SOME ASPECTS OF VISUAL SIGNALLING AND SOCIAL ORGANIZATION IN THE VERVET MONKEY (Cercopithecus aethiops pygerythrus).

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Submitted in patial fulfillment of the
requirements for the degree of Doctor of
Philosophy in the Department of Psychology,
University of Natal, Durban.
June, 1982.

ACKNOWLEDGEMENTS.

This thesis is dedicated to my parents and John Lucas.

At the University of Natal I thank David Basckin, Peter Goodburn, Jane Kvalsvig, Christine Liddell, Frank Sutton and Shirley Tollman for friendship and assistance at various stages of the project.

At the University of St. Andrews several colleagues read and discussed drafts of this thesis. I thank especially Dick Byrne, Ivan Leuder, Jeff Graves and Andy Whiten.

Professor Roger Short and Doctor Irwin Bernstein gave detailed replies to specific questions. I am grateful for their help.

The project was supported by an H.S.R.C. postgraduate bursary. Opinions expressed and conclusions reached are those of the author and are not to be regarded as reflecting the opinions and conclusions of the H.S.R.C.

Finally, by putting up with me in the final stages of the write-up, Dave and Anne established British tolerance and imperturbability as a fine art. Undying gratitude hardly evens the score.

CONTENTS.

ABSTRACT.

This study uses data from three free-ranging and one caged troop to describe the visual signals identified in the South African subspecies of vervet monkey (Cercopithecus aethiops pygerythrus) and to then compare them to those seen at other localities and in other species. It further assesses some signals used specifically by adult males - those involving secondary sexual characters - in terms of male social strategies. In the pursuance of this four aspects of the literature were reviewed in detail. It is concluded that:

1. Natal vervets use fewer visual signals that do other species living in more open habitat. These signals are, however, very similar to those recorded in East Africa, while differing more from those isolated in the West African representative of the vervet group.

2. Vervet troops are not closed units and 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.

3. The signalling function of the genitals does not accord with that ascribed to them by Wickler (1967). Penile extensions are closely associated with aggressive behaviour by the signaller, and scrotal retractions with submissive behaviour. Associated with these structures are displays that facilitate their presentation to the recipients.

4. While males yawn more than any other age-sex class, largely for social and not physiological reasons, there is no clear evidence that yawns serve specifically to display the canines. Nevertheless, by being strongly associated with certain interactions they are presumed to accrue signal value.

5. As males move into troops where they must compete with unrelated males for the same resources, it is concluded that the genital signalling system has evolved to mediate male relationships. This is of special significance as the 'multimale' system of vervets is regarded as being less developed than those of Papio or Macaca monkeys.

CHAPTER 1.

THE AIMS OF THE STUDY.

Social life, with all the competition and cooperation that comprise it, is not possible without communication among the participating individuals. Insofar as animals must interact to achieve both proximate and ultimate goals, an understanding of how they do so is not possible without an understanding of the ways in which information is made available.

Consequently, when research on primate social behaviour escalated in the early 1960s one dominant line of investigation picked up Darwin's pioneering interest in 'expressive movements' while reassembling it within an ethological framework (see van Hooff, 1962). Following the work of Altmann and Hinde and Rowell a number of behavioural repertoires were compiled, comparisons of which revealed that primates place great reliance on the visual signalling modality (Wilson, 1975) and that there is aclear evolutionary development in complexity within the order (Andrew, 1963a,b). Arising from this are basic questions concerning both the fixedness of form and usage of visual signals and the way in which specific signals are utilized - and have evolved - to advance an individual's reproductive fitness through the mediation of social relationships.

The vervet monkey (Cercopithecus aethiops) is an excellent candidate for research into such questions. It has been studied in a number of localities and two comprehensive ethograms exist for it (Struhsaker, 1967b; McGuire, 1974). It is also a species of the 'forest edge', subject to lower levels of luminance, something that may well affect the structure of its visual signals. Vervet social organization is additionally interesting in that, unlike other guenon species (excepting Miopithecus talapoin), in that it is 'multi-male'. This is to say that groups of females have associated with them more than one adult male (Crookand Gartlan, 1966). The implication of this must be that vervet males interact differently than do males in species with 'uni-male' heterosexual groups, despite the fact that they share with many of them conspicuous sexually dimorphic characters (coloured genitalia, large canine teeth) that have already been posited to have visual signalling capabilities (Wickler, 1967; Gautier and Gautier, 1977).

While data were gathered from four vervet troops, it is principally information gathered from a free-ranging troop, under observation since 1973, and a caged group, established in 1975, that is utilized in pursuance of two specific research objectives.

1. The minor aim of this study is to compare the behavioural repertoire of vervet monkeys in Natal, South Africa with those isolated in other populations and to then compare the facial expressions of vervets with those seen in other species.

With the exception of the rhesus macaque (Reynolds, 1976), species signal 'vocabularies' have usually been based on one or two studies only. Given evidence of the order's behavioural plasticity (Stephenson, 1973), it seems important that repertoires be compared at several different sites, especially since much of the work on social organization relies on such accounts. The comparison of Natal vervets with other subspecies - and it is here assumed that C.a. sabeus is at least a member of the vervet superspecies - will allow the degree of variability to be assessed and provide a reference that may be consulted by future workers.

The interspecific comparison arises out of the suggestion generated by lists of primate expressive gestures in the literature that forest monkeys have simpler repertoires than savannah or terrestrial ones. A proper comparison has yet to be made and facial signals, given their communicatory prominence and structural regularity, appear to provide a useful focus.

The aim of this aspect of the thesis is primarily comparative and as such, given the absence of quantification in the literature used, has had to be pursued qualitatively and descriptively. While this is unavoidable it is at odds with current practise which makes it worthwhile to reiterate Vines's point (1970) that quantitative comparison of the signals of different species holds little meaning when the focus of the comparison is the signals themselves rather than their social utilization.

2. The major aim of the study is to take the sexually dimorphic characters of males as examples and to examine their signalling functions with reference to male life-history strategies.

Work on signalling systems was meant to build on the base provided by ethograms in such a way as to indicate, through the establishment of communicatory networks, the structure of the society.

In this regard the work of Struhsaker and Seyfarth on the formation of coalitions in vervets, and work on the social consequences of threat in macaques by Dittus, reveal that complex processes are mediated by relatively simple signals. Careful consideration of the social use of signals, coupled with some understanding of the pressures placed on individuals in attempting to maximise their fitness, helps to identify both the message carried in the signals and the means whereby the signaller is coping with the pressures.

Insofar as the true structure of a society can only be gauged by understanding the patterns of communication that connect individuals (Altmann, 1968) it might seem best to analyse all extracted signals in this way. However, the relative difficulty of assessing factors bearing on female sociality, where there are kinship ties and long-term dynamics not detected in short-term studies, and the general advisability of analysing the sexes separately at first in order to understand the system as a whole (Wrangham, 1980), suggest that concentration on males and on a few clear signals may provide the best illustration of the way in which all signals should be treated.

That male vervets move between troops (Struhsaker, 1967c), presumably to promote reproductive fitness through exogamy (Harcourt, 1978), and must therefore deal with potential competitors within the troops into which they move, provides us with the necessary backdrop against which to view both the evolution of the epigamic characters and their communicatory function. After data has been presented on the nature and degree of male affiliation to particular troops the contexts in which the signalling structures are displayed will be described and a message- meaning analysis (Smith, 1968) attempted for each. It will be asked how such signals mediate male interactions and why these interactions assume the forms that they do. From the data obtained an attempt will be made to define more precisely the social structure of male vervet monkeys.

CHAPTER 2.

LITERATURE REVIEW.

1. INTRODUCTION.

"Social communication is...a process involving the transmission of interpersonal signals which sets up a relationship between the behaviours of the participants" (Vine, 1970; pg. 286). In this way, for a communicatory episode to occur, we need a signaller, a recipient and a medium or channel for transmission (Smith, 1977). Visual communication is therefore the transmission of information in a way reliant on the properties of light, and dependent on the visual capabilities of the recipient for successful reception.

Almost anything an animal does - the tensing of muscles, performing of a behaviour out of its usual sequence, even normal, ongoing behaviour - can constitute a visual signal and be used by the recipient to predict the future behaviour of the sender (Hailman, 1977). This study adopts Smith's approach which is that in many obvious cases of information exchange it is difficult to assess the degree of intention or direction. By taking an information-processing perspective we are able to avoid the difficulties of a motivational approach and work, instead, with the obtaining of information through more-or-less formal means. While acknowledging the importance of informal data acquisition (as Hinde has done - Hinde, 1981) Smith points out that it is most productive to begin work on communicatory systems by working on "formalized" transmissions (cf the F.A.P.S of the ethologists) where it is easier to see what is involved (Smith, 1977).

2. THE VISUAL MODALITY.

Within the limits set by vertabrate optical systems the availability of light has allowed the majority of vertabrates to develop the visual channel Marler, 1968). Consequently it is not surprising that species have evolved signals and communicatory systems that exploit this (Hailman, 1977).

2.1. Optical Signals. Hailman (1977) differentiates optical signals into those that have a physical existence independent of their creator, such as footprints (extrinsic), and those that are part of the animal itself (intrinsic).

Intrinsic signals are described by three primary dimensions:

i. The orientation of the signaller, or some part of it, with respect to the recipient;

ii. The shape or configuration of the animal. This in itself is derived from the component parts;

iii. The movenent patterns of the sender or its parts.

Some signals will depend primarily on one of these dimensions whereas others will utilize various combinations.

These mechanisms are used to create bodily shapes , and Haiman (op cit.) identifies them as :

a. Motor adjustments of bodily parts;

b. Pilomotor responses of fur and

c. The inflation of structures with air.

In addition to behavioural transformations but often operating in conjunction with them are:

i. Structural elements that alter shapes. These include those used for other functions as well as those that appear specialized for signalling ("social releasers"; Tinbergen, 1951).

ii. Surface elements that reflect light and are divisible along two dimensions according to the kind of stimulus that they create and the degree of permanence that they achieve (Hailman, 1977).

Marler (1968) lists the stimulus variables available to such reflected light signals as wavelength (colour), intensity (brightness), degree or plane of polarization and spatio-temporal patterns of stimulus delivery. Such surface elements may be used, and have been evolved, to create specific brightness contrasts, colours, shapes or orientation of shapes. Kingdon (1980) notes that combinations of agouti banding, pigments, hair tracts and hair length have produced particular visual effects in closely-related guenons, that rely on reflecting light for their effect.

The permanence of surface elements can be considered along a continuum that extends from permanent display, through labile display of a season´s duration to modulated display that may vary withing the course of a single day (Hailman, 1977). The point along the continuum that is not mentioned, as which is of importance in primate communication, is infantile colouration that shifts slowly towards a final, adult, state (see Alley, 1980). The concept is that of a phased decay of one set of features and the simultaneous emergence of another and is one which deserves more attention.

Unitary optical signals are usually formed through combinations of structural, surface and behavioural elements. The form of such a signal in any given context is very much a function of considerations such as the need for successful transmission to a receiver, accurate identification of the signal type, selection among the potential audience for a specific class of respondent as well as the particular type of response that the signal is required to elicit (Marler, 1968). Re-stated this means that the design of a display (used here to mean the emitted combination of physical and behavioural elements) is shaped not only by the physical characteristics of the environment and the medium of transmission, but by the the specific qualities of the social milieu as well.

2.2. Comparison of Modalities. Three factors may promote the use of specific modalities: the environment of signalling, the kinds of animals involved, and the functional use of the communication (Hailman, 1977). Marler (1967) shows that the usefulness of modalities may be restricted by an animals´s habits. A nocturnal species will have less use for the visual channel than a diurnal one and tactile signals will be of less general importance in a species whose members are solitary. At the same time the different sensory modalities have certain intrinsic advantages and disadvantages.

The great sensitivity of odour receptors and the durability of chemical signals give olfaction a special advantage in communication over distances. Auditory receptors are also very sensitive and auditory signals, as with chemical ones, can have energy directed into their production so that their intensity can be raised above that of `noise´ in the environment. The intensity of visual signals, while conspicuousness can be maximised, is limited by ambient lighting (Marler, 1967; Hailman, 1977). This seems a spurious distinction insofar as signals in all modalities need to compete with other stimuli, whether social or environmental, and, while luminance may handicap visual signals, differences in performance intensity - and therefore in energy-output - are as possible in the visual mode.

Visual signals have limited nocturnal value and are more easily blocked by vegetation and other obstructions than are chemical and sonic signals. Vision therefore appears to be the least satisfactory medium for long-distance communication.

Visual signals are, on the other hand, very easy to localize. Geldard (1960) refers to vision as the "great spatial sense"as localization is less accurate with sound and generally slow and uncertain with olfaction.

Such high indexical qualities permit the use of spatial patterns to a degree inconceivable in the other modalities (Hailman, 1977). Compound signals with many simultaneous, separable elements can be exploited fully to generate an immensely complex and extensive repertoire, where independent variation of the elements is possible (Marler, 1967). That this is so, even for cognitively simple species is demonstrated by Wiley´s (1975) study of the "song-spread display" of the carib grackle (Quiscalus lugubris). Two components - beak and wing elevation - varied independently and strongly depended on the social circumstances surrounding the performance. It is concluded that this independence permits an increase of information about the performer´s state issuing from each performance of the display. This richness is increased even further when the variables of colour, brightness and patterning are considered.

Visual coding is therefore to be used when:
i.the message involves spatial orientation or guidance;
ii.fine discrimination is needed and
iii.recipients must make a relatively prompt selection of data from a large array of information (Geldard, 1960).

In summary, diurnal animals, living in a fairly open environment, with a relatively close-knit society and a complex social organization:

"are best qualified to exploit the subtleties of a signal complexity possible in visual communication. These qualifications are well met in some of the higher primates and it is no accident that some of the greatest complexities of communication in such animals as baboons and macaques are being found in visual systems" (Marler, 1967; pg 773).

There are, nevertheless, two drawbacks associated with the use of the visual channel. Firstly the signalling animal must be conspicuous, both morphologically and behaviourally, and thereafter susceptible to a greater risk of predation (Marler, 1965; Gautier and Gautier, 1977; Kavanagh, 1981. The Gautiers and Kavanagh point specifically to the conspicuousness of displaying male monkeys as an example of this). Redican (1975) regards this possibility as being counteracted by the primary use of visual signals in close-range interactions. The second complication is that the intended recipient needs to be looking at the signaller in order to get the signal.

Modalities do also not act exclusively of one-another and the interplay between audition and vision, in particular, should not be forgotten (Redican, 1975). Some primate facial expressions are even distinguished by the vocalizations that accompany them (Van Hooff, 1967) and Marler (1965) suggests that close-range vocalizations may function to get the attention of the recipient who is then in a position to get more information visually. Wickler (1978) while agreeing with Marler that such interaction is both sophisticated and a common feature of primate communication stresses that there may be constraints on the evolution of such signals. This will be due to the speed at which different modalities operate and the differential attenuation of signals over distance. As the time lag increases synchronous arrival will become less possible to guarantee if the sender does not know the exact distance or wishes to address several receivers at different distances simultaneously. There are two ways in which a sender can overcome such zonation of broadcasting: by moving around and by avoiding a stable time relationship between the components from different modalities. From this Wickler challenges Marler´s assertion that composite signals are a feature of close-range communication because subtle properties would be lost at distance. Instead, Wickler argues, because of the known visual acuity of primates, the phenomenon must be more because visual signals cannot be bound to their sound counterparts at greater distances. This makes it more efficient to choose high information density within sensory modalities.

2.3. Colour Vision. The phylogenetic development of colour vision is somewhat discontinuous; within the vertabrates it is represented in all orders, with special prominence in the teleost fishes, lizards, turtles, birds and higher mammals (Gruber, 1979).

The concept of colour includes perceptions of hue, saturation and brightness abstracted from the total visual experience and scaled along a specific dimension of colour (Gruber, 1979). From this is realized the importance of physiological mechanisms and subtle perceptual factors.

Given its convergent evolution in many unrelated phyla the analysis of wavelength variations of light must clearly be of functional significance. At least part of the selective advantage of colour vision has to do with the perception of contrast, an extremely important visual process. Hartline demonstrated that the visual system is set up to analyse contrast (Hartline and Rutliff, 1972) and Walls (1942) had already explained the way in which colour vision enhances visibility, which is a perceptual correlate of contrast.

The value of colour vision, in higher primates at least, is said, by Gruber (1979) to reside in "the approximately 160 new qualities" with which the external world can be characterized. Although the derivation of these qualities is not explained they will translate out into several million discriminable colours if all levels of saturation and intensity are included. In this way they constitute a powerful analytical mechanism.

3. THE VISUAL CAPABILITIES OF PRIMATES.

Primates are usually classified as very "visual" animals insofar as they depend largely on vision both for orientation in space and for object recognition (DeValois and Jacobs, 1971; Wilson, 1975). Most other mammals have a less well-developed reliance on this one sensory system (see Wilson, 1975). An anatomical counterpart to this visual emphasis is that in primates a very large proportion of the input to the central nervous system comes up the optic nerve (DeValois and Jacobs, 1971).

3.1. Brightness Vision. Brightness is a basic property of the visual response; comparisons of primates have used measures of spectral sensitivity and brightness discrimination and contrast. For some Old World monkeys it has been found that scotopic sensitivity peaks at about 510 nm. and drops off sharply thereafter (Blough and Schrier, 1963; Adams and Jones, 1967). Photopic spectral sensitivity curves tend to peak at 520-560 nm. (Schrier and Blough, 1966; Adams and Jones, 1967). Importantly the tests used produced very similar results in humans.

3.2. Colour Vision. Almost all studies of colour vision in the cercopithecoidea have used macaques and all have indicated that the animals are normal trichromats with excellent colour vision. This again is virtually identical to that of normal man, something which is clearly of importance when working on a particular species' visual signals.

3.3. Visual Acuity. Monkeys have a prominent area centralis, consisting of small but densely-packed cones around the central retinal axis, that permits excellent resolution of detail and depth (in conjunction with the frontality of the eye-orbits; Vine, 1970).

4. THE ELEMENTS OF PRIMATE VISUAL COMMUNICATION.

4.1. Introduction. As with so much else Charles Darwin transformed the study of expressive behaviour by applying to it the evolutionary principles that directed his analysis of speciation and by perceiving that behaviour, in the same way as morphology, was under selective pressure. His The Evolution of the Emotions in Man and Animals (1872) is the point of departure for ethological work on communication and provides a detailed and particulate description of expression underpinned by three important principles:

a. The principle of serviceable associated habits. Complex actions, of service under certain states of mind , may habitually occur, even if at a lowered intensity, whenever that same state of mind is induced. This will happen despite the fact that their evocation is not functional. These movements and the movements that may be used to check them are "expressive" through their association with particular states of mind.

b. The principle of antithesis. States of mind that are directly opposite have associated with them habitual actions that are also physically opposite . Darwin regarded these oppositions as being of no practical use and therefore primary expressive.

c. The principle of direct action of the nervous system. Excess energy in a strongly excited "sensorium" is liable to be transmitted in definite directions and the effects produced are again of predictive value.

Ironically, the major flaw in this lay in Darwin´s acceptance that non-Darwinian (Lamarckian) selection was, in part at least, necessary to explain the acquisition of reflex gestures (Barnett, 1958). He wrote:

"for although some instincts have been developed through long-continued and inherited habit, other highly-complex ones have been developed through the preservation of variations of existing instincts." (pg 42).

Not withstanding this, the recognition that non-communicatory behaviours can gradually acquire signal function was fundamental and had to wait 70 years before it was exploited by the ethologists, who either developed some of the theory (Lorenz, in particular, used the principle of direct action in developing his hydraulic model. See Hinde, 1970 for a critique of this), or showed to what degree complex behaviours could evolve purely through Darwinian selection (Tinbergen, 1951).

Of major importance to this thesis is Darwin's interest in the signalling behaviour of monkeys. While anthropomorphic ("from the expression of his eye I felt sure that he was savage") he recognises the continuity of human and non-human gestures and establishes it as complex, thereby opening it up as a topic for exploration.

Modern ethologists took Darwin's ideas and developed from them the concepts and language with which we still describe communicatory processes - fixed-action-patterns, ritualization, releaser mechanisms, displays etc (Tinbergen, 1951; Morris, 1957) - but it was not until the early 1960's that work on visual signals, especially facial expressions, began to be published (Altmann, 1962; Hinde and Rowell, 1962; van Hooff, 1962; Andrew, 1963; Bolwig, 1964).

4.2.. Facial Expression. The reason for this specific interest in facial expressions is due to their immediacy; their signal properties are apparent to any observer and morphological corroboration of this is to be found in the highly-developed facial musculature of the primates (Andrew, 1964; Bolwig, 1964).

Andrew argues that the importance of facial expressions in the evolution of primate societies is evidenced by the fact that all the main types of display components, with the exception of facial expression, appeared in primates before the development of true societies. The strong selection pressure against major changes in facial musculature and anatomy and the resulting disturbance to their other functions could only be overcome by an even stronger need for efficient communication.

This differentiated musculature controls movement of the scalp, eyebrows and mouth with such precision that the primates exhibit a subtlety and variety of expression not matched by other vertebrates and appears to have come about because:

a. In complex social systems flexibility is needed (Humphrey, 1976) and therefore signal systems capable of fine changes are advantageous and will be selected for.

b. The evolutionary trend towards greatly increased frontality of the eye-orbits (stereoscopic vision) has led to a decrease in the size of the visual field. Bolwig (1964) stated that this, combined with the use of the mouth as an offensive weapon, made it important to concentrate the area of visual expression to the smallest possible extent.

c. The musculature controlling the vibrissae and nose (Andrew, 1964) in pre-primate ancestors could be freed for signalling purposes once diurnality and binocularity had lessened the importance of the vibrissae as gatherers of information. It must be noted that this argument of Andrew's is a little at odds with his other view that facial expressions were so advantageous as to override other sources of information. It does seem more likely that the decline of the other senses has led to the accelerated deployment of visual signals.

