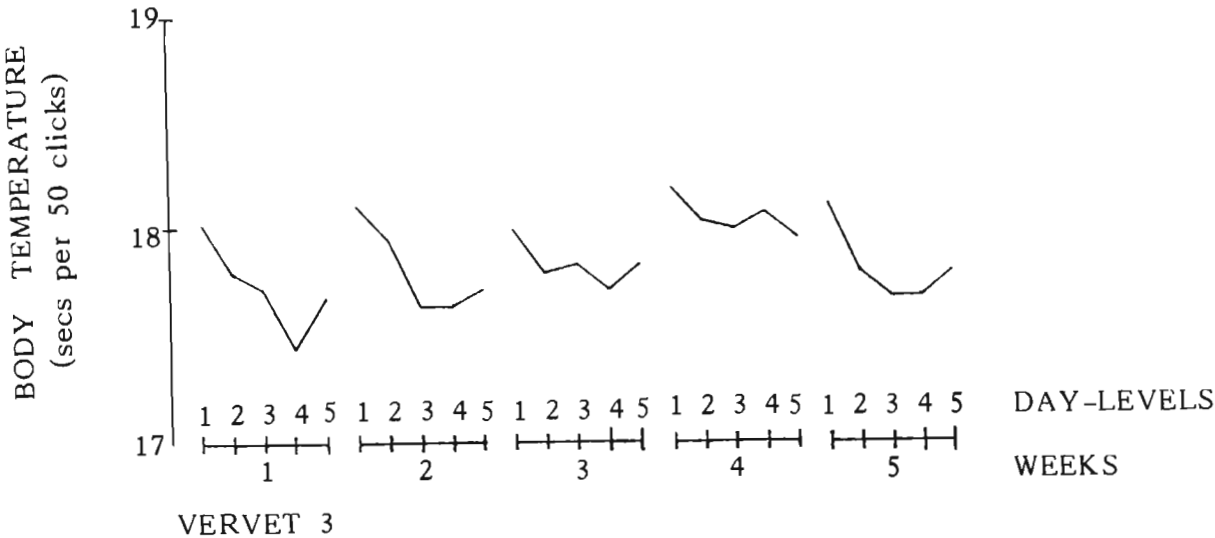SUBJECTS LIVING ALONE :

VERVET 1

VERVET 2
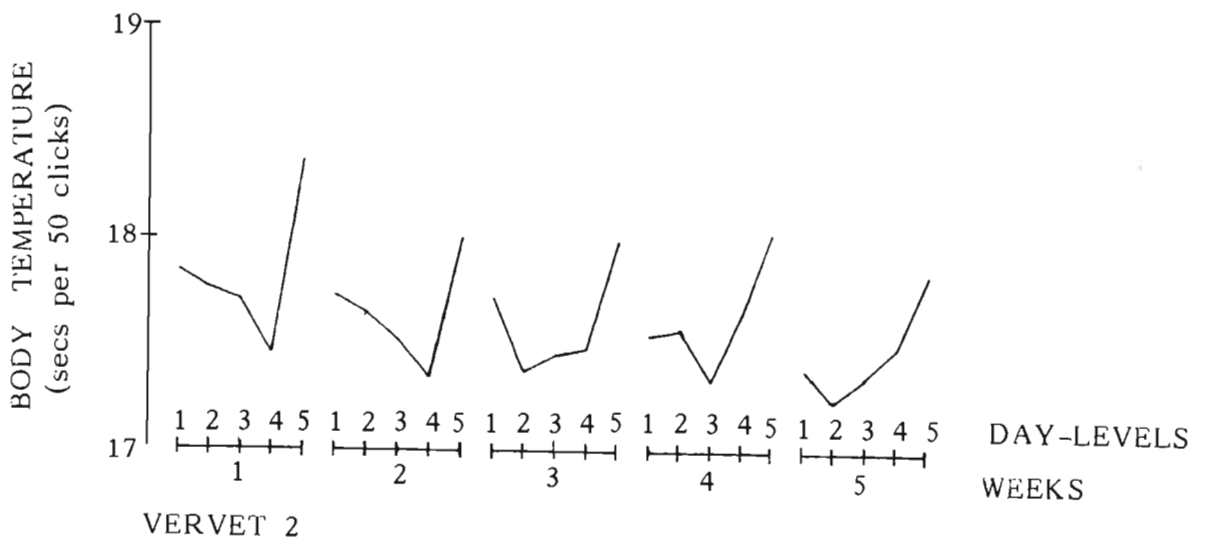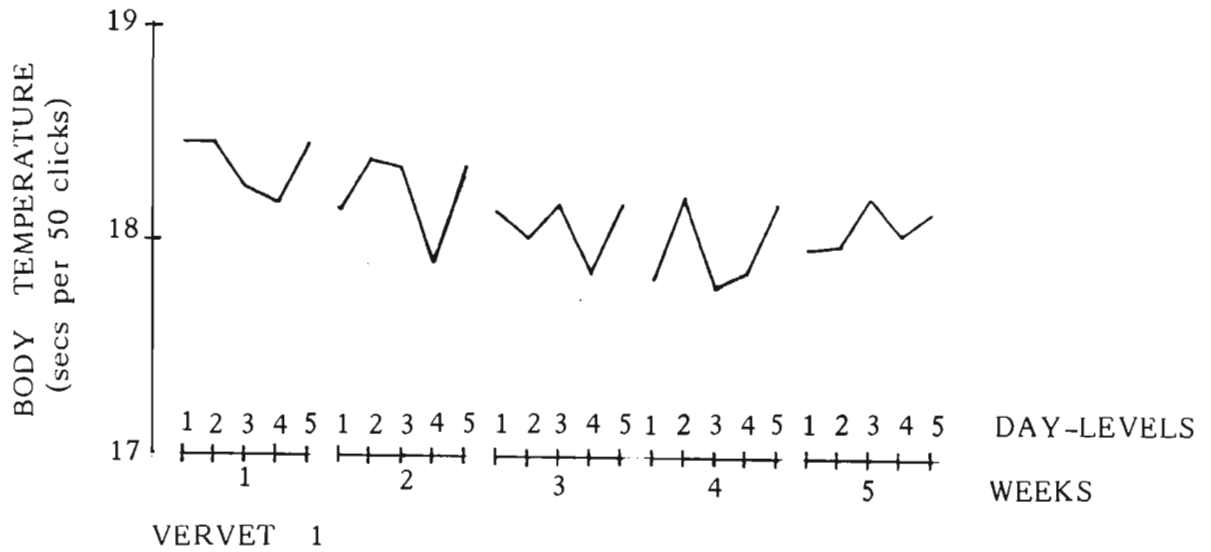
NOTE:

Day-levels:
1	07h30-09h30
2	09h30-11h30
3	11h30-13h30
4	13h30-15h30
5	15h30-17h30

SUBJECTS LIVING IN A TROOP :

VERVET 3

VERVET 4

VERVET 5

APPENDIX 3

ETHOGRAM : NUMERICAL CODING FOR ALL BEHAVIOURS
RECORDED DURING THIS RESEARCH PROJECT.

1.	Approach	23.	Investigating	45.	Threatening
2.	Attacking	24.	Interfering	46.	Threatened
3.	Attacked	25.	Joining	47.	Touching
4.	Avoiding	26.	Jumping	48.	Touched
5.	Avoided	27.	Licking	49.	Travelling perimeter
6.	Biting	28.	Lying Down	50.	Vigilant
7.	Bitten	29.	Presenting	51.	Walking
8.	Chasing	30.	Presented to	52.	Yawning
9.	Chased	31.	Ignored	53.	Chewing SA
10.	Chewing	32.	Joined	54.	Climbing SF
11.	Climbing	33.	Pushing	55.	Eating SF
12.	Coalition	34.	Pushed	56.	Grooming SF
13.	Approached	35.	Redirected aggression	57.	Investigating SF
14.	Eating	36.	Running	58.	Licking SF
15.	Following	37.	Scratching	59.	Lying down SF
16.	Followed	38.	Sexual	60.	Sitting SF
17.	Grabbing	39.	Sitting	61.	Sniffing SF
18.	Grabbed	40.	Sniffing	62.	Standing SF
19.	Grooming (auto)	41.	Standing	63.	T.P. SF
20.	Groomed	42.	Submission	64.	Vigilant SF
21.	Huddling	43.	Supplanting	65.	Walking SF
22.	Ignoring	44	Supplanted		

* SA = social agonistic
SF = social friendly

The following behaviours, which were included in the original activity matrix, were not exhibited during the present study.   It seemed that the variety of behavioural patterns had diminished with the increased time spent in the cage. This needs to be investigated.   Possibly the reduction in stimuli in an environment that was now reasonably predictable, coupled with the fact that the monitoring was confined only to adult females and done during the day accounted for the change.