Conventionally displays were seen as the ritualized intention movements of agonistic or sexual responses (Tinbergen, 1952). While agreeing that display components reflect much of the causation of the responses from which they derive, Andrew (1963a,b) has argued convincingly for the part played by "protective responses" in the evolution of signals. Essentially these account for the evolution of signals associated with fear or the likelihood of attack. Thus flattening the ears and closing the eyes provide a means of protection for these organs, while "grinning" serves to expose the teeth ready for retaliation. Similarly eye-brow lowering may protect the eyes, assist in achieving convergence of the optical axes (Andrew, 1963a,b) or exclude excessive lateral light (Darwin, 1872). Little more has been done on the evolution of facial expressions largely, one supposes, because the processes involved can only be inferred.

The primary concern of work on facial expression has been with cataloguing structure as well as signal absence or presence in a variety of species. Below are listed studies that go at least some way towards providing a comprehensive catalogue of facial expressions (and other visual signals). C indicates work on captive groups and F work on free-ranging animals.

A. MACAQUES.

M. mulatta - Hinde and Rowell, 1962.C; Reynolds, 1976.C; Altmann, 1962.F.

M. Fascicularis - Shirek-Ellefson, 1972.F; Angst, 1974.C.

M. arctoides - Bertrand, 1969.C.; Chevalier-Skolnikoff, 1974.C.

M. nemestrina - Goosen and Kortmulder, 1979.C.

B. BABOONS.

P. anubis/ursinus - Hall and De Vore, 1965.F.

C. COLOBINES.

P. entellus - Dolhinow, 1978.CF.

P. johnii - Poirier, 1970.F.

C. guereza - Oates, 1977.F.

C. badius - Struhsaker, 1975.F.

D. MANGABEYS.

C. albigena - Chalmers, 1968.F.

E. GUENONS AND ALLIES.

C. aethiops - Struhsaker, 1967b.F; McGuire, 1974.F.

E. patas - Hall, 1965.F; Hall et al, 1965.FC.

M. talapoin - Wolfheim and Rowell, 1972.C.

The form of these compilations is similar insofar as they provide information on structure of the expressions and the social circumstances associated with their use. Interspecific comparison has relied on the major synthetic analyses of van Hooff (1967) and Redican (1975) who have used both the catalogues available and incidental data to show that, with the exception of a few species-specific expressions, there is a surprising degree of uniformity in the gross physical representation of facial expressions across species although not all species use all of them (van Hooff, 1967). Table 2-1 lists the facial displays isolated by previous workers. Since different workers use different names (Reynolds, 1976) I have stuck to those provided by van Hooff, except where he does not include an expression or where there is a more-widely used alternative.

Redican (1975), in contrast to van Hooff and others lumps categories, making the important point that the various components of a facial `display´ may all occur or may (especially in threat) be seen "more-or-less" independently, making it potentially limiting to view facial expressions as fixed clusters of elements. Nevertheless these are clearly perceived and perhaps each element is best seen as having the ability to vary slightly from a modal aggregation of elements which we may regard as a `type´ expression. Barlow (1977) takes this approach in arguing that supposedly fixed "fixed-action-patterns" contain variability and are better re-defined as "modal-action-patterns" (MAPs).

From the table and the literature it is clear that the unchanging and therefore central feature in defining such MAPs is the <u>mouth</u>, and that the other facial and associated bodily

On the next 2 pages:

TABLE 2-1: A listing of the facial expressions generally isolated and regarded as communicatory.

NOTES:

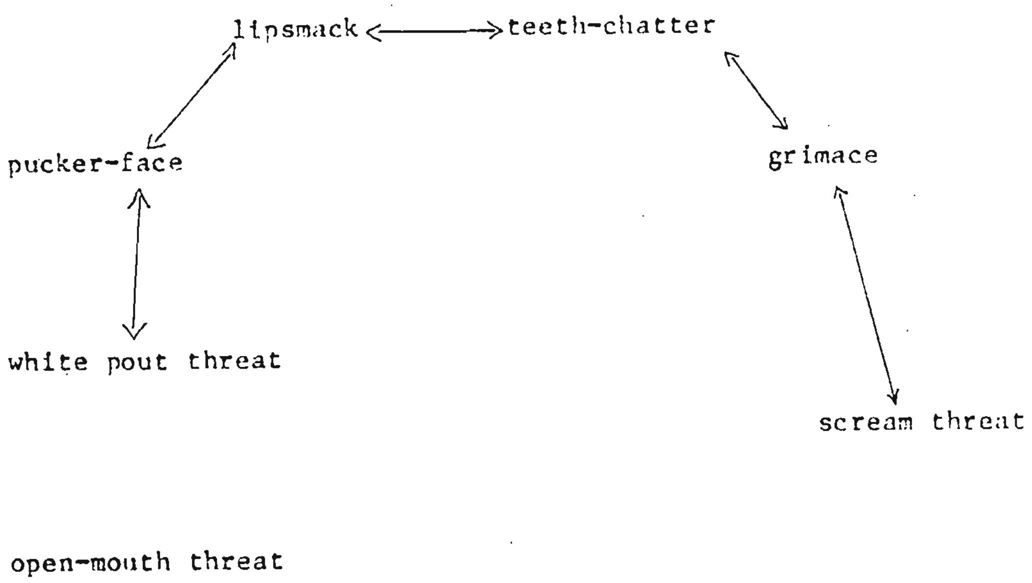
1. Van Hooff refers to this as the "relaxed open-mouth face".
2. Van Hooff does not regard this as a communicatory expression (Redican, 1975).

SIGNAL NAME.	EYES.	EARS.	MOUTH.	VOCALIZATION.	POSTURE.	CIRCUMSTANCES.
1. Relaxed Face	Neutral No rapid movement or fixed gaze	neutral	closed, relaxed	none	several, no tension	indicates relaxed animal.
2. Alert face	Fully opened	--	a degree of tension	none	raised muscle tonus	many situations, mostly concentration
3. Tense mouth F./ Threat stare.	Stare at recip, eyebrows raised. Eyelids exposed.	flattened	closed, tense. Jaw may be thrust forward. Lips forward.	usually silent	variable, bobbing.	threat - by dominant animal.
4. Staring open-mouth face	Stare, brows lifted. Lids exposed	retracted	open, lips tense. Teeth not show, jaw forward	poss. grunts or barks	variable; repeated bobbing. Piloerection possible	mostly dominant threat.
5. Silent bared-teeth face	evasive, "peeking" or stare	retracted	closed ,lips + mouth corners retracted	none	forward and erect. Also hunched	1. recipient of aggro. 2. male, during copulation 3. during greeting or est. contact.
6. Staring bared-teeth scream face	stare, brows lifted	retracted	open wide. Lips and mouth corners fully retracted	shrill scream	vary; often strongly hunched. Poss. piloerection	response to severe aggro. Redican sees as intermediate between 4 and 5.
7. Frowning bared-teeth scream face	closed; brows lowered	retracted	open as 6 above	shrill scream	hunched	reaction to imminent or actual attack and may alternate with flight.

SIGNAL NAME.	EYES.	EARS.	MOUTH.	VOCALIZATION.	POSTURE.	CIRCUMSTANCES.
8. Gecker face	as 5.	as 5.	lips may not be completely vertically retracted	"gecker" or "chutter"	variable	"mild fear" or anxiety
9. Lip smacking face	staring, but head may be turned	poss. retracted	rapid opening + closing; mouth corners forward.	tongue movement produces audible "smacking"	variable	during grooming or approaching a dominant. Seen as appeasing or placatory
10. Teeth-chattering face	staring or evasive. Brows poss. retracted	retracted	opens + closes. Teeth meet	audible teeth chatter	hunched or broadside	More intense version of lipsmack, common in macaques
11. Protruded lips face	staring or evasive but brows lifted completely	retracted	closed. Lips protrude + mouth corners forward	none noted	forward tendency. Head tilted up	Peculiar to a few macaques. Used by male during mating and alternates with 9 in social encounters
12. Pout face	Directed to partner ; brows lifted	not noted	slightly open, corners pulled forward + lips protruded	"oooo"	relaxed or forward	typically an infant expression suggested to express need for comfort or food.
13. Play face[1]	mostly not fixed	not noted	wide open, lips generally cover teeth	none	variable - "play"	occurs during play.
14. Yawn[2]	open but closed at climax	back	opens smoothly, lips cover teeth until mouth at widest point and then they draw back to reveal teeth.	none	variable, head thrown back	elicited as display during conflict or stress. When directed is regarded as canine display

elements vary within precise limits (see Goosen and Kortmulder, 1979).

Shirek-Ellefson (1972) anticipates Stringer (1973) in suggesting that while element clusters provide clarity, they are still morphologically linked along a continuum which makes it easy to shift expression to match slight changes in motivational state. This is illustrated in her diagram represented below:



The fact that she does not link open-mouth threat to white pout threat suggests a jump to a different level. While such linkage allows great flexibility it does not result in ambiguity, largely because interpretation is reliant on an assessment of social "context".

It remains to be seen whether the alternative stance - that facial expressions are static but may be more precisely defined than they are now - will be validated. This approach, that there will be a one-to-one mapping of expression and response, was followed by Goosen and Kortmulder (1979) who subsequently isolated more facial expressions in *M. nemestrina* than reported in any other primate. However, examination of their data still reveals considerable variability in the transition frequencies of responses to facial expression and, in addition, they have to collapse categories to make the data amenable to analysis. Such variability is important and Shirek-Ellefson is correct to point out that responses to signals have not been well-studied. It remains to be seen how much of the variation is significant and responded to and how much of it is an artefact of descriptive methods.

One thing not in doubt is the central importance of eye-contact in facial-visual communication. A direct stare is a universal component of threat. While merely looking at another animal is not threatening, it can become so through even a slight prolonging of the gaze (Struhsaker, 1967b; Altmann, 1962; Bertrand, 1969; Chalmers, 1968b). Its efficacy has been demonstrated physiologically by Wada (1961) who found that a macaque could, and did, suppress an electrically induced brainstem response as long as the experimenter's gaze was fixed on it.

Along the same lines, and following Darwin's antithesis principle, is the finding that the most frequent response to eye-contact and threat is immediate gaze-aversion. Chance (1962) suggested that such aversion literally "cuts-off" any threatening social stimuli and prevents further perceptual arousal, thereby reducing the tendency to flee without having to move physically. Redican (1975) rightly adds that gaze-aversion must have vital effects on the motivation of the other individuals involved insofar as they are not presented with threatening stimuli. It is regarded as a submissive gesture in primates (Altmann, 1962; Rahaman and Parthasarathy, 1968).

Of equal interest is the debate as to whether a yawn constitutes a facial expression. Darwin (1872), regarding the exposure of the canine teeth as having a "secondary intimidating effect", thought that it did. More recently some workers have denied it a serious communicatory purpose generally (van Hooff, 1967 - by exclusion) or because it did not appear as such for the species on which they worked (Hinde and Rowell, 1962; Struhsaker, 1967a; Poirier, 1970; Shirek-Ellefson, 1972; Cevalier-Skolnikoff, 1974; Dolhinow, 1978). Its relevance as a signal has, on the other hand, been clearly established in other species (Hadidian, 1980; Gautier and Gautier, 1977; Redican, 1975; Chalmers, 1968b; Hall et al., 1965; Oates, 1977; Wolfheim and Rowell, 1972; Hall and De Vore, 1965).

Altmann (1967), in accepting the implication of social function, listed three types of yawn in primates: "true" yawns; yawns occuring in conflict or anxiety-producing situations; and yawns which carry semantic messages (threats involving a show of teeth). Since the motor patterns involved with the behaviour do not vary from one type to another the classification of yawns must be made on a contextual basis (Hadidian, 1980).

Tension yawns are characteristic of animals under stress - such as that induced by the arrival of human observers - and are typically "non-directed" (Hall, 1967; Hadidian, 1980). As such they appear to be indicators of arousal. Threat yawns are more specifically directed towards the recipient and, in baboons, may be accompanied by threat gestures such as ear-flattening and eye-brow raising (Hall and De vore, 1965). Chalmers (1968b) demonstrated that black mangabeys were more likely to flee after giving non-directed yawns than after directed ones. This lends support to Hall's distinction between the former as a sign of stress and the latter as a threat.

The fact that adult males yawn more frequently than any other age-sex class (Hadidian, 1980; Dixson, 1977; Wolfheim and Rowell, 1972; Struhsaker and Gartlan, 1970; Durham, 1969), coupled with the pronounced sexual dimorphism in the size of canine teeth among the cercopithecoidea (males have the larger - Napier and Napier, 1967), suggests that the yawn functions to display male canines and that this display, in turn, is deployed in social circumstances where it is immediately amenable to the operation of sexual selection (either intra- or inter-; see Crook, 1972).

Hadidian (1980), who produced a quantified account of yawning in M. nigra, denies its exclusive function as a canine display as it occurs prior to the emergence of adult canine teeth and is also used by females, although at a lower rate, in the same circumstances that elicit them in males. He sees it as serving to reveal all the teeth (which are a monkey's most prominent weapons; see Saayman, 1971), but concedes that the message content of the display is still far from clear. Nevertheless, Gautier and Gautier (1977) on information got from Deputte feel that it might function less as a threat (in Ce. galeritus at least) than as an indicator of status among males.

Packer's (1979b) data on P. anubis is the most pertinent to the sexual selection hypothesis. He found that the frequency of performing a non-directed yawn within 5m. of another male was correlated with the condition of the displayer's canines but not with his age. "Thus males with the best canines displayed them most often to other males, and males, therefore, had the opportunity to appraise eachother's canines" (pg 42). He further found that in each of three pairs of males of the same age the male with the better canines was also the male with the higher overall consorting activity. This is likely to arise out of the importance of canine condition for fighting competence and, consequently, the ability to ward off competition during consortship. In contrast, Alexander and Hughes (1971) showed that while canines might have played a role in the self-defence of low-ranking males, their extraction did not hinder the attainment or maintainance of high rank in corralled Japanese macaques. From this it can only be concluded that the message-content varies among species or that, if unitary, is still only imprecisely delineated.

4.3. The Body.

4.3.1. Static Features. Without its behaving in any way, a monkey's species, age, sex and individual identity are available to any informed observer. Different species, even sub-species, have pelage colouration and structures sufficiently distinct (see Napier and Napier, 1967) to allow conspecifics to recognise one another, even where closely-related groups are sympatric.

Kingdon (1980), for example, discusses the geographical overlap of two C. mona-group species that has come about because of the rejoining of forest communities. While they are so closely-related that hybrids are occasionally seen, they are differently coloured and have differently shaped ear tufts. These, in combination with highly-ritualized movements, are presumably adequately sufficient to keep the species distinct.

Pelage colour also changes ontogenetically, allowing reasonable age estimation (Rasmussen, 1979; Krige, 1975) and the elicitation of age-appropriate interactions (see Krige, 1975). Neonatal infants are, in particular, usually strikingly different in colouration from adults and it is likely that this, with other infantile characteristics such as relative body and ear size, serves to evoke caregiving and inhibit aggression (Alley, 1980). It appears that male C. neglectus may retain juvenile colouration beyond puberty, Kingdon (1971) suggests that this could delay/inhibit the antagonism of the harem male, allowing the subordinate to remain in the group longer than would normally be possible.

Sexual identity may be gauged by the structure of the secondary sex characters and by body size (The cercopithecoidea are somatically sexually-dimorphic - Napier and Napier, 1967). Individual differences in colouration and, particularly, in physiognomy subserve individual recognition (Struhsaker, 1967b; see chapter 3 below).

4.3.2. Dynamic features. Dynamism is introduced into the signalling capabilities of somatic characters when their configurational relationship to other characters requires effort on the part of the signaller. This effort may be transitory or relatively sustained.

All locomotion conveys information: the internal state represented by a slow walk is unlikely to be equivalent to that associated with a gallop. Different patterns when combined, as in foraging and movement between food patches (Rose, 1977), may give information not contained in either on their own. Furthermore, movement can be associated with a particular facial expression, such as a `forward-dart´ with a threat face, and thereby form part of the expressive cluster. Sade (1973) demonstrated that movement within a particular plane is related to specific tendencies (Submission - frontal plane; amicable approach - low-to-high movent in the sagittal plane; querying - oblique movement; play - rotary plane). Status can even be the quality of the movement as in the `confident walk´ of dominant macaques (Altmann, 1962; Rahaman and Parthasarathy, 1968).

A few movement patterns seem sufficiently high-profile and distinctive to suggest that their communicatory value has become `formalized´ (Smith, 1977). One of these is `play´, easy to recognise but hard to define (Hinde, 1974; Fagen, 1981). Nevertheless, patterns associated with locomotory play are generally vigourous, exaggerated, repetitive and with a more variable ordering than when used out of this context (Fagen, 1981). Play is often initiated with a `lolloping´ gait that is very distinctive (see Wolfheim and Rowell, 1972).

Another pattern of relevance is the "branch-shaking" (Hinde and Rowell, 1962) or "jump displays" (Poirier, 1970) characteristic of adult males (Struhsaker, 1967a; Gautier and Gautier, 1977; Kavanagh, 1981). In performing it, generally in response to the presence of strange conspecifics, a male will jump noisily through the canopy and/or stand and vigourously shake a branch. It is a highly conspicuous action pattern, making optimal use of visual (its movement and that of the substrate) and acoustic (vocal and non-vocal) sources. It is usually seen as generally intimidatory (Gautier and Gautier, 1977)although Rahaman and Parthasarathy (1968) see it as serving "to warn the members of the troop to refrain from quarrelling" (pg. 262).

Like locomotion, maintained postures may regularly occur with particular activities - resting, foraging, and social encounters - for an observer to be potentially able to use the relationship to predict future behaviour (Rose, 1977; Wolfheim and Rowell, 1972, Altmann, 1962; Gautier and Gautier, 1977).

Some postures are immediately and directly social and may be emphasized by being coupled to movement. One such cluster is genital signalling and is discussed in greater detail below. Another is the soliciting for grooming. Grooming is a fundamental aspect of social cohesion (see Seyfarth, 1980) and animals may often request it by conspicuously orienting a part of the body towards its partner or by lying down in front of it (Hinde and Rowell, 1962; Wolfheim and Rowell, 1972). The stereotypy is more obvious if the protagonists are relative strangers (Gautier and Gautier, 1977. Presumably this stereotypy is more an absence of smoothness of gesture). Such presentations are classified as `invitations to groom´ as they are not maintained for more than a few seconds if the groom is not forthcoming (Wolfheim and Rowell, 1972).

An interesting finding, often reported, is that dominant male monkeys carry their tails differently to the rest of the troop (Altmann, 1962; Bertrand, 1969) and that this difference reflects the increased muscle tonus associated with dominance and also often reflected in their walk. As it occurs in the stumptail macaque, whose tail is vestigial, there is good reason to suspect that it is primarily communicatory (Bertrand, 1969).

However Hausfater (1977) analysed data on baboons and concluded that age, not status, is responsible for the style of carriage usually associated with the latter. Even if this is so, it in no way diminishes its signalling value.

Bernstein et al. (1978) applied context analysis to determine, in vervet monkeys, the messages tied to a number of tail positions. They found that correlation between position and activity did exist: with the more anterad positions a vervet might forego non-agonistic behaviour to attack, and, with the more posterad, to withdraw.

Detailed analysis such as this shows that information can be conveyed subtlely, but Rowell (1972) rightly cautions against too liberal a set of interpretations: tails are also very important for locomotion and may be carried `conspicuously´ merely to facilitate balance (see Gautier and Gautier, 1977). Also social use may not be evident in species, such as P. johnii (Poirier, 1970), where this would have been predicted (Jay, 1965, discusses tail use in the closely-related P. entellus).

Lastly we must consider the ability of cercopithecoidea to perform pilo-erection, thereby increasing their apparent size. When this is not being done as a response to cold weather, it is generally seen during agonistic encounters (Angst, 1974) but is apparently not preferentially connected with either approach or flight (Gautier and Gautier, 1977). Bertrand (1969) sees it as combining aggression and fear.

5. GENITAL SIGNALS.

Genital signalling may be said to occur when the visible presentation of an animal´s secondary/external sexual organs influences, or has the potential to influence, the behaviour of signal recipients. Such signals occur in a variety of forms within the primates and are often given special prominence through the evolution of enhancing structures and ritualization of the mode of presentation (Wickler, 1967).

The immediate implication of such signalling is that it must be linked, in some way, to reproduction and reproductive effort.

An investigation, therefore, of the degree of signallig elaboration achieved by a species and the social use to which these signals are put, becomes central to an understanding of the pressures facing an individual attempting to maximize its fitness. This section of the review differs from others in that the scantiness of relevant information makes it desirable to include data on New-World monkeys as well as other orders. Additionally, this information is catalogued species by species so that the state of research can be appreciated.

5.1. New-World Monkeys.

Within the platyrrhines two major types of genital display occur, each associated with one of two families.

6.1.1. In the *Callitrichidae* species that display their genitals (scrotal sac and labia) do so by lifting their tails and orienting their rump towards the intended receiver (Oppenheimer, 1977). Both hands and feet are kept on the ground. The literature does little more than describe the displays but Epple (1975) notes that after the tail is raised pheromones may be released. The display is performed by both sexes and is regarded as constituting an aggressive threat.

6.1.2. More work has been done on the form and function of the genital display in the *Cebidae* where it is performed frontally with the chest raised, legs spread and penis or clitoris erect.

The squirrel monkey, *Saimiri sciureus*, has been especially prominent in such studies . Ploog and MacLean (1963), working on caged groups, were the first to record that male squirrel monkeys display penile erection under a variety of conditions. The introduction of a new animal into the monkey room may often precipitate a "distant display", something which also occasionally occurs among old inhabitants in different cages. During the display the male inclines his head to one side and abducts one thigh as the penis gradually reaches partial or full erection. A small amount of urine may be produced concurrently. Typically the signaller also scratches its body and vocalizes (the "churr"; Winter, 1968). With each vocalization the penis may be thrust forward.

If a mirror is held before a male full erection will be achieved more rapidly, apparently facilitated by the simultaneous erection seen in the reflection. Habituation to the mirror does not readily occur. Ploog and MacLean point out that olfactory cues are necessarily excluded in the "mirror display", as support for the inference that vision alone plays the key role in eliciting the behaviour.

Within an established group the signalling male may direct the erection to an individual of either sex. In the "open posture" the sender moves into the visual field of another animal and displays from betweeen 10cm. and 4m. away while looking at the recipient (Winter, 1968). Thigh spreading may infrequently be seen without an accompanying erection.

In the "closed position" a male approaches the recipient head on and places one or both hands on its back, spreads his thigh and thrusts his penis towards the face of the other monkey. The gaze is directed away from the recipient and the whole act normally lasts less than ten seconds. The recipient sits hunched and, although it may thigh spread, will never develop an erection.

When the above display is directed towards females it may precede copulation although alpha females have been seen to respond with similar postures and clitoral distension.

Developmentally the genital display is one of the earliest behaviours to emerge, occasionally seen on day 1 but always present by the end of the first month (Rosenblum, 1968).

It is generally concluded that the `distant´ and `open´ displays serve as forms of greeting, while the `closed´ form appears to have aggressive connotations. This latter is born out by the assault of non-quiescent signal recipients. The opinion is that this display is used to exert and maintain dominance. As such it seems to be a more exact indicator of hierarchy than does competition for food. Since dominance is not a feature of male/female relationships (Baldwin, 1968), and since the display when given to a female is not followed by aggression, a communicatory significance in courtship behaviour is suggested.

Baldwin (1968) and DuMond (1968), working on less restricted animals, confirm that, during the mating season, a strongly-contested, linear, penile display dominance hierarchy is established among males. Baldwin suggests that hormonal activity in subordinate males may be inhibited by pheromones released in a dominant males's urine during a penile display. Green et al. (1972) who found that hormonal supplementation did not affect display in dominant animals agree that it would be interesting to see the effect of similar treatment on the behaviour of subordinates.

There is little elaboration of the penile displays in the rest of the _Cebidae_, although they are recorded as occurring in all except _C. capuchinus_ and _C. nigrivittatus_ (Oppenheimer, 1977). In the spider monkeys (_Ateles_ spp.), males have been seen to perform pelvic thrusts, with an erect penis, to females prior to copulation. However, in the wild, such displays were not associated with sexual activity but with grooming, play or even homosexual hugging (Klein, 1971). The female spider monkey possesses a long, pendulous clitoris and it has been suggested that this, through its tendency to retain urine, has evolved to mark the environment wherever it touches. It is assumed that this makes it easier for the male to locate the female (Klein and Klein, 1971; in Oppenheimer, 1977). No visual significance is posited.

In howler monkeys (_Alouatta_ spp.) both the male and female may have erections during sexual encounters (Oppenheimer, 1977). Jones (1980) reports on the existence of stereotyped "scrotal" and "vulval" displays where the tail is raised, during status interactions, to reveal the perianal areas. They are interpreted as being appeasement behaviours, ritualized because of the energetic constraints imposed by a folivorous diet. Altmann (1959 - in Oppenheimer, 1977) witnessed scrotal retractions in *A. villosa*, whose scrotum is differentiated in colour from the surrounding fur (Carpenter, 1965).

Genital signalling as a sexual present by females occurs in New-World monkeys and consists of crouching, with the tail held aside, and/or backing into the male (Oppenheimer, 1977).

5.2. Old-World Monkeys.

5.2.1. Most of the guenons are characterized by blue scrota and red penises, the vividness of which make them, along with the forest baboons (*M. sphinx* and *M. leucophaeus*), unique among mammals (Young, 1971). Scrotal blue (and presumably vulvar colour in the female vervet) is accounted for by a deep dermal deposition of melanin in melanocytes. It modulated by the state of hydration in the dermis (Price et al., 1976) and does not appear to be under the control of testosterone (Dixson and Herbert, 1974). Vascularization of the epithelial layer of the dermis results in the red of the penis (see Dixson and Herbert, 1974).

Data on the genital signals of forest guenons are sparse, both because of the types of problems that researchers are working on, and because of observation difficulties (see chapter

3). Nevertheless there is some information.

Kingdon (1971) records that _C. mitis_ males sometimes sit and face the observer with legs splayed to reveal the pale, grey-blue genitals. In females the overtly sexual nature of 'presenting' is absent but they do solicit by half-crouching and raising their tails over their backs. A more complex presentation was seen in _C. neglectus_ where males would drop onto their elbows, raise their rumps with feet widely parted, and look over their shoulders. The presenter then, especially if a subadult male, backs up to the recipient and, looking through its legs, waves its rump or tail. It is regarded as the "forcing" of an appeasement gesture insofar as it hides the white beards of adult males, the display of which constitutes an aggressive signal (Kingdon, 1971). Subadult males have reddish-brown perianal pelage (said to mimic that of adult females) which is conspicuously displayed during this presentation. Kingdon tested an adult male on its responsiveness to colours and found that it was very interested in orange-brown but agitated by blue (assumed to be due to its resemblance to scrotal colour).

In the talapoin monkey (_Miopithecus talapoin_) the male's glans penis, which normally protrudes and is conspicuous against the blue scrotum, is retracted when the animal is frightened. Sexually-aroused males develop jerking erections but there is no evidence that this is of signal value to females (Wolfheim and Rowell, 1972; data taken from a captive colony with one mature male). Unlike other guenon/guenon allies female talapoins develop pink sexual swellings that, like those of baboons and macaques, increase to a maximum during the follicular phase of the menstrual cycle (Rowell and Dixson, 1975; 2 troops of wild talapoin). This is associated with a "squat present" on the part of sexually soliciting females. It is held very briefly and involves squatting with the back to the other animal and looking at it over one shoulder (Wolfheim and Rowell, 1972). That the swelling serves as a visual signal to males is indicated by both the increase in visual inspection occasioned by it and by the fact that, once the breeding season had begun, the more females there were in the group with large swellings, the more males were associated with the group (Rowell and Dixson, 1975). This explanation does not consider the possibility that olfactory stimuli (pheromones) may be eliciting the associated male behaviour.

The presentation of the ano-genital region in a sexual context is known for several guenons (Gautier and Gautier, 1977), whereas non-sexual presentation has been seen being performed by young males towards adult males in C. nictitans, C. cephus and C. pogonias. In two of these species, at least, the latter presentation derives from sexual solicitation (Gautier and Gautier, 1977; Kingdon, 1980) and relies on a combination of genital presentation with signals from the facial pole (pouting in C. pogonias and head-flagging in C. nictitans)

The primacy of the genital region in C. diana is indicated by the concentration of colour and complex design in this area.

However, the blue scrotum is virtually hidden by the red or cream-coloured fur surrounding it (Kingdon, 1980). The male often employs "stopping" postures where the forelegs are dropped and the tail arched in a way that emphasizes the hindquarters (Morike, 1973). Additionally the animal may throw a momentary handstand while running, thereby flashing the "brilliant buttocks". Kingdon regards it as deriving from an exaggerated juvenile presentation where the handstand forces the ano-genital region into the recipient's visual field.

The terrestrial, open-ground patas monkey male, E. patas, displays its genitalia either by standing bipedally, by bouncing up and down on the same spot, or by "see-sawing" in a rocking bounce where the tail is held erect or to one side (Kingdon, 1971). In the laboratory, Hall (1967) found that the adult male in his caged group attacked a younger male whose mature genital colouration had become visible only two weeks prior to the attack. It was also noticed that the blue scrotum of the adult male was a source of interest and attraction to the younger males (Hall and Meyer, 1967). This was confirmed on free-ranging animals (Gartlan, 1973, 1975) and Gartlan emphasized that the recipients of such attention displayed no aggression. Females were never seen to respond in this way to male scrota.

Gartlan (1973) argues that the formation of all-male groups of patas appears to be permitted by the presence of a characteristic, highly-visible and attractive ano-genital region. While he does not explain the mechanism in detail it would appear, if true, to be producing an effect very different from that postulated for its action in closely-related genera. Females have no genital colouration and do apparently not present the region either sexually or appeasingly (Hall, 1965).

Brain (1965) also reccorded male interest in other males' scrota in vervet monkeys, *C. aethiops*, and was the first of a number of investigators to comment on the social significance of scrotal colour, seeing it as a "status symbol". He noted that the intensity of the blue was variable and possibly related to the general state of well-being of the animal and its level of dominance.

Wickler (1967) and Bolwig (1978) point out that vervet males utilize a sitting posture where the thighs are spread and while this is not accompanied by penile erections in tame animals it is in wild males "keeping watch beside the group" (Wickler, 1967). Such erections occur in situations of high arousal such as the approach of humans or other monkeys. The penis may jerk against the stomach on occasion, emphasizing its already conspicuous colouration.

Struhsaker (1967a,b,c) presents the most comprehensive set of data on the structure and function of genital signals yet presented for any species. Working on free-ranging vervets he isolated three signalling patterns:

i. Penile erection.The erection, in a non-sexual context, was either immobile or sagittally jerking. It was observed during grooming and sometimes during intra-group agonistic encounters where it was developed almost exclusively by the aggressor. Struhsaker concludes that while the erection was conspicuous its function was not evident.

ii. Penile display. This was an infrequent pattern, involving two males, where one stood bipedally with his hands on another's shoulders, directing his inguinal area towards its face. When the penis could be seen it was almost invariably erect. The common form of termination was for one of the animals to walk away and it was felt that this behaviour most closely resembled the closed display of the squirrel monkey (see above), without a function being apparent.

iii. The 'Red-White-and-Blue' display. Encounters included in this category involved "a dominant male displaying his red perianus, the medial strip of white pelage between the perianus and scrotum, and his turqoise or powder-blue scrotum to a subordinate male" (1967b; pg. 16). It involved all males except younger juveniles and infants.

The displayer would walk confidently back and forth in front of, or encircle the recipient while holding his tail vertical or , at least, above the horizontal. Occasionally the displayer would stand bipedally or pause and direct the ano-genital plane towards the recipient. This latter pattern was similar to sexual presenting.

The recipient, during all this, would crouch, grimace, vocalize ("waa" and "woof-waa" calls) and hop backwards and away from the displayer while maintaining eye-contact. Infrequently he would shake his head from side to side or initiate a "false chase" which consisted of a slow, hesitant and jerky gallop that never resulted in the capture of the animal pursued.

The roles (sic) assumed in these displays depended on the relative ranks of the participants. The dominant male always displayed to the subordinate and role reversal was never seen (Struhsaker, 1967c).

The frequency with which the display was performed varied seasonally and was directly related to the mating season. As there was a direct relationship between dominance and mating activity Struhsaker (1967b) suggests that the display is used to assert dominance, something which is critical during the mating season and which would facilitate the differential reproductive success that selects for dominance.

The RWB display, while seen by Struhsaker in a number of East African localities, was never observed by Cartlan (in Struhsaker, 1967a) in Uganda, nor in a translocated population of Green monkeys (C. aethiops sabeus) on the Caribbean island of St. Kitts, where the scrotal colour is much paler ("yellowish", Poirier, 1972; "chalk-like to sky-blue", McGuire, 1974). While it may be that this is a consequence of isolation and gene-pool dimunition, a recent study of C. a. sabeus in Senegal has revealed the same absence of scrotal colour and the RWB display (Harrison, pers. comm.). Penile erection was, however, seen during agonistic encounters (McGuire, 1974; Harrison, pers. comm.).

Struhsaker (1967b) also commented briefly on the infrequent adduction of the testes performed by males while walking or climbing, but saw this as a non-social, non-communicative behaviour and one for which no explanation could be forwarded.

Female vervets use an active `present´ (orientation of the hindquarters towards a male, sometimes simultaneously glancing over the shoulder) as a means of signalling oestrus condition (Struhsaker, 1967b; McGuire, 1974). While she is distinctive among the guenons in having coloured genitalia (red perineum, blue vulvar margins) there does not appear to be support for Wickler´s (1967) observation that this colour becomes more intense when the female is sexually receptive (Struhsaker, 1967b; Butler, 1966). Presenting in a non-sexual context has not been recorded for the species.

5.2.2. The savannah baboon male (Papio spp.) has a pink penis which, when extended, is very visible against the grey scrotum (Wickler, 1967). Baboon males are commonly seen sitting in the open, often facing away from the centre of the group, with their thighs spread and their penises extended. Hall (1960) has shown that these males give immediate warning of the approach of other troops. As this has also been seen in patas and vervet groups (Hall et al., 1965), Wickler (1967) suggested that males adopting this posture are serving as "optical markers" of the presence of the group or its territorial boundaries, largely as a warning to conspecifics. As Fig. 3/19 in Hall and DeVore (1965) and Fig. 3 in Redican (1975) show, penile extension or erection do at least also occur during tense or aggressive situations.

The oestrus cycle in female baboons is marked by swellings of the perineal skin. During maximum turgescence the skin, owing to increased blood supply, becomes iridescent pink, and attracts males (Saayman, 1970; Kingdon, 1971). Male ischial callosities are generally light coloured although those of P. hamadryas are "luminous red".

Both male and female baboons orientate their hindquarters towards other conspecifics. Hall and DeVore list it as occuring:

i. By a sexually-receptive female to a male. She stands in front of him and turns her tail to the side. This is a sexual present and the male is likely to differ in his response depending on the stage of her cycle.

ii. Anoestrus females present more briefly as do juveniles, who may do so to a dominant male.

iii. Adult females may present to mothers with young infants. This will be accompanied by a lip-smack.

iv. Adult males may walk to other adult males and lower their hindquarters. It is often the more dominant animal that does this.

The most notable variants on these are seen in P. hamadryas where females may present to the unit male after an altercation with another female, or where a male may notify his unit leader of the direction of his departure by walking away slowly with the hindquarters exposed (Kummer, 1968). Here, and in other genera, non-sexual presenting is almost always regarded as an "appeasing" gesture designed to dampen aggression annd allow for the reduction of inter-personal distances (Wickler, 1967; Marler, 1968).

The gelada baboon, *Theropithecus gelada*, is recorded as using penile erection, genital presentation of the male and presentation of the hindquarters in circumstances where they may be regarded as having social communicative value (Dunbar and Dunbar, 1975). Crook (1972) sees little evidence for Wickler's (1967) view that the "bleeding hearts" of male geladas are mimics of female genitalia for use in appeasing displays.

The forest baboons, *Mandrillus sphinx* and *M. leucophaeus*, are more strikingly coloured than their savannah counterparts. Males of both species have bright genitalia. The circumanal region is red; lateral to the callosities there is a blue patch fading into lilac; the posterior scrotum is lilac, the anterior pink; the pubic region is scarlet and the glans penis is pink. In addition, the male mandrill, *M. sphinx* has a red nose and brilliant blue paranasal swellings that run longitudinally. the females of both species have relatively unpigmented sexual swellings that do not reach the gross proportions of savannah baboons (Napier and Napier, 1967).

Sadly, little is known of these species, although Darwin

(1876) quotes an anecdote concerning the use of presentation by a captive mandrill. Jouventin (1975) saw mandrills in the field and reported that, in dark undergrowth, the "luminous" hindquarters were very conspicuous. From work with decoys and captive animals the colouration of the scrotum and penis revealed themselves as components of a dominance display when the penis may be erect and the behaviour accompanied by yawns. Bolwig (1978) noted that captive drills use the "open-posture" almost as frequently as baboons while they presented to both oestrus females and challengers.

No biological meaning is evident for the presence of colour on the mandrill face. Wickler (1967) suggests that although presenting is not established as a behavioural pattern in mandrills all a male would need to do to achieve the same effect would be to look at someone.

5.2.3. Data for the mangabeys are rather more sparse than for other genera. Chalmers (1968a,b) saw sexual and non-sexual presenting in <u>Cercocebus albigena</u> although the latter was not performed with the same frequency by all age/sex classes. Sexual presentation was not an inevitable part of mating interactions.

Gautier and Gautier (1977) found penile displays - directed and in association with open-postures - in <u>Ce. albigena</u> and <u>Ce. galeritus</u>, associated, at least, with provocation by humans. From their Fig. 12 it is easy to see that, at close distances, the penis, although chromatically undifferentiated, is easily seen to be erect. These displays are regarded as relevant to group protection.

5.2.4. The genus Macaca have genital signals, which to a large degree, resemble those of savannah baboons. All species have females with pink to red sexual swellings and males with relatively pale penises. Sexual and non-sexual presentation is common (Hanby, 1976). Both scrotal retraction and penile display have been seen (Altmann, 1962; Bertrand, 1969; Bernstein, pers. comm.).

5.2.5. Oates (1977) and Marler (1972) both noted the occurence of penis extensions in male Black and White colobus, Co. guereza, during inter-group encounters or the presence of the observer or other primates. Associated with it was the "stiff legs" posture where the signaller sat with his back straight and his legs held out stiffly from the body. It was adopted most commonly by adult males but was recorded for all classes except infants. Erections were sometimes seen in non-sexual encounters but never in conjunction with the `stiff legs´ posture. Oates (1977) sees penile extension as a probable threat signal towards other groups. It is often accompanied by yawns.

Both guereza males and females use the present in sexual and non-sexual contexts and the hindquarters are simply turned towards the recipient. Marked lowering of the body typical of most sexual presents was not an obvious component of non-sexual usage. Female guereza do not develop a sexual swelling (Struhsaker and Leland, 1979).

Female red colobus, Co. badius, on the other hand do develop moderate swelling and, additionally, possess a large, prominent clitoris. (Struhsaker, 1975). Male genitalia are not distinctively coloured. No reference is made to penile extensions or displays but Struhsaker (1975) does differentiate three different presents on the basis of the degree of elevation of the body and the correlation of these with different contexts. Essentially, their non-sexual usage is designed to reinforce the dominant position of high-ranking males or enhance the bond between adult males, especially at times of imminent physical aggression.

Females of the genus *Presbytis* (Asian colobines) do not show external signs of oestrus and males have relatively non-distictive genitalia (Napier and Napier, 1967). In *P. entellus* penile erections are seen in non-sexual contexts and , again, presents are used for more than sexual soliciting. The performance of a present is not necessarily correlated with relative rank, status or sexual receptivity (Dolhinhow, 1978). In *P. entellus*, at least, the penis is very visible against a dark scrotum (see colour plate 5 in Hrdy, 1977).

In *P. johnii*, Poirier (1970) reports male interest in the genitalia of other males and the use of presenting in the same way as in *P. entellus*.

5.3. Great Apes.

Within the great apes it is only the chimpanzee that has undergone any marked development of the size and visiblity of the external genitalia (Short, 1979). The scrotal region is rendered conspicuous by a hairless, unpigmented patch of skin and the long, pink penis, when erect, is easy to see against the bare, white skin of the preputial area. Oestrus in the female is accompanied by very pronounced perineal tumescence. Non-sexual penile erection was sometimes seen as a component of feeding and greeting behaviour, but not during aggressive encounters (von Lawick-Goodall, 1968). Female chimps present sexually and socially (Hanby, 1976).

5.4. Other Orders.

Visual genital signalling is rarely commented on in work on non-primate mammals. That it might well be more common than thought is evidenced by some examples from the literature.

In canids a common action in greeting is to twist the trunk around so that the groin is presented and causes the recipient to initiate genital investigation (Fox and Cohen, 1977). No special visual structures are associated with this and the primary reason for its presence may be to facilitate the transmission of olfactory information.

In feral horses, Equus caballus, Feist and McCullough (1976) recorded 59 penile extensions in situations connected with neither copulation or urination. Flexion often occured after extension and stallions of all statuses were involved. Some extensions arose indirectly out of sexual interactions but several were due specifically to aggressive encounters with other males. In such cases the action was associated with a specific posture, "stand-stare", that commonly developed in the early stages of a fight.

Similarly, in the red lechwe antelope, Kobus leche, the more dominant male may have an erection during male-male encounters. It is seen in conjunction with the "broadside" posture where the signaller's body is oriented laterally with respect to the recipient (Williamson, 1979). This posture is widespread in the artiodactyla and is characteristic of dominance encounters and may progress into a circling walk (Walther, 1977).

Orientation of the hindquarters in the artiodactyla is often associated with conspicuous rump colouration and may be used to elicit mounting, a diminution of aggression or a following response (Walther, 1977). Schaller (1980) notes in passing that the white scrotum of the urial, Ovis orientalis, is exceptionally conspicuous, flashing from the distance "like a heliograph" (pg. 141).

The only major theoretical examination of the structure and function of these socio-sexual signals has been made by Wickler (1967). In brief his argument has two tenets. Firstly, that in "restricted groups of individually acquainted members" a need exists for some process of appeasement to counter-balance disruptive intra-group aggression. Non-sexual presents provide this, which suggests, together with the "mimicry" of female structures by males (*P. hamadryas*, *C. aethiops*), that the provision of an 'attractive' signal will, in agonistic encounters, act as a sign-stimulus releasing a response in the aggressor that is motivationally antithetical to attack. Within the same framework intra-group penile displays are seen as rising out of the relationship between sex and aggression, thereby being available for use as dominance signals.