Individual Behaviours

defaecating	fishing	playing
digging	investigating	sexual
drinking	orientation	urinating
face rubbing	paddling	vocalising

Social Behaviours

exposing eyelid SA
nursing SF
intervening SF
muzzle-muzzle SF

APPENDIX 4

FUNCTIONAL CATEGORIES : BEHAVIOURS INCLUDED IN EACH CATEGORY.

| FACTOR NO	CATEGORY	BEHAVIOURAL ELEMENTS
1	ACTIVE	Approach, approached, attacking, attacked, avoiding, avoided, biting, bitten, chasing, chased, chewing, chewing sa, climbing, climbing sf, eating, eating sf, following, followed, grabbing, grabbed, grooming (auto), grooming (allo), groomed, ignoring, ignored, investigating, investigating sf, interfering, joining, joined, jumping, licking, licking sf, presenting, presented to, pushing, pushed, redir. aggr, running, scratching, sexual, sitting, sitting sf, sniffing, sniffing sf, standing, standing sf, submission, supplanting, supplanted, threatening, threatened, touched, vigilant, vigilant sf, walking, walking sf, yawning.
2	PASSIVE	Huddling, lying down, lying down sf, touching.
3	PASSIVE CONTACT	Huddling and touching.
4	SOCIAL	Approach, approached, attacking, attacked, avoiding, avoided, biting, bitten, chasing, chased, coalition, chewing sa, climbing sf, eating sf, following, followed, grabbing, grabbed, grooming (allo), groomed, huddling, ignoring, ignored, investigating sf, interfering, joining, joined, licking sf, lying down sf, presenting, presented to, pushing, pushed, redir. aggr, sexual, sitting sf, sniffing sf, standing sf, submission, supplanting, supplanted, threatening, threatened, touching, touched, trav. per sf, vigilant sf, walking sf.
5	NON- SOCIAL	Chewing, climbing, eating, grooming (auto), investigating, jumping, lying down, running, scratching, sitting, sniffing, standing, travelling perimeter, vigilant, walking, yawning.
6	SOCIAL FRIENDLY.	Approach, approached, coalition, climbing sf, eating sf, following, followed, grooming (allo), groomed, huddling, investigating sf, joining, joined, licking sf, lying down sf, presenting, presented to, sexual, sitting sf, sniffing sf, standing sf, touching, touched, trav. per. sf, vigilant sf, walking sf.
7	SOCIAL AGONISTIC	Attacking, attacked, avoiding, avoided, biting, bitten, chasing, chased, chewing sa, grabbing, grabbed, pushing, pushed, redir. aggr., submission, supplanting, supplanted, threatening, threatened, yawning.

*   sa - social agonistic

    sf - social friendly

APPENDIX 5

STATISTICAL ANALYSES : DETAILS OF PRINCIPAL AXES FACTOR ANALYSES, WITH GRAPHS PLOTTING EIGENVALUES AGAINST FACTOR NUMBERS FOR THE APPLICATION OF THE SCREE TEST.