Secondly, in the optically oriented higher primates, visual genital signals will also have evolved from the use of the uro-genital system in providing olfactory information concerning status and domain (e.g. territory marking). This would account for the use of open posture displays which are assumed to be a component of vigilant behaviour. He sees the males as "optical markers" of the presence of the troop as a whole.

As mentioned above, Crook (1972) showed that the suppositions regarding the gelada are not entirely correct and that while the female chest pattern is used in copulatory sequences its colour phasing does not match that of the perineum.

Grubb (1973) denies that mandrill colour mimes that of the genital system. He feels that it is unlikely that there was a selective advantage in acquiring colouration for this reason and proposes, instead, that convergence has occurred, with an advantage in increased facial conspicuousness, because the physiological methods for the production of somatic pigments and structural colours are limited.

Finally, Clutton-Brock and Harvey (1976) point out that in accepting Wickler's mimicry hypothesis we would expect convergence to be greater in multi-male species. However it is seen at its most elaborate form in hamadryas baboons yet does not occur in the talapoin monkey.

6. THERMOREGULATION AND THE SCROTUM.

In 1952 Portmann questioned the long-held view that the primary function of the scrotum is to regulate testis temperature. He argued, instead, that it served most importantly as a visual sexual signal, producing as evidence the correlation between a well-developed visual sense and the presence of conspicuously coloured scrota.

This argument was criticised by Ruibal (1957) who pointed out that in the great majority of scrotal (permanent or seasonal) mammals the scrotum is relatively inconspicuous and/or the visual sense is of minor importance in sex recognition. He did not deny that the scrotum may serve as a signal in some species but disputed that this was its primary adaptive role.

Cowles (1958) emphasized that there is a narrow temperature range, in both plants and mammals, where gametogenesis is possible. Moreover, the adaptive value of homoiothermy and the adoption of high somatic temperatures by endotherms has led to a "thermal conflict of interest" (pg. 360) where the optimal temperature for reproduction is lower than core body temperature.

Since increased temperature can adversely affect spermatogenesis and androgen production (VanDemark and Free, 1970; Cowles, 1976) it is held that mammalian testes have achieved a separate thermoregulatory system through the evolution of the scrotum. The scrotum, in the higher mammals, is a pendant sac completely isolated from the peritoneal cavity, as a part of which it has its origin (Waites, 1970). The skin is thin, often bare, and has its surface area under the control of two powerful muscles, the <u>tunica</u> <u>dartos</u> and the <u>cremastor</u> (Setchell, 1978).

While most reviews regard the adaptive significance of the scrotal state as being directly related to the functioning of the testes, Bedford (1978) has advanced an alternative theory which is of interest as it takes mating strategies into account. He argues that the data no longer support the older view that raised temperatures cause testis malfunction and that, instead, descent into the scrotum has been influenced primarily by the need for migration of the <u>cauda</u> <u>epididymis</u> to this cooler location. Testicular descent then becomes a mechanical event enabling the epididymis to project from the body.

The epididymis is instrumental in sperm storage and Bedford puts forward evidence that a scrotum characterizes polygynous species in which a dominant male achieves all or most of the fertile matings in a large group, as well as those known to engage in multiple, ejaculatory coitus with one female. The possibility is raised that the scrotal state may be linked to the sexual capacity of the male as optimal sperm storage is essential if fertile ejaculates are to be produced repeatedly within a short space of time.

7. THE PROCESS OF DISPERSAL IN OLD WORLD MONKEYS.

Despite Carpenter's (1944) data on several primate species and his acceptance of a non-group phase in an individual's life history, De Vore (1963 - in Lindburg, 1969) and others could still regard primate groups as "closed", highly inbred social units. Thus,.."a rhesus monkey in the natural state typically spends all its life in the natal troop" (Bernstein, 1964).

However, the accretion of data since the 1960's has entirely corroded this view (Lindburg, 1969; Itani, 1972). Primate groups are neither closed or stable and dispersal, either in the form of arrival into, or departure from a social unit, or in the presence of extra-group animals, has been recorded from a wide variety of species and genera (Baldwin, 1969; Struhsaker, 1967c, 1975; Poirier, 1969; Lindburg, 1969; Rudran, 1973, 1978; Packer, 1979a; Marsh, 1979; Dittus, 1975; Dunbar and Dunbar, 1973; Altmann and Altmann, 1970; Kummer, 1968; Sugiyama, 1976; Hrdy, 1977; Cartlan, 1974; Bourliere et al., 1972). The apparent ubiquity of the process (but see recent data on Barbary macaques by Taub, 1980) indicates that it should be regarded as a fundamental feature of social organization and not as an anomaly or curiosity (Slatkin and Hausfater, 1976).

7.1. Characteristics of Emigrants.

7.1.1. Sex Differences. In most of the studies listed above the common migrants were found to be males. The important exceptions to this are:

i. in *P. hamadryas*, where both males and females move from the natal troop although the dynamics differ for each sex (Kummer, 1968);

ii. in *C. badius*, where females transfer more commonly than males (Marsh, 1979; Struhsaker and Leland, 1979).

7.1.2. Age at first emigration. In most animal populations dispersal in subadulthood is the rule (Wilson, 1975; pg 95) and is so for primates (Packer, 1979a; Dittus, 1975; Sugiyama, 1976; Harcourt, 1978). Where both sexes migrate the slower maturation of males means that they leave their natal troops after females of the same age (Harcourt, 1978).

7.1.3. Status of Migrants. Data indicate that dominant animals do not leave and migration is therefore associated (especially in multiple- transfer adults) with a loss of status or failure to increase sufficiently in rank within a given time. Status may be lost either through the violent take-overs characteristic of uni-male species (Rudran, 1973; Hrdy, 1977; Struhsaker, 1977) where the loser leaves immediately to avoid death, or through status shifts in multi-male troops (which can be violent) where departure by the loser is not automatic (Dittus, 1975; Sugiyama, 1976).

Failure to accede to high status within the resident troop is a characteristic of males in multi-male systems and of adolescent males generally, although males may remain in the natal troop and become dominant (Sugiyama, 1976; Harcourt, 1978). While subadult males from both high and low-ranking lineages leave *M. fuscata* troops it is possible that the few which remain rely on kinship for their status climbs (Sugiyama, 1976; and see Meikle and Vessey, 1981). In this light it is interesting that during the pre-peripheralization phase in *P. entellus*, male "weanlings" are often threatened by the dominant male. This causes them to live away from their mothers for varying lengths of time and rapidly reduces the strength of the mother-male infant tie (Mohnot, 1978).

7.2. Fates of Emmigrants.

7.2.1. Immediately after emmigration.

Emmigrating animals have three options open to them:

i. They can transfer immediately to another bisexual group, something that many Japanese macaques and baboons do (Packer, 1979a; Sugiyama, 1976);

ii. join all-male groups which are commonly seen in langurs, patas and red-tailed monkeys, and occasionally in macaques (Rudran, 1973; Poirier, 1969; Hrdy, 1977; Gartlan, 1974; Struhsaker, 1977; Sugiyama, 1976; Simonds, 1973) or;

iii. travel alone. This has been recorded for baboons, C. mitis, patas, mandrills and Japanese macaques (Slatkin and Hausfater, 1976; Gartlan, 1974; Gartlan, 1970; Rudran, 1978; Sugiyama, 1976).

7.2.2. The number of transfers per individual. Where data is available it is apparent that transfer occurs more than once (Rudran, 1973; Dittus, 1975; Packer, 1979a; Sugiyama, 1976; Lindburg, 1969). Movement is generally into adjacent troops, with subsequent transfers often taking the animals further and further from their natal troops. Nevertheless, particular individuals may well return to groups in which they had previously been resident even though this is not a common occurrence (Packer, 1979a; Sugiyama, 1976; Dittus, 1975; Lindburg, 1969).

7.2.3. Nature of the groups into which animals transfer. Packer's data (1979a) indicate that baboons choose to move into troops where they have access to an increased number of adult females but work on macaques does not support this (Koford, 1966; Lindburg, 1969). However, Meikle and Vessey have recently shown that rhesus males do better, reproductively, and stay longer, if they move into a troop where they have a high-ranking brother (1981).

7.2.4. The concomnitants of extra-group existence. Migration increases the mortality of adult males who migrate (Koford, 1966; Dittus, 1975; Gartlan, 1974; Sugiyama, 1976) because:

i. they are forced into ecologically poorer zones. This has been recorded in both deciduous forest and savannah species (Rudran, 1973; Sugiyama et al., 1965; Gartlan, 1974) where the abundance of food and water show marked seasonal variation. This is unlikely to be a problem in habitats where resources are more stable. Excluded *C. guereza* males even travel within the home-range of bisexual groups, in what is an environment of relatively uniform resource dispersal (Wrangham, 1980). Moreover, Slatkin and Hausfater (1976), following a single male baboon, concluded that a solitary male, even if injured, is not necessarily intended to die or incur a lower reproductive potential. However, isolated animals are unlikely to be able to exploit large clumped food sources as efficiently as a larger foraging group can (Wrangham, 1980).

ii. Susceptibility to predation is increased. Anti-predator vigilance, especially in smaller species, is more efficiently managed in larger groups (see Siegfried and Underhill, 1975). Higher levels of predation on migrating animals have been recorded for *C. badius* (Marsh, 1978) and, outside the primates, in the Hunting Dog, *Lycaon pictus* (Frame and Frame, 1976).

7.3. The Process of Dispersal.

7.3.1. *Timing of movement.* In the macaques movement, both into the troop and out of it, is strongly associated with the breeding season, and appears to be designed to exploit the availibility of oestrus females (Sugiyama, 1976; Lindburg, 1969; Dittus, 1975). Sugiyama feels that it is aided by the fact that food is plentiful at this time of the year.

There is less information on species lacking a discrete breeding season but Packer (1979a), working on *P. anubis*, which has no such season, showed that males transferring for the first time moved into groups regardless of the number of females there, while older males chose groups with more oestrus females. The timing appears, therefore, to be governed by season only insofar as this reflects the number of sexually-receptive females.

In the red colobus, where females move, Marsh (1979) speculates that it may have something to do with the prevention of infanticide, although this does *not* occur in the grey langur, where infanticide is commonplace (Hrdy, 1977).

7.3.2. *Synchrony*. The data collected from habituated troops of Japanese and rhesus macaques show that males have a preference for transferring together (Drickamer and Vessey, 1973; Sugiyama, 1976), something also occasionally seen in *P. johnii*, *C. ascanius*, *P. anubis* and *P. ursinus* (Poirier, 1969; Struhsaker, 1977; Packer, 1979a; Cheney and Seyfarth, 1977).

It has been held that, in the macaques at least, synchrony is an artefact induced by the presence of a breeding season and adjacent troops (Harcourt, 1978), but Meikle and Vessey (1981) have shown that reproductive advantages accrue to those rhesus males that move with a brother. However, in the absence of a breeding season, baboon males usually travel on their own

(Altmann and Altmann, 1970; Packer, 1979a).

7.3.3. *Nature of the departure*. In the first instance, departures may be peaceful, which is to say that animals are not forcibly evicted by competitors. Sugiyama (1976) states that young males may even leave troops in which there are no adult males (who would be most likely to attack them). Packer (1979a) shows that there is no obvious eviction of males from their natal troops. Departure has also been reported as being voluntary in *M. mulatta*, *M. sinica* and *C. badius* (Drickamer, 1974; Dittus, 1975; Marsh, 1978).

In two uni-male species of guenon it becomes more important to distinguish between males moving for the first time and fully-mature males. In *C. campbelli* and *E. patas* mature males are driven out after a successful take-over by a challenger whereas subadult males leave for reasons not understood but less associated with direct aggression (Bourliere et al., 1970; Gartlan, 1974). In several other species adolescent males are apparently forced out by the resident adult male (Sugiyama, 1965 - *P. entellus*; Poirier, 1969 - *P. johnii*) in the way that adult males are. In the hamadryas baboon, young females are kidnapped from the natal unit by adult males who then incorporate them into their own units (Kummer, 1971).

7.3.4. *Responses of residents and the behaviour of immigrants.*

In *P. anubis* the arrival of sexually-mature males in the vicinity of a troop leads to the transferred males of that troop chasing females away from the newcomers who are then themselves chased, often for several hundred metres. this has the effect of deterring most attempted immigration. However, one male actually managed to belong to two troops simultaneously and was able to move back and forth between them (Packer, 1979a).

Females in the new troop were not aggressive and cooperated when the new males started consortships, something which could even happen on the first day. Consort formation by new males often appeared to be a response to the approach of a resident male, serving, in consequence, to inhibit aggressiveness in the latter.

In the hamadryas baboon new males were also threatened by unit-leaders. The response, however, was not to run off but to behave like a female and run towards the attacker. As with Packer´s baboons, older males were more tolerant of `followers´ (Kummer, 1968). However the latter have little access to females and females, whose social activity is lower than in other baboons, have little to do with them.

Long-distance chasing has also been seen in rhesus and shifting is only accomplished after a transition of four or five days, during which time groups demonstrate their intolerance of the intrusion (Lindburg, 1969). The use of `group´ is ill-advised here since Lindburg provides evidence that females are eminently willing to copulate with new males during the transition phase. Boelkins and Wilson (1972) and Meikle and Vessey (1981) have noticed that males can accelerate their acceptibility by forming a relationship with a resident male, who is likely to be a brother. In M. fuscata immigrant males are always the lowest ranking and their status increases as dominant males disappear.

The process is markedly different in uni-male species, such as the colobines and guenons, where the arrival of males is marked by intense violence and, often, the defeat of the resident male. In P. senex such interactions lead to severe wounding and possible death. Male turn-over results in the exclusion of all immature animals of both sexes, something not seen in P. entellus (Rudran, 1973) where violence is followed by the departure of the resident adult and subadult males (Sugiyama, 1965; Hrdy, 1974). In P. johnii there appears to be less intense agonism following the arrival of strange males. This is surprising in the light of Poirier's own data which shows that 84% of all dominance sequences was accounted for by male-male encounters. However, he also recorded an unusual amount of play during "merging" and suggests that this is a behaviour facilitating the entry of immigrant males. Unlike the males, females were unconcerned by the arrival of new males (Poirier, 1969).

In the African colobines the process appears a little less traumatic. In C. badius an influx of males is noticeably peaceful (Marsh, 1979), while in C. guereza, where male take-over was an ultimate consequence of the presence of newcomers, it did not always follow immediately. New males did remain on the periphery, though, and may have interfered with reproduction (Oates, 1977).

With the apparent exception of P. johnii, langur take-overs commonly result in the killing of resident infants by the new male (Sugiyama, 1965; Mohnot, 1971; Rudran, 1973; Hrdy, 1977). Hrdy's account is the most detailed and she, seeing it in 70% of all take-overs, interpreted it as a male reproductive strategy insofar as an infant's death causes its mother to resume cycling, thereby enabling the male to impregnate her almost immediately. Female response to this is to attack new males and/or leave the troop. Infanticide in the African colobines is presumed on the basis of circumstantial evidence and must remain speculative until there are better data (Marsh, 1973; Oates, 1977).

Owing to the range of social systems within the guenons we would expect that the behaviour of immigrants and the response of residents will vary. What evidence there is supports this. In C. campbelli, a uni-male species, Bourliere et al. (1970) noted that the resident male responded aggressively to the presence of strange, migrating males but that females were less concerned. It is assumed that take-overs are violent.

Struhsaker's study of C. ascanius (1977) revealed that harem-male replacement could occur in two ways:

1. As a slow process in which the resident male is challenged

more-or-less successfully by an animal of equal strength, for example. Neither male is ousted nor has exclusive access to the females. This break-down of dominance leads to an influx of solitary males who do not work in concert but, instead, compete with eachother for females.

ii. One male replaces the resident male suddenly and aggressively. Interestingly, when this is completed it is followed by infanticide.

In two other uni-male species, the terrestrial _E. patas_ and the arboreal _C. mitis_, the data is sparse but suggestive of aggressive take-overs (Hall, 1965; Gartlan, 1974; Rudran, 1978). Vervet monkeys, which commonly live in multi-male groups, respond a little differently to immigrants in that males are soon integrated into the dominance framework. There is certainly no recorded attempt at infanticide and infants are generally ignored (Struhsaker, 1967b).

CHAPTER 3.

METHODS.

1.SAMPLING TECHNIQUES.

The primary requirement of this study was the provision of precise descriptions of behavioural acts at the empirical level (see Lehner, 1979). In addition it was necessary to be able to assess, for some of these acts, the way in which they were used socially. It is only through such quantification that function can be accurately postulated.

It is not possible to observe all subjects all the time; it becomes necessary, therefore, to sample behaviour and to sample it in such a way that the resulting data base is representative of the the total behavioural output (Lehner, 1979). Sampling procedures in behavioural research have become increasingly sophisticated and refined; comprehensive evaluations of the different techniques enabled the selection of those most appropriate prior to starting the study (Altmann, 1974; Dunbar, 1976).

Data were gathered by both `ad libitum´ and `focal-animal´ sampling. While ad lib. sampling, in which no constraints are employed, is regarded as being inadequate for the collection of quantitative data, it was well suited for obtaining information on the form of visual signals (see Chevalier-Skolnikoff, 1974). Employment of the technique, both on its own, as at Stainbank and Westville, or as two-minute bouts interspersed with focal-samples as at the Cage and Burman Bush, rapidly increased the number of required descriptions. It also facilitated the sighting of rare events, one of its acknowledged advantages (Altmann, 1974). As importantly, when used in conjunction with focal-samples, it greatly aided an understanding of the prevailing social mood and interactions, without which the point of focal-observations would have been missed. In this sense the data collection was actively biased towards the collection of information relevant at the time. This is a use of the method not discussed in critiques. However, since the sources of bias are so many, only those data which were important and rare (eg hetero- and homo-sexual activity, intertroop encounters, troop movement) were added to the focal-sample data.

Quantitative data were provided by focal-animal sampling. Here a single animal was followed and all its behavioural acts recorded in as much detail as the speed of events allowed. After some trial-and-error sample duration was fixed at three minutes. Longer sample times would have been less biased against protracted intractions but were not feasible at Burman Bush where visibility was restricted by the nature of the environment and by the animals being semi-arboreal and free-ranging. It is for this reason that data collection on forest monkeys is normally achieved through systematic scan samples (Aldridge-Blake, 1970; Rudran, 1978), which unfortunately are not capable of generating data of the type necessary for this study. Fortunately the animals at Burman Bush were sufficiently habituated to make focal-sampling possible. Short-duration samples have also been shown to give reliable estimates of total frequency (Baulu and Redmond, 1978). During focal-samples attention was additionally paid to what was going on elsewhere provided it was being attended to by the focal animal or did not interfere with collecting data from it (Hausfater, 1975, refers to this as `concurrent sampling´).

It was not possible to do all-day observations and data collection blocks were confined to periods of approximately one hour at a time. While these could not be correctly randomized it was attempted, as far as possible, to distribute them equally. The diurnal and seasonal distribution of observation minutes is given in Table 3-1.

Subjects, on the other hand, were randomly assigned to sample order using random number tables. Since they took time to find at Burman Bush not all subjects could always be sampled within an observation block, as was possible at the Cage. This was taken into account when analysing the relative frequency with which behaviours occurred.

2. DATA COLLECTION.

Once a sampling system has been chosen the data may be recorded in a number of ways. Of those potentially suitable for

	MONTHS												
TIME	J	F	M	A	M	J	J	A	S	O	N	D	
6-9	0	60	270	240	480	510	120	180	300	300	280	300	3040
9-12	225	60	240	360	510	360	360	120	60	180	160	270	2905
12-3	315	370	670	420	540	270	120	180	180	180	120	300	3665
3-6	270	360	360	180	360	330	0	420	60	60	180	120	2700
TOT.	810	850	1540	1200	1890	1470	600	900	600	720	740	990	12310

TOTAL HOURS: 205 hours 10 minutes.

a. Burman Bush.

	MONTHS												
TIME	J	F	M	A	M	J	J	A	S	O	N	D	
6-9	140	140	70	0	0	0	0	0	0	120	60	0	530
9-12	375	210	70	70	0	60	60	0	0	360	195	390	1790
12-3	205	0	0	0	0	0	85	0	0	120	195	0	605
3-6	490	280	70	0	0	0	0	0	0	120	260	325	1545
TOT.	1210	630	210	70	0	60	145	0	0	720	710	715	4470

TOTAL HOURS: 74 hours 30 minutes.

b. The Cage.

TABLE 3-1: The distribution of observation minutes at The Cage and Burman Bush, from which quantitative data were obtained.

this study, note-taking was rejected as being too slow and distracting, event-recorders and check-sheets required prior determination of the acts to be recorded, and videotaping was found to be too slow, clumsy and obtrusive. It was decided to make a spoken commentary of ongoing behaviour onto audio-tape (Phillips portable cassette). This could then be taken from the field and transcribed verbatim. It enabled me to concentrate on the subject at the time of recording, and had the advantage of allowing all perceived behaviours to be preserved in the form of a transcript. Unfortunately an hour of recorded data took up to four hours to transcribe, another thing that limited the number of hours spent in the field. A randomly-chosen sample transcription (Burman Bush, 13/9/1977) is given below:

"TROOP: Troop comes down to CZ (contact zone) from behind ablution block. TOG comes down after TE who was one of first. Most on ground. None of the other troops visible. TOG goes across road. OTR already there. TOG sits. Troop spread -some to CZII-foraging and resting. Females sit alone. GMR goes across road. More follow. Almost all over after awhile. There is an infant with a wounded head (hole in top of head; first sighting).

WTR. On fence, eating, hindleg-hunched. Surrounded by others - over road - her infant is 1m. away. Comes to ground, walks, tail 45deg. - hindleg sit, vocalize "krkrrk" (other females go "urf"). Looks to me, circles show - puts food in mouth and goes back across road. LT (Lower Troop) is arriving. Tail 45deg.tip down as walks. LT vocalizing "krr" as come down from bush. She stands, orientates in that direction, eats. All of UT (Upper Troop) back across road now. GEO goes "Waa" as TOG comes past with slight extension (penile). Intertroop encounter begins. WTR doesn't join in but observes."

On arriving at the study site the troop was located (not necessary at the Cage) and given 10 minutes to habituate. During this time the climatic conditions and the location of the troop were recorded. The sample session was always begun with an ad. lib. sample and then followed by a focal-sample. This cycle was repeated until the observation block had ended. When a focal-animal could not be located prior to the start of its sample it was sought for five minutes before being replaced by the next subject. If, during a sample, the subject disappeared from view that sample was discarded.

No animal was ever observed from closer than 2.5m. and if the subject additionally showed signs of discomfort at the closeness of the observer, the viewing distance was immmediately and appropriately increased. Leitz trinovid 8*32 were employed to watch events and animals further away. After some sessions photographs were taken with a Canon F1 camera and 200mm lens.

That the observer would eventually become a "neutral" part of the vervet milieu was not borne out in reality. Habituated animals, rather than ignoring a known individual would choose to interact in a number of ways, the most serious of which was the re-direction of aggression by individual animals and by the troop as a whole. The reception of social signals was recorded but responded to only by cut-off signals similar to those used by the vervets themselves. Thus a visual threat would be responded to by averting the eyes and, if necessary, walking away. The obvious consequence of this is that the observer, by sending subordinate-type messages was probably regarded more as a low-ranking camp-follower than an inanimate object. It may well be that no sympatric species are neutral in the way that is assumed in the literature. Vervets pay close attention to events going on around them and were certainly seen, for example, to utilize the vigilant behaviour of species with which they were not directly interacting.

3.THE RECOGNITION OF INDIVIDUALS.

Any comprehensive analysis of social processes needs ultimately to be based on individuals (Kummer, 1971; Wilson, 1975), something which is not possible if the animals are not individually recognisable. In primate research recognition has been most commonly achieved by getting to know subjects through the natural variation of physical characteristics. Kawai's (1979) description of this process in his study of gelada baboons is typical:

"The first condition is to create a suitable situation providing sufficient time observing the animals at close quarters under thorough habituation. After spending every day with the baboons we were able to recognize intuitively the gestalt of their facial expressions. It should be stressed that the identification of monkeys rests not only on a recognition of morphological features as the key, but also requires an accurate understanding of their lives." (pp.xiii-xiv).

Hrdy (1974) indicates that among the more "subtle" physical differences she used to identify animals were the shape of the tail-tip, colouration, freckles, ear-shape and facial exression.

While the ability of a human observer to reliably identify her study animals has been demonstrated (Bateson, 1977) it nevertheless remains that some will be better at it than others and that inter-observer reliability might be difficult to maintain with personnel changes. It could also be that some groupings within the society, such as juveniles or closely-related kin, are difficult to tell apart (Sharman, pers. comm., relates the tale of two juvenile vervets in a Kenyan study group that had been given the same name; a mistake which was not discovered for some time).

More seriously, though, is the possibility that the `subtle´ features used in constructing a gestalt are not exclusively those of the individuals that display them but are instead characteristics of the positions animals can occupy within the society. This is so at least for locomotion (e.g.the "confident" walk of dominant animals; Altmann, 1962) and tail position (where specific carriage styles may be due to status - Altmann, 1962; Ojha, 1974, or to age - Hausfater, 1977). The obvious consequence of using such criteria in identification is that animals sharing the same position may be mistaken for one another, especially if shifts in position occur.

Another practise has been to use animals with distinctive features such as scars or deformities (Hrdy, 1974) either as subjects or as "marker individuals" for troop identification. While the latter is acceptable, provided the animals used don't move, the former is seriously flawed in that such animals could be showing abnormal behaviour and/or releasing it in others (Tinbergen, 1953) and may not, in the longer term, adequately represent the range of phenotypes in the society.

For these reasons the programme of which this study was a part, was based where possible, on marked animals.

3.1.Trapping. The major objection to marking is that the animals would have to undergo an unnatural and traumatic experience (McGrew, pers. comm.). This was risked, however, but a trapping regime planned that strove to minimize it.

Collapsible "crush" traps, constructed from chicken wire with a trigger-released guillotine door, were set up in core areas of the troops' home ranges and baited with bananas, bread and samp. No trapping was attempted until the animals showed themselves to used to the traps by entering and leaving them without hesitation.

Once a vervet was trapped and the rest of the troop had moved off (unless it was clear that they were not going to do so), the trap was collapsed and the animal, while thus immobilized, given an intra-muscular injection of ketalar (Ketamine hydrochloride). Ketalar is an tranquilliser with a rapid action and a wide safety margin which, depending on the dosage, could keep a vervet unconscious for up to 90 minutes. While anaesthetised it was marked, weighed and examined to establish general physical condition. None of the handled vervets was left on its own until it had recovered sufficiently to climb a tree and had shown that it was capable of remaining up it.

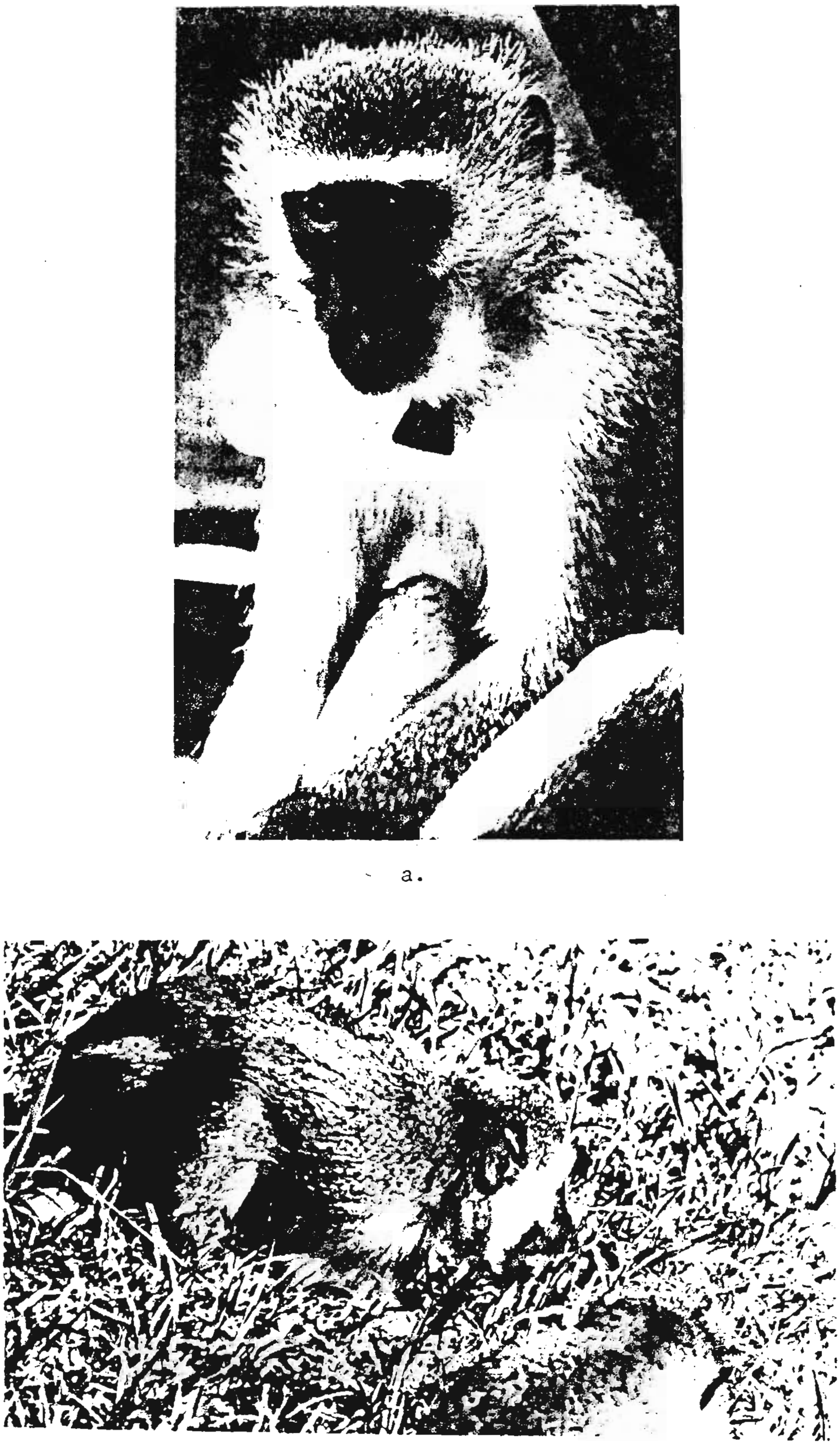
On being approached, the trapped monkeys would rush frenziedly from one side of the cage to the other, receiving cut hands and feet and lacerated eyebrow ridges as a result. While these were never serious they were immediately treated with antiseptic as a precaution. Fortunately the retroactive amnesia that accompanies the administration of ketalar (D.Perrett, pers. comm.) prevented the animals from remembering their own distress, something demonstrated on several occasions by their being re-trapped later the same day.

The response of the rest of the troop was dependent on their having remained in the area and then on the identity of the trapped animal. It ranged from indifference to the treatment of adult males to severe aggression (especially from the mother and alpha male) when infants or young juveniles were captured. It is true to say that the trapping regime did result in increased wariness by the troop but this was not long-lasting and was dealt with by using non-researchers to do the processing whenever posssible.

3.2.Marking. Two systems were used. At the Cage, and initially at Burman Bush, perspex pendants of four different colours and eight different shapes were hung around the vervets´ necks on a nylon-rope collar (fig. 3-1a.). The major shortcoming of such a scheme was that it did not efficiently cope with age-related changes in neck girth. Collars that were loose enough for adults slipped off younger animals. It was also noted that collars, although constructed to specifications accepted by the S.P.C.A., became too tight for some adults at Burman Bush, causing open-sores through chafing.

For this reason these animals had their collars removed and were given eartags, as were animals caught subsequently. A tag consisted of single-flex wire with single or multi-coloured plastic sheathing. A hole was punched in one of three positions in the monkey´s ear (top, middle-edge or bottom) using a sterilized awl, and the wire threaded through it and secured (fig.3-1b.).

The advantage of tags over pendants is that they are not as obtrusive, much less likely to damage the monkey and enable a subject to be identified while facing away from the observer.



a.

b.

FIG. 3-1. Identification markers.

The two disadvantages are that they are less visible at a distance and relatively less permanent, either falling out or being ripped off. However, an examination of the females in Upper Troop (who do not migrate) revealed that of eight tags attached in 1976, three were still in situ in 1981 (pers. observ.). This loss of one a year is much better than that reported in another study where bigger tags were used (Scott et al., 1976).

It is felt that, despite the invasive nature of trapping, marking paid dividends sufficient to justify it. It allowed the immediate collection of data from known animals and the utilization of information gathered by other workers (the death of GMR was reported by a member of the public who had seen the tag). The markers also served as independent checks that an animal <u>was</u> being recognised by its `gestalt´. Misgivings about the accurate identification of known but unmarked adults were probably not justified for, six months after the study commenced, all adults at the Cage and Burman Bush could be recognised without their markers being visible. Young juveniles and infants retained their anonymity throughout and were identifiable only if tagged.

CHAPTER 4.

SUBJECTS.

1. TAXONOMIC AFFINITIES AND CHARACTERISTICS OF THE GENUS.

The focus of this study is the vervet monkey. It is one of approximately 20 species of the genus *Cercopithecus* (LINNEUS,1758), that, together with the closely-related *Allenopithecus* and *Miopithecus*, comprise the group of African monkeys known as guenons. The guenons are medium-to-large, mildly sexually-dimorphic monkeys, all but two species of which normally inhabit forests. Their fur is thick, soft and short with many of the coats showing ticking or flecking. The group is characterized by flashes and bars of brilliant colours and striking adornments such as nose-spots and beards.

The species groups are anatomically homogeneous and hybridization has been recorded. The face is moderately orthagnathous, the tail is longer than the combined head and body length and the ischial callosities are small and well separated. Cheek pouches are present (Napier and Napier, 1967; Kingdon, 1971; Thorington and Groves, 1970; Aldridge-Blake, 1968; Murray, 1975).

2. THE VERVET MONKEY.

Of the two species that are found outside of forests one is C.mitis, which may occur in woodland savannah, and the other is the vervet monkey, C.aethiops (Gartlan and Brain, 1968). This latter species is the most widely-distributed guenon and consequently probably the most numerous (Tappen, 1960). It is unique within the genus in being found throughout much of the African woodland while being generally absent from forest areas (Kavenagh, 1980). It is also much more terrestrial than the others, something which is reflected in its comparatively generalized limb structure (Napier and Napier, 1967; Gartlan and Brain, 1968).

The evidence shows that the C.aethiops group consists of inter-breeding allopatric forms and must therefore be regarded as a single, polytypic species, although it is most conveniently divided into five sub-species on morphological grounds (Thorington and Groves, 1970; Dorst and Dandelot, 1972). The characteristics of each of these are described:

a.C.a.sabeus. Like the other sub-species it is a greenish-grey animal with a white-fringed face. The facial skin is black and there is no white band on the forehead. The tip of the tail is yellow and the genitalia are much paler than those of the other sub-species. It is found from Senegal to Ghana and has also been introduced onto the Caribbean island of St. Kitts. It has been studied in Senegal (Harrison, in prep.) and on St. Kitts. (Poirier, 1972; McGuire, 1974).

b.C.a.tantalus. It has a very conspicuous headband and the whiskers are sharply demarcated in colour from the crown. The perineal area is orange and the tip of the tail is whitish. It is widely distributed in the broad belt of savannah from Ghana to Uganda and has been studied by Kavanagh (1978; 1980).

c.C.a.aethiops. Its whiskers are pure white and distinctively long and fluffy. The tail tip is whitish. It is found primarily in Ethiopia and has not yet been the subject of intensive study.

d.C.a.cynosurus. It is the only vervet with a pale face. The tip of the tail is black. It has never been studied and occurs from southern Zaire and Angola to north-west Zambia.

e.C.a.pygerythrus. It has a conspicuous headband that blends with the whiskers which are not sharply demarcated in colour from the crown. The feet and the tail tip, especially in males, are noticeably blacker than in other sub-species. It is found from Ethiopia and Somalia down to South Africa and is the most widely-studied of the aethiops group, and therefore of the guenons (Struhsaker,1967abc; Gartlan, 1968; Gartlan and Brain, 1968; Lancaster, 1971; Krige and Lucas, 1974). Fig.4-1 shows the distribution of the group by sub-species.

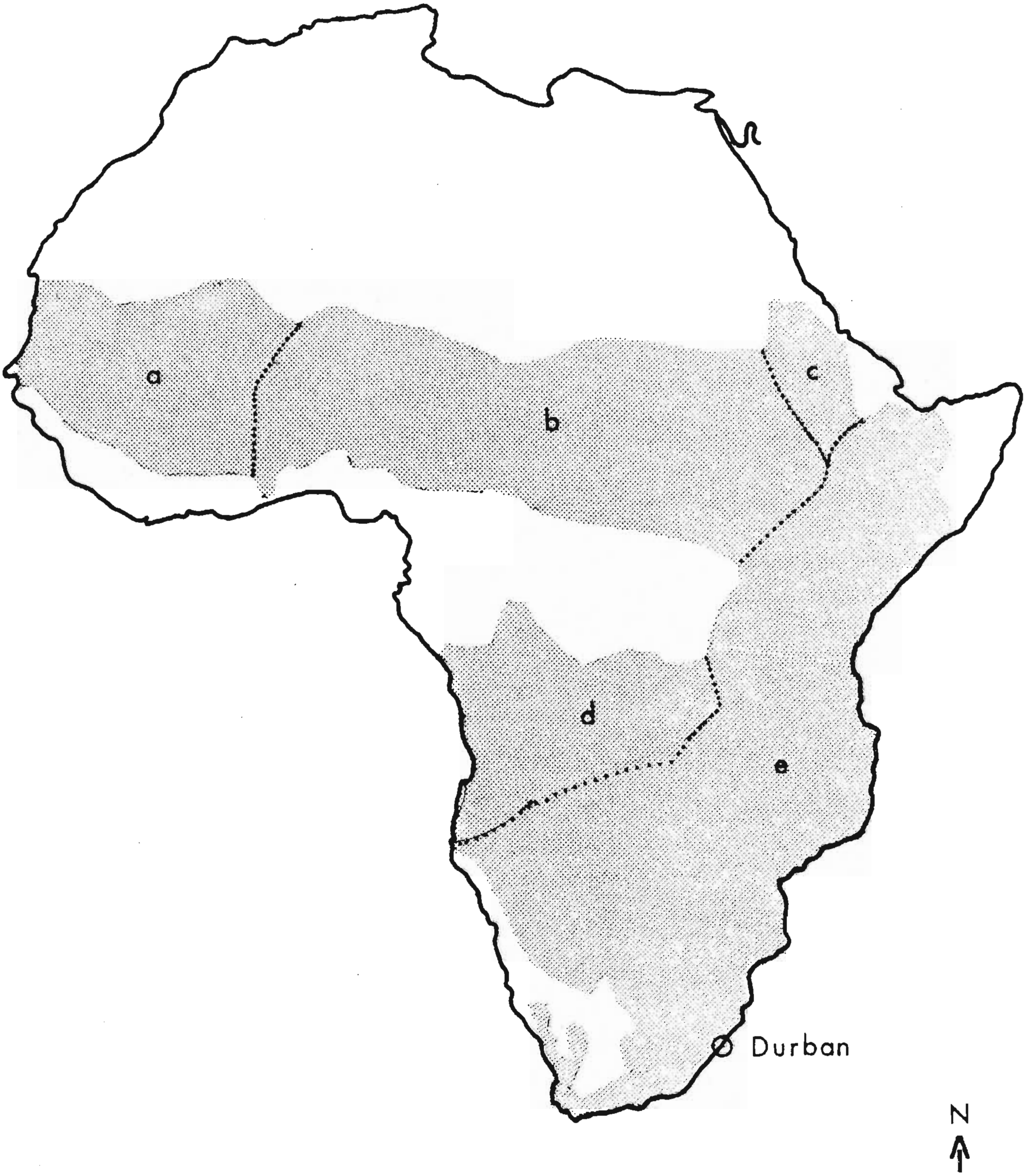


FIG. 4-1: African distribution of <u>C. aethiops</u>.

a. <u>C.a. sabeus</u>
b. <u>C.a. tantalus</u>
c. <u>C.a. aethiops</u>
d. <u>C.a. cynosurus</u>
e. <u>C.a. pygerythrus</u>

3. HABITAT AND ECOLOGY.

The vervet is regarded as the most adaptable guenon. It is capable of utilizing riverine and gallery forest, various grades of savannah, mangrove swamp, farmland within the rainforest and even urban parkland (Gartlan and Brain, 1968; Kingdon, 1971; Kavanagh, 1980; Henzi, 1979). Such habitats, despite their diversity, are generally more open than primary forest, thereby affording greater visibility and exposing the animals to increased predation (Cheney et al, 1981).

Their feeding style has been described as "eclectic" omnivory (Kavanagh, 1978); the resultant flexibility being demonstrated by the large inter-monthly variation in food sources. Such eclecticism allows them to capitalize on any sudden abundance of items within the dietary range (Struhsaker, 1967d; Moreno-Black and Maples, 1977; Kavanagh, 1980). Its distribution may well be based only on the availability of trees as a source of refuge and the presence of water (Wrangham, 1981).

4. SOCIAL ORGANIZATION.

The current view is that vervets are best described as territorial, multi-male, female-bonded societies (Wrangham, 1980). Crook and Gartlan (1966) graded *C.aethiops* as a "multi-male" system arising as a response to the increased pressure of a non-forest existence. Eisenberg et al (1972) argued that such a classification in the case of vervets was partially unfounded and that they could be more precisely categorized as falling along a multi-male/age-graded male continuum. Age-graded systems can be considered a phylogenetic step towards a true multi-male system by having a level of male tolerance that allows several young males to mature within the natal troop. It nevertheless remains a variant on the uni-male theme.

True multi-male species are identified by their having an "oligarchy of adult males that are roughly equivalent in age" and all functionally reproductive (Eisenberg et al, 1972). This has not yet been demonstrated insofar as Struhsaker has shown that males move between troops and that inter-male relations are not those expected of an "oligarchy", being characterized rather by dominance interactions and the resultant formation of linear hierarchies. McGuire (1974) noted exceptions to this in one of his troops on St. Kitts where adult males were seen to travel and play together. Generally, though, males are less socially active than females, receive more social acts than they give and spend much of their time behaving `vigilantly´ (Bernstein, 1971; Gartlan, 1968; Bramblett, 1973).

Play with juveniles has been seen (Struhsaker, 1967b; Bolwig, pers. comm.), while males are generally indifferent to infants who may, occasionally, manifest interest in the colourful genitalia of fully-adult males.

Wrangham (1980a) has criticized earlier analyses of the evolution of specific social structures, where inferences on the ultimate causes of group life are based on correlates of group size with ecological variables. From the exceptions to the correlations and the inability of explanations focussing on both sexes together to explain species differences in which sex migrates, a more useful approach might be to examine the distribution of individual rather than group characteristics. He proposes a classification of primate social systems in terms of social relations within the sexes. Vervets thereby fall within the group of "female-bonded" societies since females breed in their natal troops and are consequently bound to other females by close kinship ties (Lee, quoted in Wrangham, 1980a; pers. observ.).