	DURATIONAL DATA					FREQUENTIAL DATA			
Factor	Communality	Eigenvalue	% variance	Cumulative %	Factor	Communality	Eigenvalue	% variance	Cumulative %
1	.295	2.775	8.7	8.7	1	.320	3.100	7.8	7.8
2	.256	2.432	7.9	16.6	2	.345	2.668	6.7	14.4
3	.196	2.175	6.8	23.4	3	.237	2.285	5.7	20.1
4	.206	1.939	6.1	29.4	4	.242	2.098	5.2	25.4
5	.147	1.680	5.3	34.7	5	.453	1.858	4.6	30.0
6	.481	1.593	5.0	39.7	6	.332	1.615	4.0	34.1
7	.186	1.509	4.7	44.4	7	.282	1.565	3.7	38.0
8	.240	1.321	4.1	48.5	8	.293	1.475	3.7	41.7
9	.259	1.233	3.9	52.4	9	.231	1.392	3.5	45.1
10	.224	1.164	3.6	56.0	10	.245	1.325	3.3	48.4
11	.204	1.088	3.4	59.4	11	.115	1.264	3.2	51.6
12	.226	.980	3.1	62.5	12	.290	1.166	2.9	54.5
13	.227	.933	2.9	65.4	13	.264	1.120	2.8	57.3
14	.215	.901	2.8	68.2	14	.160	1.087	2.7	60.0
15	.135	.883	2.8	71.0	15	.249	1.040	2.6	62.6
16	.406	.838	2.6	73.6	16	.198	1.008	2.5	65.2
17	.258	.790	2.5	76.0	17	.137	.967	2.4	67.6
18	.431	.764	2.4	78.4	18	.512	.907	2.3	69.8
19	.291	.746	2.3	80.8	19	.321	.869	2.2	72.0
20	.584	.688	2.1	82.9	20	.224	.846	2.1	74.1
21	.341	.658	2.1	85.0	21	.569	.813	2.0	76.2
22	.296	.618	1.9	86.9	22	.432	.791	2.0	78.1
23	.140	.578	1.8	88.7	23	.171	.750	1.9	80.0
24	.579	.562	1.8	90.5	24	.240	.746	1.9	81.9
25	.169	.520	1.6	92.1	25	.151	.685	1.7	83.6
26	.587	.488	1.5	93.6	26	.182	.670	1.7	85.3
27	.302	.468	1.5	95.1	27	.275	.629	1.6	86.8
28	.287	.426	1.3	96.4	28	.576	.608	1.5	88.4
29	.239	.388	1.2	97.6	29	.361	.528	1.3	89.7
30	.229	.309	1.0	98.6	30	.493	.517	1.3	91.0
31	.500	.272	.8	99.4	31	.171	.488	1.2	92.2
32	.499	.182	.6	100.0	32	.589	.467	1.2	93.4
					33	.151	.438	1.1	94.5
					34	.428	.415	1.0	95.5
					35	.335	.405	1.0	96.5
					36	.288	.362	.9	97.4
					37	.303	.292	.7	98.1
					38	.317	.287	.7	98.9
					39	.430	.247	.6	99.5
					40	.515	.210	.5	100.0