Female relationships within such societies are predicted to be highly differentiated (Wrangham, 1980a; Struhsaker and Leland, 1979), something which appears to be the case for vervets. There is a linear dominance hierarchy, suggested by Lancaster (1971) to be separate from that of males. Grooming is frequent, more so than among males, and is commonly directed towards more dominant animals. Since coalitions play an important part in vervet female agonistic interactions, this may help in retaining the services of more dominant kin (Struhsaker, 1967c; Lancaster, 1971; Seyfarth, 1980; Fairbanks, 1980). Indeed, Seyfarth (1980) demonstrated that high rates of grooming were significantly correlated with high rates of alliance formation and/or proximity. It has been argued by Fairbanks

(1980) that Seyfarth´s conclusions ignore the effect of kinship. This is certainly confounded with dominance (see Hausfater, 1980) and may be very important in its own right.

Apart from the exploitation of particular ecological niches, female interactions are also assumed to be relevant to the rearing of offspring. Vervet mother-infant pairs have been found to be highly attractive to other females (Krige, 1975; Seyfarth, 1980) and allomaternal care is common and well-developed (Krige and Lucas, 1974). Mothering is intense and protective and is aided by the ability of mothers to distinguish their semi-dependent offsprings´ vocalizations (Cheney and Seyfarth, 1980; pers. observ.).

Adult male-female interactions have been less clearly delineated in the literature. Sexual behaviour is generally seasonal, relatively rare and may be initiated by either sex (Gartlan, 1969; Lancaster, 1971; Struhsaker, 1967b). The male dominance of females reported by Struhsaker (1967c) has not been as clearly observed in other studies (Gartlan, 1968; Lancaster, 1971). Females appear to be responsible for the initiation of friendly interactions (grooming) while males largely limit their interactions, at least in the breeding season, to the olfactory monitoring of sexual state (see Gartlan, 1969). Wrangham (1980a) goes so far as to postulate that females, in territorial female-bonded species are responsible for regulating the number of adult males in a troop.

Although vervet troops have home ranges that overlap with those of their neighbours they are territorial in that they will actively defend boundaries on contacting transgressors. The territories are maintained all year round and defended by all age/sex classes with the exception of infants (Struhsaker, 1967c). Nevertheless, play and grooming have been seen to occur between members of different troops (pers.observ.) while adult males have been reported to move between troops (Struhsaker, 1967c; Gartlan and Brain, 1968).

Table 4-1: Troop Size

	June 1974	June 1978	Annual increase %	Ratio of adult males to adult females	
				1974	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

5.SAMPLE POPULATIONS.

Within the province of Natal *Cercopithecus aethiops pygerythrus* is widely distributed along the coast and in the midlands where it even reaches the foothills of the Drakensberg Mountains. Given sufficient cover it may also be found within the boundaries of towns and cities (Pringle, 1974).

Urban populations of the species are important for a variety of reasons, and their continued presence is reliant on the establishment of reserves and the curbing of antagonistic human activity (Henzi, 1979). One beneficial consequence of their prolonged exposure to humans is that they are habituated to the presence of observers. This allows close and detailed following of individual animals which helps to counter the poor observation conditions inherent in working on semi-arboreal animals in a wooded environment. (Gartlan records that 2073 hrs. of observation time in a forest yielded 198 contact hours-Gartlan and Struhsaker, 1972).

Data for this study, which commenced in July, 1976 and ended in June, 1978, were collected from four different troops at four different localities within a 20 km. radius of Durban, a city on the east coast of South Africa (see figs. 4-1 and 4-2).

5.2.*Burman Bush.* Burman Bush is a 44.3 ha. nature reserve lying within the Durban suburb of Morningside. It was designated a Park and Open Space in 1962 and falls under the jurisdiction of the Durban City corporation. It lies approximately three km.

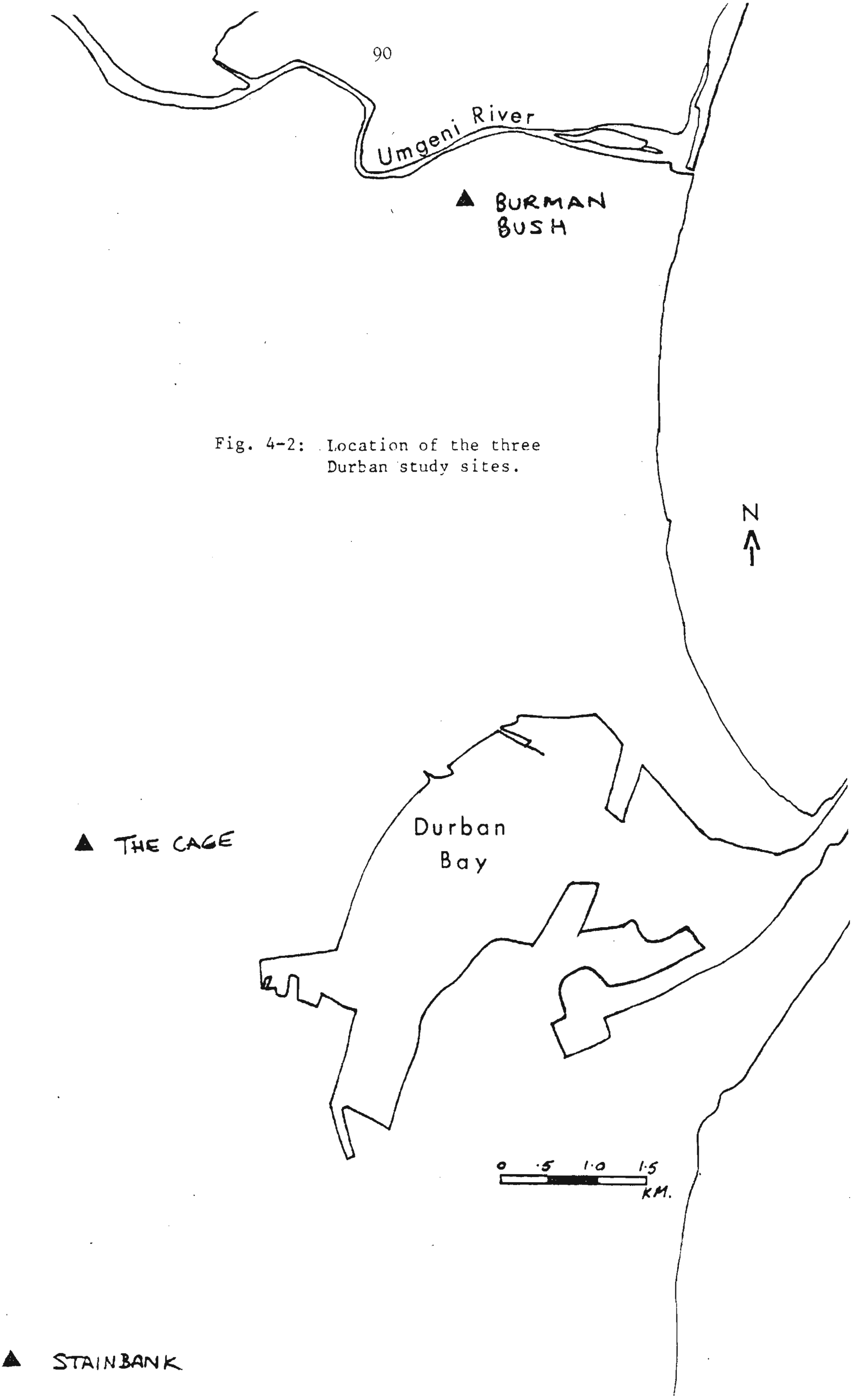
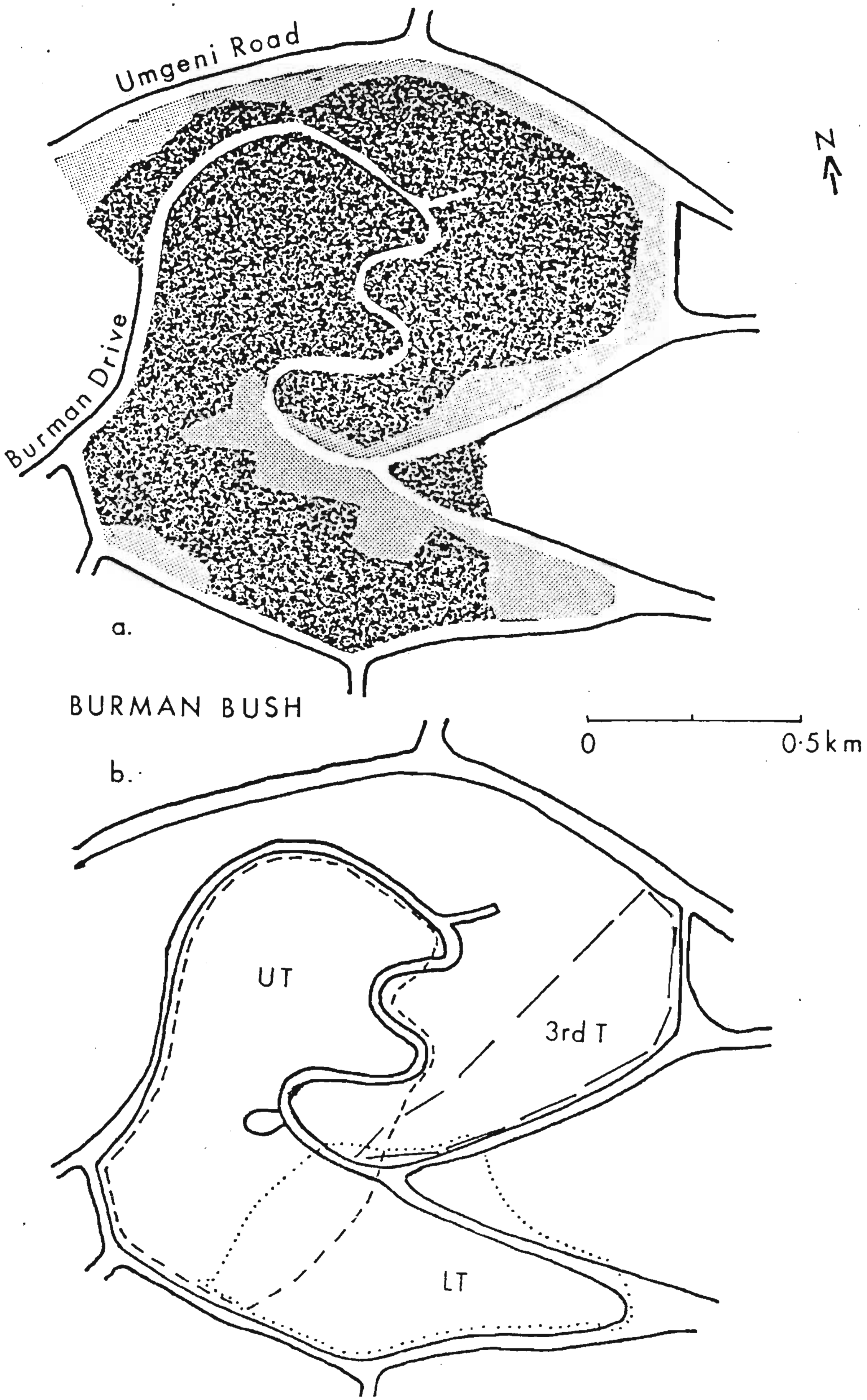


Fig. 4-2: Location of the three Durban study sites.

FIG. 4-3. Burman Bush. a. Habitat structure, dark shading = forest, light shading = clearings.
b. Home ranges of the 3 observed troops.



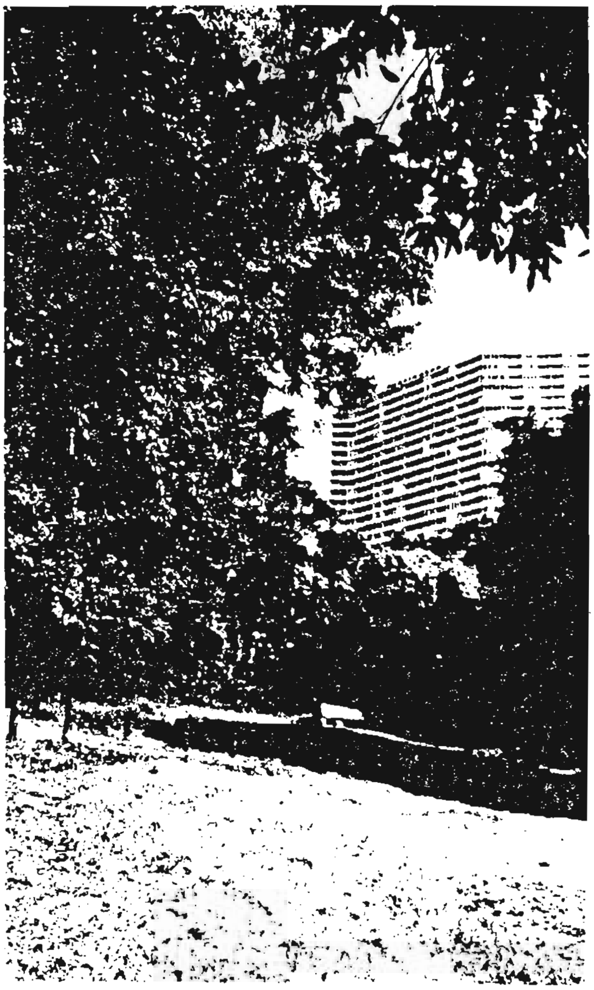


FIG. 4-3 c. Scenes at Burman Bush.

from the sea, rises to about 60m. above sea-level, and is bounded on three sides by light industry and residential areas. The fourth side is adjacent to the Umgeni River, vegetation along the banks of which connects the Burman Bush monkeys to vervet populations further away (fig. 4-3a). A busy road runs through the reserve and tourists and picnickers frequent the maintained clearings on either side of it.

The area is covered by subtropical coastal forest which has been disturbed to various degrees. The canopy is closed or partially closed and may be vertically stratified as follows (Bourquin, 1968):

i. Upper canopy of trees and climbers at approximately 8-10m.
ii. Short tree layer between 3.5-8m.
iii. <u>Isoglossa woodii</u> shrub layer between 1.5-3.5m.
iv. Sparse ground cover under trees and grass in the open.

Apart from the vervets the area is poor for mammals, although both red duiker (<u>Cephalophus natalensis</u>) and blue duiker (<u>Cephalophus monticola</u>) were occasionally seen. A pack of domestic dogs wandered through the park from time to time and only they, giant eagle owls and pythons could possibly predate on the vervets.

Four troops live within the reserve although one of these was only infrequently seen. Table 4-1 indicates the population size and its change over time for the other three, and gives some indication of the ratio of adult males to adult females. The troops- Upper Troop, Lower Troop and Third Troop- occupied adjoining territories and exhibited a fair degree of home-range overlap (Fig. 4-3b). Fig.4-3c provides some views of the area.

The monkeys were a source of interest to the public and were as a consequence offered a variety of foodstuffs. This supplemented their diets sufficiently to maintain them in good physical condition and allow the population to increase at a rate comparable to those of other provisioned troops (see Dittus, 1977; Drickamer, 1974). Surprisingly little human-monkey interaction occurred during observation periods. There were possibly more over week-ends.

Although all three observable troops were monitored from 1974 to 1978 for data concerning inter-troop movement and were observed during inter-troop encounters, only one troop, Upper Troop, was regularly sampled. This was done from July, 1976 to June, 1978 to get qualitative data on the variety and structures of visual signals and quantitative data on their social deployment. Only a portion of the troop, selected to match the age-sex composition of the Cage troop, was sampled. This was later broadened to include all the adult males. With the exception of some of the males all the sample animals were tagged (see below). Non-tagged adults were, however, all individually recognisable. Table 4-2a lists all adults; sample members are underlined.

5.2.The Cage. The Cage is a hemispheric enclosure constructed out of piping and covered with wire-netting. It has a diameter

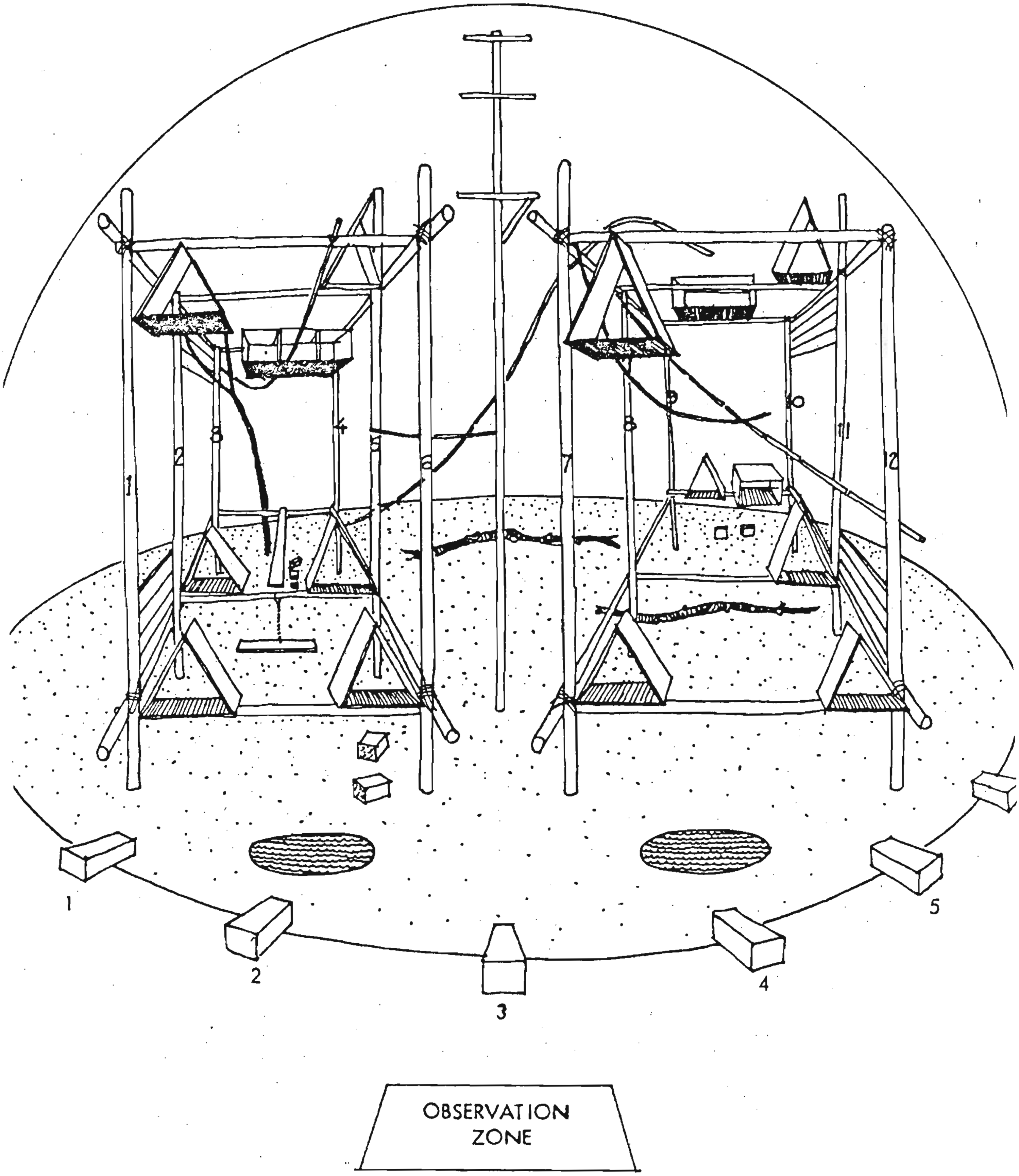
NAME	AGE/SEX	REMARKS.
TOG	AM	Arrived 6/76. Tagged on right ear.
TE	AM	Left 6/78. Missing assumed dead, 7/78.
TY	AM	Arrived 6/76. Left 5/77. Tagged on Left ear.
GEO	AM	Arrived 5/77. No tag.
PER	AM	Arrived 4/78. Unmarked.
POI	AM	Arrived 4/78. Unmarked.
NN	AF	Top-ranking female. Unmarked.
UNM	AF	Unmarked.
CRP	J/AF	Had cripple hand. Gave birth 11/77.
LBN	AF	Old. Unmarked. Missing assumed dead, 7/78.
WTR	AF	Tagged on right ear.
WML	AF	Tagged on left ear.
OTR	AF	Tagged on right ear; fell out 11/77.
GNT	AF	Collar and pendant.
BS	AF	Collar and pendant. Killed 5/77.
GTR	AF	Tagged right ear.
GTRJ	J/AF	Tagged right ear. Gave birth 1977.
GMR	JM	Tagged right ear. Killed 4/78.
GTL	JM	Tagged left ear.
SUB	JM	Unmarked. Disappeared 4/78, presumed migrant.
GBL	JM	Tagged left ear.
YBL	J/AF	Tagged left ear. Gave birth 11/77.
GBR	JF	Tagged right ear.

TABLE 4-2a. A listing of the recognisable adults and juveniles at Burman Bush. A - adult; J - juvenile; M - male; F - female. The names of sample members are underlined.

ALF	AM	Pendant. Dominant male. Escaped after completion of study.
TOM	AM	Pendant.
U	JM	Pendant.
DISC	JM	Pendant.
CROSS	JM	Pendant.
OMEGA	JM	Pendant.
OBL	AF	Pendant. Dominant female.
BOLT	AF	Pendant.
TEE	AF	Pandant.
SQ.	AF	No marker.
VEE	AF	Pendant. "Stress"-related death after completion of study.
LB	IM	No marker. Son of BOLT. Born 10/76.
TT	IM	No marker. Son of TEE. Born 11/76.
DS	IF	No marker. Daughter of SQ. Born 10/76.

TABLE 4-2b. The members of the Cage troop during the study period. I - infant.

Fig. 4-4: The Cage.



of 13m. and a maximum height of 6.5m. (refer to Tollman and Lucas, 1979 for a more detailed account). It was constructed in 1975 and is located in the Natal University gardens. It stands in a small clearing and is surrounded by trees. These give some protection against the weather and obscure human activity in the surrounding area (Tollman, 1977). Casual visitors were not allowed in the vicinity of the Cage during the study period.

The interior was designed to provide for all the major activities seen in free-ranging animals but organized in such a way as to promote maximal visibility (Fig 4-4). The provision of 14 small shelters gave the vervets protection against the elements and other animals, and resting places that could accomodate varying numbers of monkeys. Food which consisted of bread, eggs, vegetables and fruit was given through five separate food shutes in order to minimize food-based aggression. The cement floor was built with two shallow depressions which serve as pools and provide a continuous supply of water.

The advantages of this construction over more conventional enclosures are that it is structurally stable, constitutes the most economical way of covering the most space, eliminates corners where animals may get trapped during agonistic encounters and allows within it a complexity of structure that goes some way towards meeting the needs of its occupants (Tollman, 1977).

The monkeys were observed from an observation hut situated 3m. from the cage. It was not possible to effect an unnoticed entrance into the hut, nor to completely conceal activity within it. To minimize this latter problem the interior was painted black and the windows covered with mosquito gauze.

The Cage was originally conceived to assess the ways in which free-ranging vervet monkeys respond and adapt to confinement. Tollman (1977) described these processes in detail and concluded that by the time the present study began the confined troop had successfully adapted, exhibiting all the behaviour patterns seen by her in the field with the natural exception of troop movement. The retention of some patterns were undoubtedly caused by the fact that the Cage was situated within the home-range of a small troop of free-ranging vervets that interacted with the confined animals on a daily basis.

The caged troop consisted of 11 animals trapped and removed from a feral troop living on the Beachwood golf course, 17km. north of the university nursery. These animals and the three infants born in 1976 were observed as part of the present study (Table 4-2b). Systematic observations at the Cage commenced in June, 1976 and ended in April, 1977.

5.3.Kenneth Stainbank Nature Reserve. This reserve lies 9km. south-west of the city centre. It lies between 30m. and 150m. above sea-level, comprises some 240ha. of coast forest and grassland and is entirely bounded by suburban development (Campbell, 1966). It is floristically similar to Burman Bush, although in much better condition and faunistically far richer.

Four troops of vervet monkey occur within the reserve. One of these did not range outside the reserve and was chosen for observation. This was done to increase the sample size and to investigate the nature of the visual displays between relatively unhabituated animals and a human observer. Time constraints prevented any attempt to systematically follow, count or recognise individuals within the troop. During the months January to March, when the troop was followed it was roughly estimated as having 24 members, 3 of whom were adult males. Of the 112 hours spent in the field, 62 involved visual contact with the animals.

5.4.Jan Hofmeyr Road, Westville. The burough of Westville lies some 21km. west of the city centre. Diminishing areas of forest, scrub and secondary growth within its boundaries still harbour a few troops of vervet monkeys. One of these regularly visited the property of R. and J. Senogles to whom they had become habituated, and by whom they were fed, thereby facilitating the gathering of data.

The animals were observed for more than 100 hours between October, 1977 and March, 1978. The troop, consisting of 14 animals, was observed both to gather general information on visual signals and in connection with the presentation of models.

The climate of the research areas may be described as sub-tropical with hot, humid summers and mild winters. Table 4-3 presents the monthly means of some relevant climatological parameters.

In the Durban area there were discrete mating and, consequently, birth seasons. Fig. 5-37 shows the annual distribution of observed mounts (as a percentage of the total), corrected for the number of observation hours and number of males in the troop. The birth season commenced in October and usually peaked in November.

MONTH	RAINFALL(mm.)	TEMP.(C)	HUMIDITY(%)
January	118.2	24.5	81
February	177.1	25.7	81
March	152.7	23.6	83
April	91.0	21.0	80
May	80.6	18.7	77
June	21.4	16.7	74
July	25.3	16.9	65
August	41.7	17.0	60
September	61.8	19.3	64
October	107.4	21.0	71
November	106.7	21.5	73
December	110.9	23.1	79

TABLE 4-3: Climatic data for the study region. Data was obtained from the Weather Bureau, Lois Botha Airport, and averaged, by month, over the study period.

CHAPTER 5.

RESULTS

5.1. THE ELEMENTS OF VISUAL SIGNALLING.

5.1.1. Obtaining information.

It was clear from observation that the vervets were finely attuned to visual signals. Their visual acuity was excellent and they often demonstrated that they were capable of discriminating, strange from familiar dogs, for example, over distances of up to 500m.

Their reliance on the visual channel is indicated by their use of a number of ways of improving reception.

i. Scanning. Animals briefly, and apparently spontaneously, interrupted activities in order to visually scan the environment. It was also an invariant response to alarm and interest vocalizations (Cheney and Seyfarth, 1980).

ii. Bipedal stances. If interested in something happening at a distance, vervets of all age-sex classes except young infants, stood on their hindlegs , using the tail as a brace, and attended to the object of interest (Fig. 5-1). The posture, while usually brief, could be sustained. Adult males also performed a `hop' while running which allowed them to scan the environment (Struhsaker's "hop and gallop"). It was especially used when they were running down to meet a troop or en route to an

Figure 5-1: An example of the bipedal stance used when scanning.

aggressive encounter.

iii. During agonistic encounters, animals sometimes tapped opponents with their hands and then, when eye-contact had been established, delivered a facial threat. It was clearly a means of counteracting the visual "cut-off" (Chance, 1962) which recipients of threat used to eliminate visual input. It was employed by all age-sex classes except infants.

5.1.2. Facial Expression.

The adult vervet face is black and surrounded by the pale fur of the headband and cheektufts. This isolates it from the rest of the body, and makes it easy to locate, even in low luminance. The teeth and unpigmented eyelids and orbital rings, when exposed, stand in contrast to the face and make conspicuous expressions with which they are associated.

Table 5-1 lists facial expressions which were used by vervets in the study population. The orbital rings were present in all except the neutral and lipsmacking faces. Some examples are given in Figs. 5-2 - 5-6. It is evident that threat grades more finely than does `fear'.

Animals responded to threat either by looking away, returning it while defensively postured, or by screaming. Screams produced faces that resembled grimaces except that vocalization was present and intense. Silent grimaces were seen on two occasions, both given by the same female on the sudden

	EXPRESSION.	EYES	EARS	MOUTH	VOCALIZATION.	POSTURE.	CIRCUMSTANCES.
1.	Neutral	not fixed	-	relaxed	-	relaxed	A relaxed animal. The resting state of the face.
2.	Alert	focussed on object of attention	normal	closed	-	variable	Paying attention to something that does not yet, if social, directly involve it.
3.	Stare	directed to opponent	normal to back	closed	-	variable	Mild aggression although response to it may vary, depending on the status of the recipient.
4.	'Hardlook'	directed to opponent.	back	closed, jaw thrust forward. Headband retracted	silent, although may be preceded by "hurr".	variable, hunched if defensive. Head may be bobbed	Aggression of variable intensity. Most common threat.
5.	Open-mouth threat	"	"	open. Lips pressed tightly over teeth. Jaw forward.	"	As above. Headbob often more intense	Presumed to be more intense than 4. but probably dependent on individual differences.
6.	'Look away'	Averted	normal	closed	none	variable. Hunched if received 4 or 5	The usual response to a direct gaze or threat. Served to 'cut-off' encounter.
7.	Lipsmack	averted	normal	slightly open, lips pursed, tongue flicks in and out	"lipsmacking": sound of tongue hitting lips.	variable, often standing.	conciliatory; used when taking infant from mother or in approaching more dominant vervet.
8.	Open-mouth scream threat	directed to opponent	back	open, lips retracted and teeth visible and apart.	a variety of screams depending on age and sex	hunched chase or hunchedsit	response to aggression.
9.	'Chutter' face	directed at object	normal to back	as in 8 above	"chutter"	variable	Fear - given to potential predators. Not given in connection with behaviour of other vervets.
10.	Play-face	Averted	normal to back	open, lips generally cover teeth but not pressed down	none	associated with play	Play. Given by both although not always preceeding bout.
11.	Pout Face.	directed or scanning	normal to back	closed-lips forward forming "O"	"rrr"	variable	Seen in infants when anxious. Results in retrieval by mother.

Table 5-1: A list of facial expressions isolated in vervets. Not included id the yawn which is discussed in detail below.

Figure 5-2: Illustrates a neutral face that shifts into an alert, staring one.

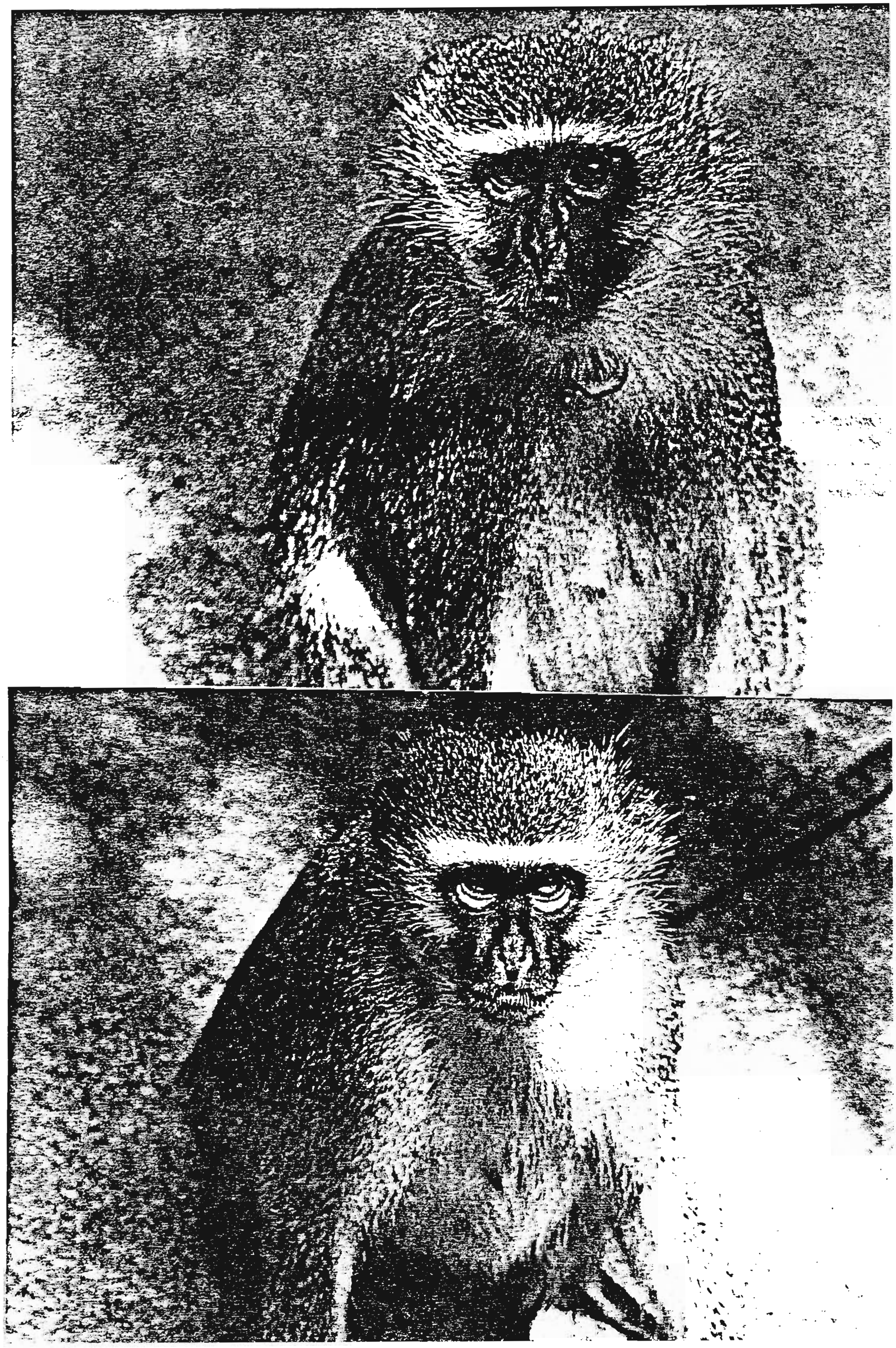
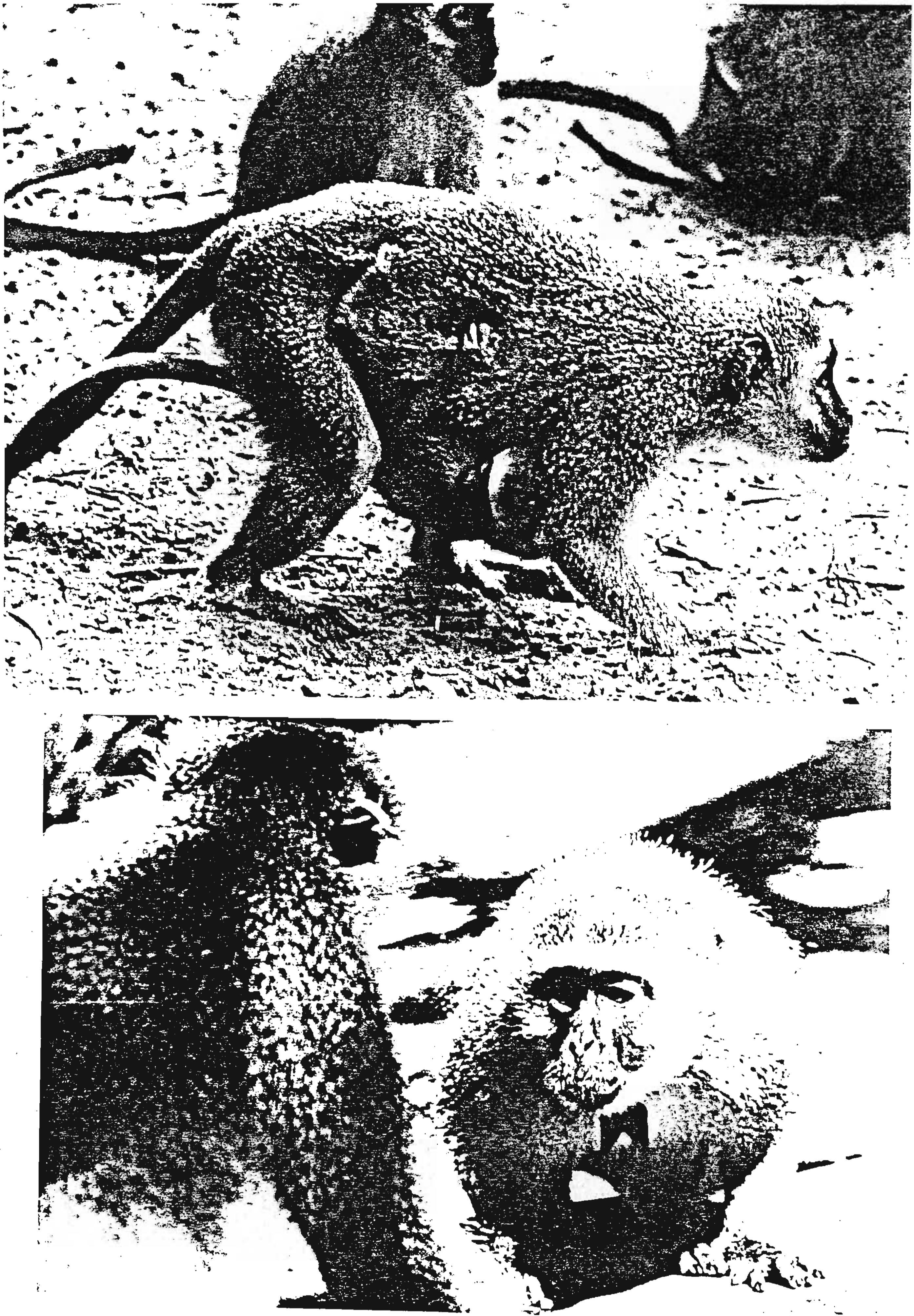


Figure 5-3: The Hardlook (a) and the same face (b) given while in a defensive posture.



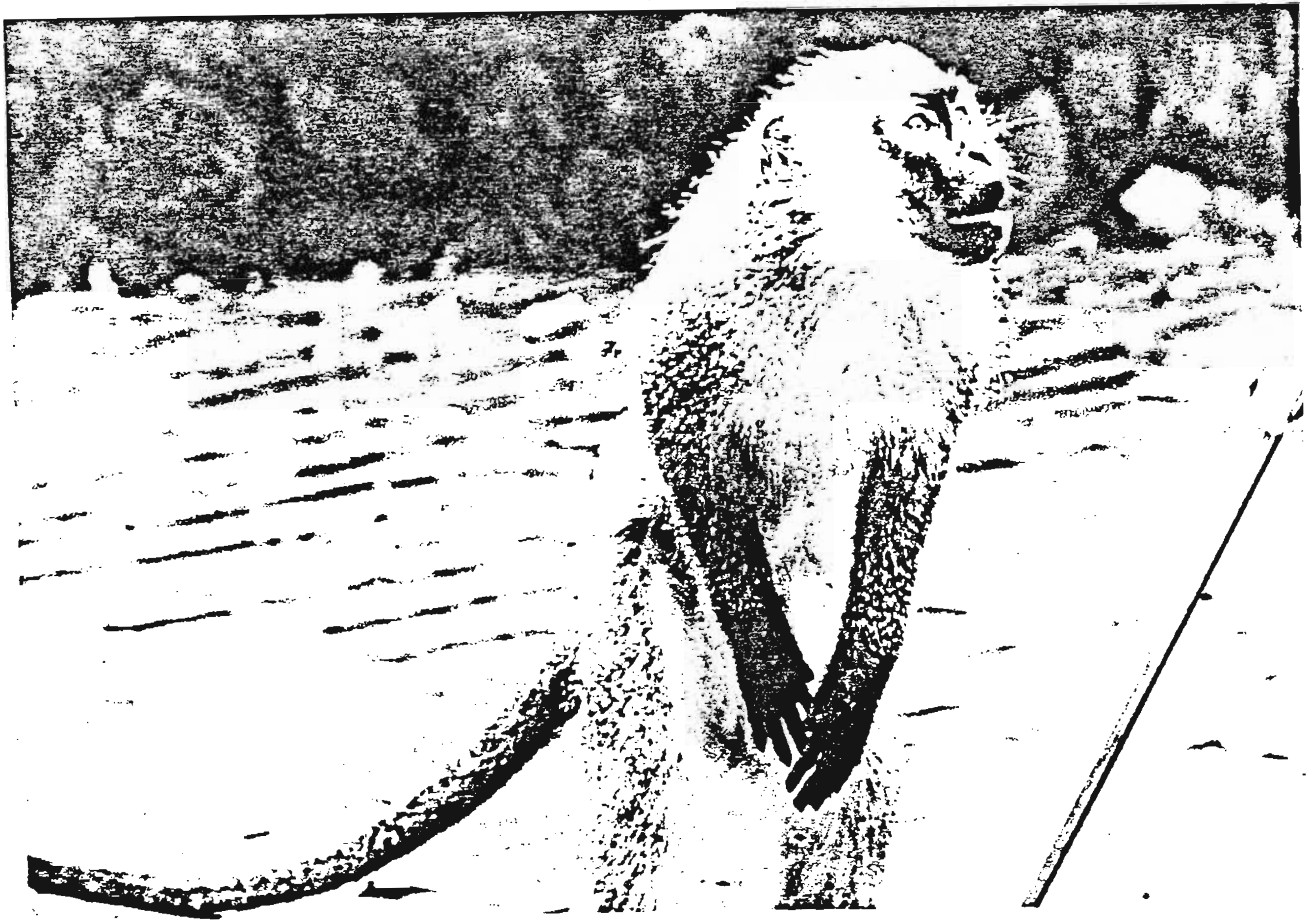


Figure 5-4: Open-mouth threat, given with an extreme 'bob' which resulted in the animal rising onto its hindlegs.

Figure 5-5: The chutter.

Figure 5-6a. : Two scream faces, given by an adult male and an infant.

arrival of the alpha female. When given the eyes were averted and the body hunched. By comparison with the other expressions it was extremely rare and therefore not included in the table. Lipsmacking, while not strictly an expression, is included here because it has an obvious visual component.

The increase in the physical intensity of threat is presumed to be related both to the nature of the context and to the motivational state of the signaller. However, it appeared that situations that solicited severe threat from some animals hardly resulted in anything from others. Further study should focus on the interrelationship between individual identity and status, context and recipient identity. It may well be that individual idiosyncracies account for much of the observed variability. As a general rule, higher ranking animals had more effect with less intense signals.

Also recorded was a head movement - the `headflag' - that, while not an expression, was performed at a typical intensity and was very conspicuous. It is discussed below in the section on genital signals.

Developmentally, infants used only the play face, seen appearing as a `bite' by the second week, or a version of the scream face where the vocalization was shrill and the mouth less widely open than in adults. Also seen was the `pout face' that resulted when infants gave the "rrr" vocalization. It did not occur in the absence of the vocalization.

The developmental change in infant colouration catalogued by Krige (1975) was verified in this study by weekly assessments of the colour of infants of known age. She derived four categories:

I. Black infant (0 - 6 weeks). The pelage was black and the face naked and pink. The duration of this phase was confirmed.