DURATIONAL DATA
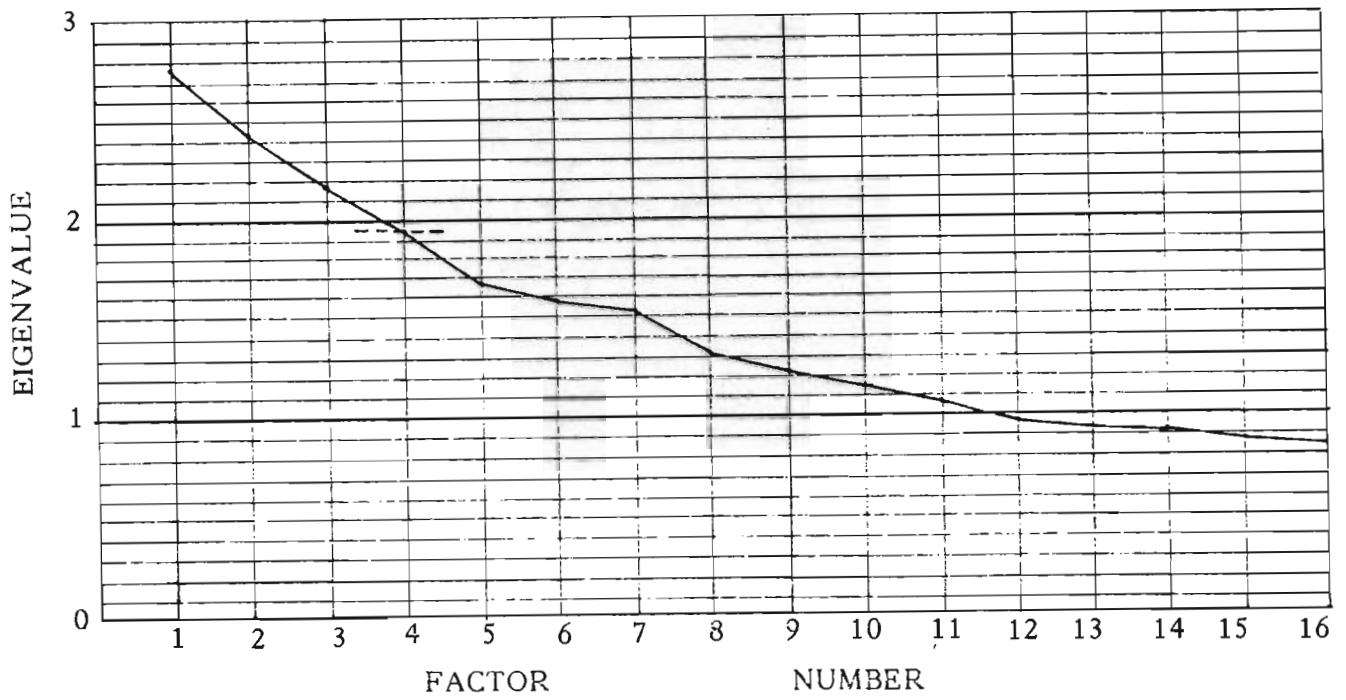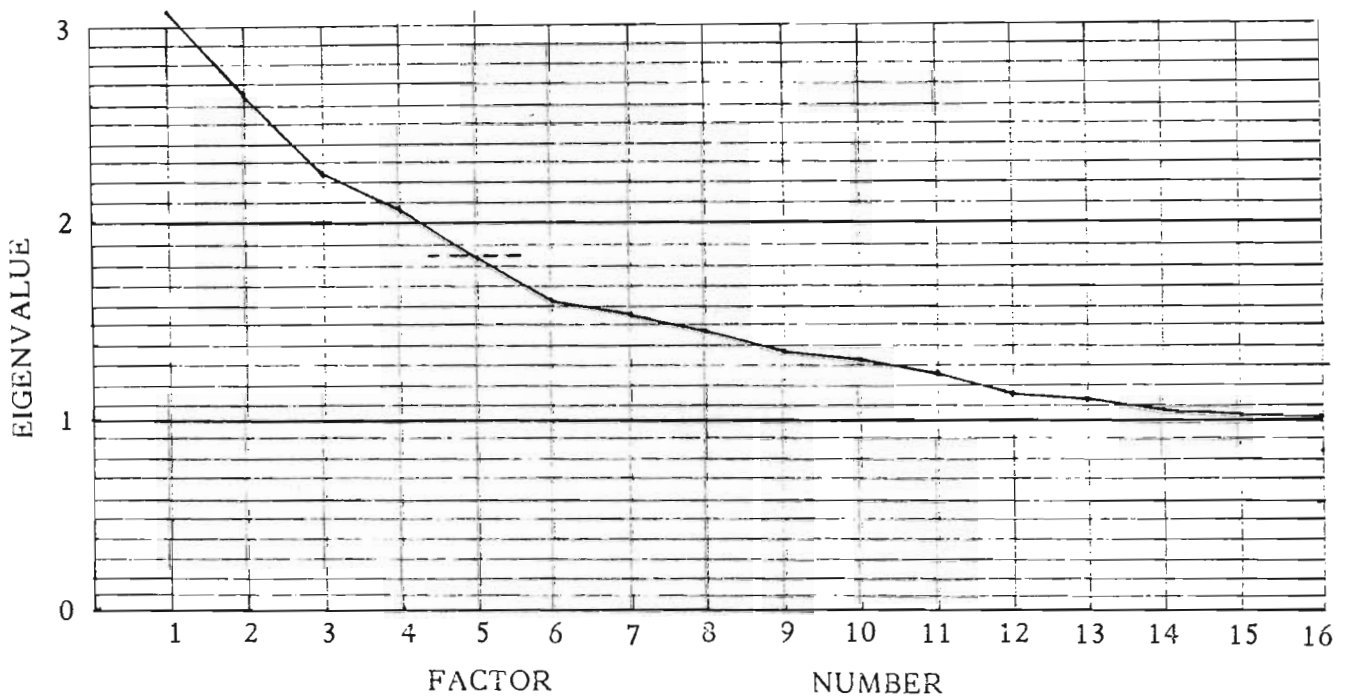
FREQUENTIAL DATA

GRAPH 6.1

SCREE TEST : PLOT OF EIGENVALUES WITH FACTOR NUMBERS.

APPENDIX 6

DERIVED FACTORS : BEHAVIOURAL LOADINGS FOR FACTORS FROM DURATIONAL AND FREQUENTIAL DATA.

1.   DURATIONAL DATA

Factor 1		Factor 2		Factor 3		Factor 4	
sitting	+0,55	climbing SF	+0,81	vigilant	+0,48	avoided	+0,67
trav. per	+0,49	vigilant SF	+0,65	scratching	+0,42	chasing	+0,38
standing	+0,45	walking SF	+0,62	sitting	+0,37	presenting	+0,34
walking	+0,37	huddling	+0,40	grooming	+0,34	walking	+0,30
running	+0,36	sitting SF	+0,37	(auto)		sniffing SF	+0,29
climbing	+0,35			yawning	+0,28	standing SF	+0,23
vigilant	+0,30			sitting SF	+0,20	grabbed	+0,22
eating	+0,20					trav. per	+0,22
				standing	-0,20	eating	+0,21
coalition	-0,28			eating	-0,20	joined	+0,20
groomed	-0,29			running	-0,46		
grooming SF	-0,70			trav. per	-0,47		

2.   FREQUENTIAL DATA

Factor 1		Factor 2		Factor 3		Factor 4		Factor 5	
walking	+0,65	climbing SF	+0,87	trav. per	+0,75	scratching	+0,51	standing SF	+0,43
sitting	+0,64	walking SF	+0,72	running	+0,65	grooming	+0,47	trav. per SF	+0,44
standing	+0,50	vigilant SF	+0,55	avoiding	+0,35	(auto)		grabbed	+0,37
eating	+0,42	huddling	+0,38	sniffing SF	+0,25	sitting	+0,43	sitting SF	+0,35
investigating	+0,39	sitting SF	+0,31	standing	+0,22	vigilant	+0,37	followed	+0,33
avoided	+0,31	coalition	+0,21			presented	+0,30	avoided	+0,30
climbing	+0,29			grooming SF	-0,20	to		sniffing SF	+0,26
vigilant	+0,28			avoided	-0,21	yawning	+0,22	joined	+0,25
jumping	+0,27					grooming SF	+0,22	grooming SF	+0,24
running	+0,20							groomed	+0,22
						eating	-0,28	touched	+0,20
groomed	-0,20					eating SF	-0,28		
coalition	-0,21								
grooming SF	-0,33								

* trav. per. = travelling perimeter
  SF   = social friendly

APPENDIX 7

SOCIAL BEHAVIOUR : CATEGORISATION OF BEHAVIOUR FOR USE WITH SOCIOGRAMS (see Chapter Seven).

FRIENDLY INTERACTIONS

INITIATOR		RECIPIENT		COACTION	
Matrix No.	Behaviour	Matrix No.	Behaviour	Matrix No.	Behaviour
1	approach	13	was approached	11	climbing
15	following	16	was followed	12	coalition
17	grabbing	18	was grabbed	21	huddling
19	grooming	20	was groomed	38	sexual
25	joining	30	was presented to	47	touching
40	sniffing	32	was joined	55	eating SF
		40	was touched	59	lying down SF
		40	was sniffed	60	sitting SF
				62	standing SF
				63	traversing perimeter SF
				65	walking SF

AGONISTIC INTERACTIONS

INITIATOR		RECIPIENT	
Matrix No.	Behaviour	Matrix No.	Behaviour
2	attacking	3	was attacked
6	biting	9	was chased
8	chasing	18	was grabbed
17	grabbing	34	was pushed
33	pushing	44	was supplanted
35	redirecting aggression	46	was threatened
43	supplanting		
45	threatening		

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