II. Dusky-faced infant (6 - 18 weeks). Face gradually turned black, except round the eyes and mouth (by 12 weeks). This was not confirmed. Infants observed from 1976-1978 retained paler faces until they were at least 7 or 8 months old. There was also some variability in the rate at which the face changed colour and all young juveniles (~12 months) had paler skin around the mouth. The change of colour in the ears matched this.

The beginnings of a white headband by 8 weeks and its development by week 12 was the same as seen by Krige. However she says that only a few of her infants developed a thin yellow line on the forehead as a precursor to the headband. My data indicate that all infants developed this during the third or fourth week and that it was the first real colour change to appear.

III. (12 -18 weeks). Infants in this category were regarded as being only slightly darker in pelage to adults. I suggest above that the face is still differently coloured.

IV. (18 - 24 weeks). Regarded as resembling miniature adults. With noted exceptions, this is essentially true.

5.1.3. Locomotion.

i. Walk. The usual form of loccmotion, both on the ground and arboreally, was the quadrapedal walk; with the right forelimb and left hind limb moving together and alternating with the opposite set of limbs. It was generally indicative of a socially relaxed animal, although when approached in this way by a dominant vervet a subordinate might well have moved off. In doing this, it was said to have been displaced. High-ranking vervets, especially males, walked `confidently' (spine concave), while lower-ranking ones appeared more hunched.

ii. Run. Walks could increase in pace until the animal was galloping (the forelimbs moved in unison and met the hindlimbs, also moving in concert, on the substrate under the body). Animals ran in a variety of circumstances (see `homage' and `tree display' below) and could generally serve to cue observers that something of relevance was happening.

iii. A chase was a run or gallop directed towards a specific recipient during agonism or play. When performed by a subordinate animal in response to a more dominant one, the body was generally held lower and shorter steps were taken.

iv. Jump. The performer left the substrate entirely either leaping onto, or down from a tree, or onto a play partner. It was also a means of rapidly getting away from an opponent.

v. Climb. Trees were ascended head first but descended in this way only if the distance was short or the trunk angled. Descent over longer distances was tail first.

vi. Back off. When threatened, an animal often backed off by moving its legs back a little and then moving the hands back to meet them. The body was hunched during the movement. It allowed the animal to continue facing the aggressor, and thus keep it in visual contact, while increasing the distance between them.

vii. Dart towards. In aggressive encounters, especially between troops, vervets would take a few short, rapid steps towards an opponent, while maintaining eye-contact. This dash was followed by a stationary threat or a bipedal stand.

viii. Play. The movements associated with play form an obvious complex involving combinations of the above plus `wrestling', where the play partners established physical contact and grappled with each other.

ix. Tail carriage during locomotion depended on both status and context. Alpha males and alpha females habitually carried theirs curved `down and out' while the rest of the troop carried theirs more slackly. TE was an exception to this and continued to carry his tail curved after his decline in status. During aggressive interactions, the aggressor, even if not high-ranking, curved its tail while threatening. It is presumed that curved carriage indicates increased muscle tonus (Altmann, 1962). It did add to the apparent size of the animal by lengthening the line of the back (see Fig. 5-6) and may have been used for this reason during agonism, as piloerection was. Genital display was also facilitated by curved tail carriage. Natal vervets only infrequently raised their tails vertically or curved them back towards the head.

5.1.4. Posture.

i. Lie. A resting posture and also one adopted by recipients of grooming. The animal was recumbent, its torso on the substrate and its legs either tucked in underneath it or held out to the side.

ii. 4-leg sit. These sitting postures were distinguished from others in that all four limbs rested on the same substrate. The variants include extended limbs or limbs placed up against a vertical surface. They were used in a number of contexts, with some being resting postures and others, notably the 4-leg-up also serving in other communicatory capacities (see Fig. 5-7 and the section on penile extensions below). The 4-leg-hunch was adopted in response to aggression.

iii. Hindleg sit. The arms were lifted off the substrate, either in use or resting on the legs. The legs were either bent, extended or dropped and, additionally, could be held together or splayed (Fig. 5-8). this group of postures was adopted when using the hands, resting or displaying the genitals.

iv. Bob-sit. During aggression, again especially in intertroop encounters, the bob-sit sequence was common. The animal darted forward, gave a facial threat while bobbing the head and forequarters and then immediately sitting or standing straight up (see Fig. 5-4). Apart from introducing a movement component to the threat it served to `flash' the white ventral surface which, by contrasting with the otherwise dark body, added to the conspicuousness of the display.

v. Stand. All four legs were on the substrate while the torso was raised off it. It was sometimes used in a display context (see `broadside' below).

vi. Bipedal stand. The forelimbs were lifted off the ground while the hindlimbs were extended vertically.

vii. The present. This display was seen in a sexual context and very infrequently as a submissive gesture. It is considered below.

viii. Grooming solicitation. The vervets made pointed use of some of the above postures in order to solicit grooming from others. This was most commonly done by walking up to, and lying down in front of another animal. It was also achieved by sitting up in front of a potential groomer, or by merely coming and standing in close proximity to it. Refusal by the recipient to groom was often met by the adoption of alternative solicitation postures.

5.1.5. Genital signals.

These are considered in detail below.

5.1.5. Miscellany.

During intertroop aggression, females frequently bunched together en masse while threatening members of the other troop. Such a phalanx of animals (Fig. 5-9) was imposing and apart from any other purpose, it created the illusion of a `superorganism' such as that described by Kingdon (1971) for the banded mongoose. The cooperation of animals in creating a single

Figure 5-6b: Two examples of curved tail carriage. The top vervet is an adult male and the lower one a juvenile.

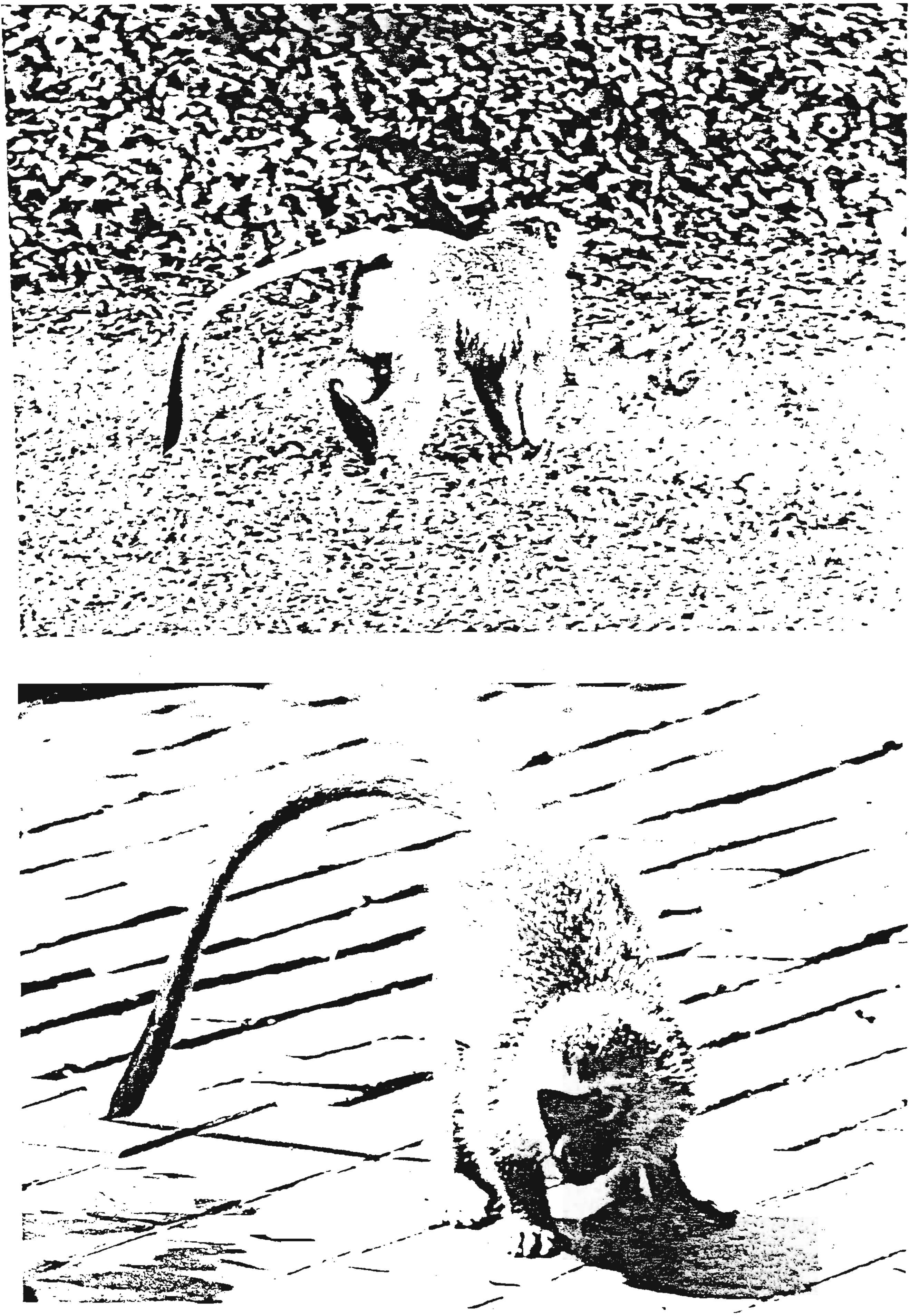
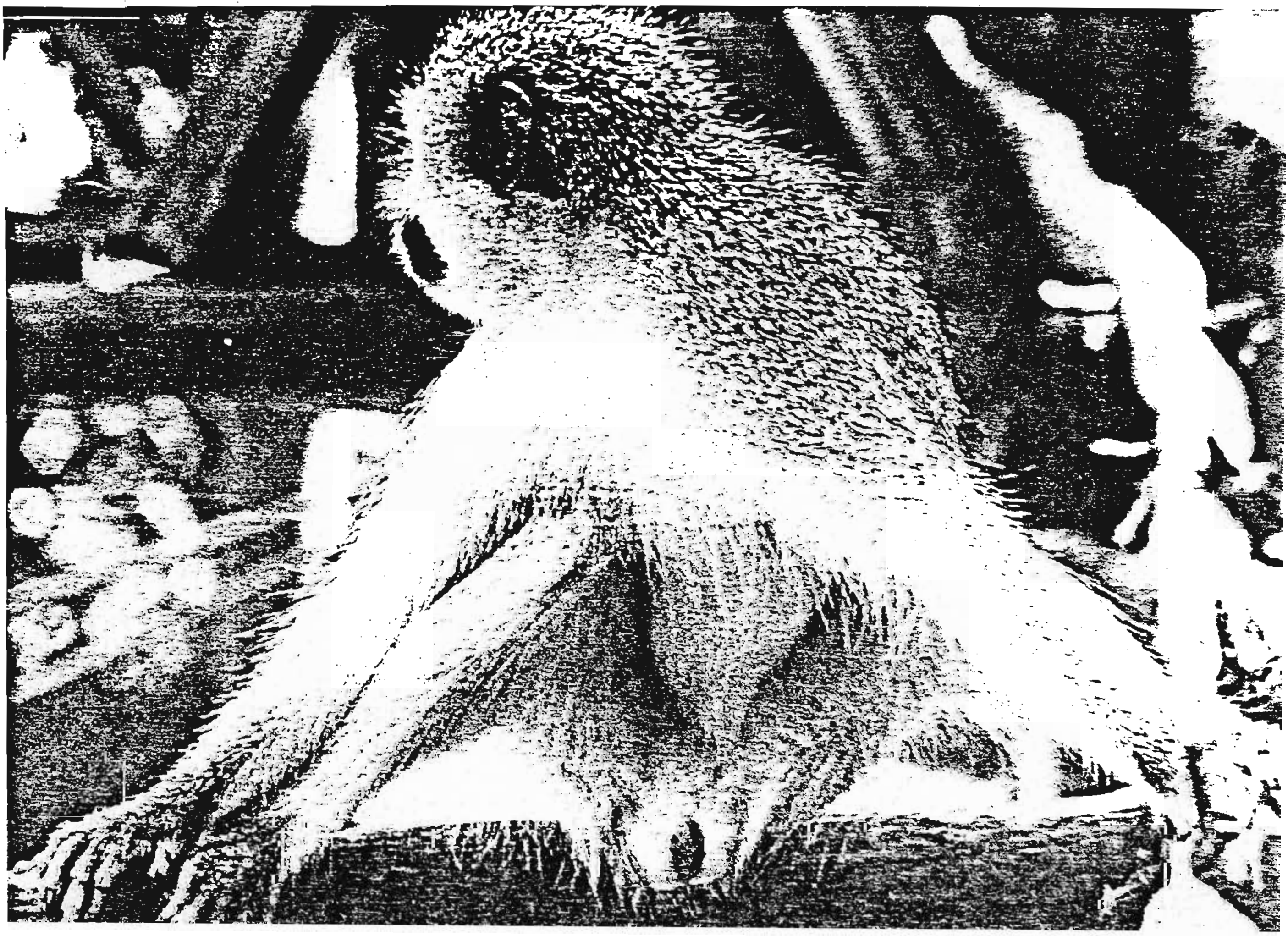


Figure 5-7: A four-leg-up sit.

Figure 5-8: A splayleg sit.



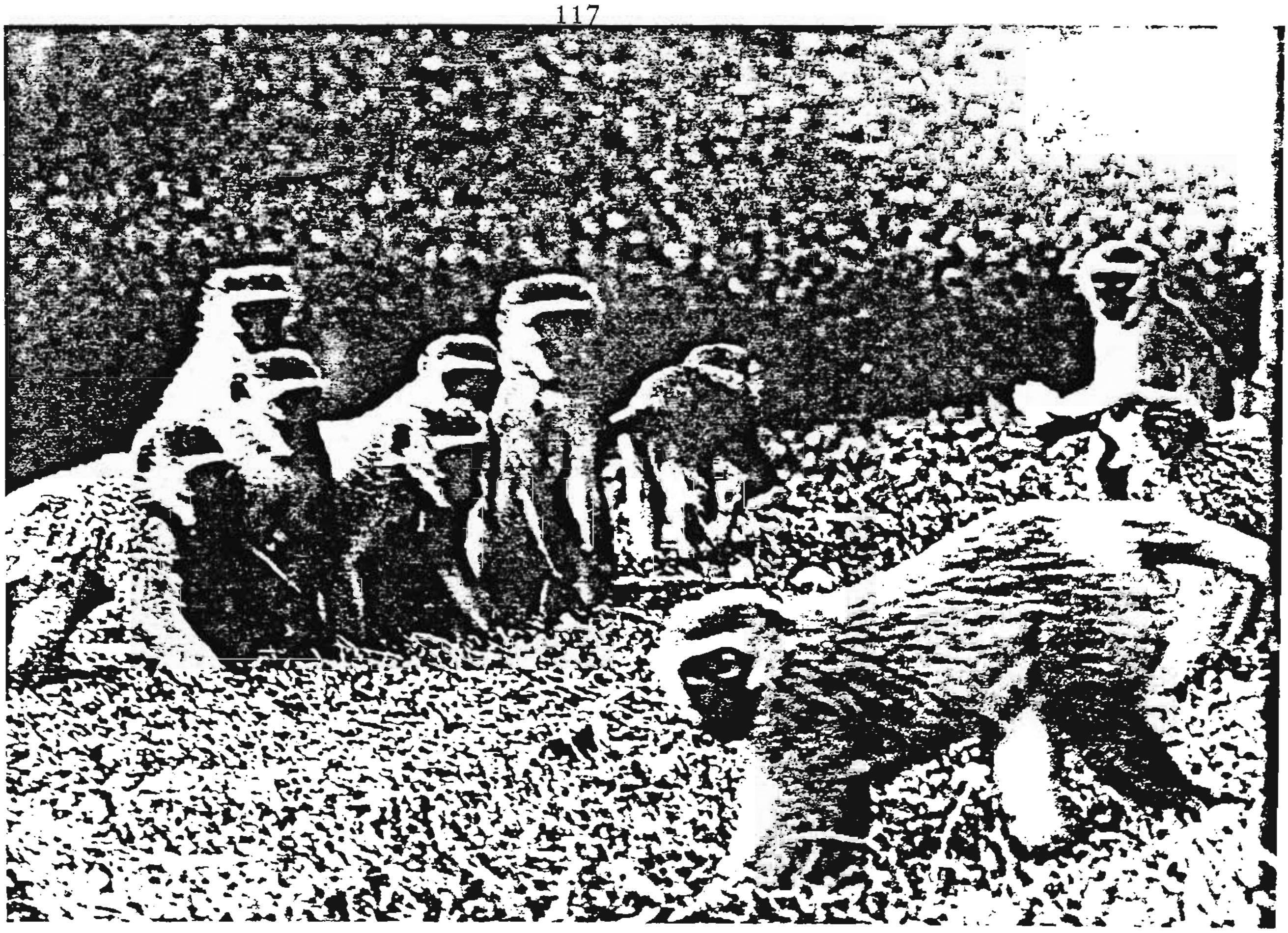


figure 5-9: Adult females grouping together during intertroop aggression.

Figure 5-10: An infant with its ears pulled forwards.

visual effect has rarely been described for mammals. Single vervets increased their apparent size through piloerection.

Although development aspects are not a concern of this thesis, one interesting and previously unrecorded manipulation of an infantile character was seen. In contrast to adults, infants younger than six months had disproportionately large and pale ears. Such antithetical elements (Darwin, 1872) are presumed to remove infants from the fray of adult life and is demonstrated by the license with which infants operated, doing things that would have resulted in violence had they been older. As these characters are temporally fixed (relative to the adoption of atithetic postures, for example) they have generally been regarded as static elements. Infants in Natal, however, when stared at by a human observer, and during threat, used to bring the ears forward (Fig. 5-10), thereby emphasizing them. It is not known what muscles were employed but the phenomenon was absent in adults and older juveniles, appearing to decrease in frequency as the ears got darker. The process should be studied further.

5.1.7. A comparison of the behavioural repertoires of different vervet populations.

Two other studies have focussed on the behavioural repertoires of vervet monkeys (Struhsaker, 1967b; McGuire, 1974). Table 5-2 uses Struhsaker's original listing to compare the Natal population with these.

Table 5-2: A comparison of the communicative behaviours of Amboseli, St. Kitts and Natal vervets. The behaviour categories come from Struhsaker (1967b) and the St. Kitts data from McGuire (1974) Lower case letters give the contexts in which they were seen at Amboseli and, if following ticks in the St.Kitts or Natal columns, indicate that the same contexts applied there.

BEHAVIOUR	AMBOSELI	ST. KITTS	NATAL
1. Grooming	Y	Yabc	Yabc
a) Solicitation for grooming			
b) Not apparent			
c) Intergroup encounters			
2. Solicitation for grooming	Y	Yab	Yab
a) Not apparent			
b) Intergroup encounters			
3. Mounting (complete and incomplete)	Y	Yacd	Ybcd
a) Grooming prelude			
b) Homosexual behavior			
c) Heterosexual behavior			
d) Intergroup encounters			
4. Hands-on-shoulders	Y	Ya	Ya
a) Grooming prelude			
5. Hand-on-head	Y	Ya	Ya
a) Grooming prelude			
b) Red-white-blue display			
c) Intergroup encounter			
6. Face-in-inguinal region	Y	Yac	Yac
a) Grooming prelude			
b) Homosexual behavior			
c) Intergroup encounter			
7. Muzzled-scrotum	Y	Yacd	Yabcd
a) Grooming prelude			
b) Homosexual behavior			
c) Heterosexual behavior			
d) Infant social interactions			
8. Touched-genitals	Y	Ybd	Yabcd
a) Intergroup encounter			
b) Grooming prelude			
c) Homosexual behavior			
d) Infant social interactions			
9. Embrace-and-straddle-from-behind	Y	Yc	Ybc
a) Grooming prelude			
b) Homosexual behavior			
c) Heterosexual behavior			
10. Embrace from in-front	Y	N	Y not in this context.
a) Grooming prelude			
11. Mouthing-of-the-lateral-neck-surface	Y	Ya	N
a) Grooming prelude			
12. Muzzle-muzzle	Y	Yab	Yab
a) Grooming prelude			
b) Intergroup encounter			
13. Handling infant	Y	Ya	Ya
a) Grooming prelude			
14. Staring	Y	Ya	Ya
a) Intense agonism			
15. Exposure-of-eyelids	Y	Ya	Ya
a) Intense agonism			
16. Jerking-of-head	Y	Ya	Ya
a) Intense agonism			
17. Jerking-of-forequarters	Y	Ya	Ya
a) Intense agonism			
18. Chase	Y	Ya	Ya
a) Intense agonism			
19. Attack	Y	Ya	Ya
a) Intense agonism			

Table 5-2 continued.

	AMBOSELI	ST. KITTS	NATAL
20. False chase	Y	Ya	Yab
a) Intense agonism			
b) Red-white-blue display			
21. Sideward-jerking-of-forequarters	Y	N	Ya
a) Intense agonism			
22. Sideward-display	Y	Ya	N
a) Intense agonism			
23. Penile-erection	Y	Yab	Yabcd
a) Intense agonism			
b) Grooming			
c) Red-white-blue display			
d) Homosexual behavior			
24. Grabbing-or-slapping-toward	Y	Ya	Ya
a) Intense agonism			
25. Hitting or slapping	Y	Ya	Ya
a) Intense agonism			
26. Grabbing	Y	N	Ya
a) Intense agonism			
27. Biting	Y	Ya	Ya
a) Intense agonism			
28. Rapid-glancing	Y	Yab	Yabc
a) Intense agonism			
b) Supplantation encounters			
c) Red-white-blue display			
29. Crouching	Y	Ya	Yab
a) Intense agonism			
b) Red-white-blue display			
30. Gaping	Y	Ya	Ya
a) Intense agonism			
31. Grimace	Y	Ya	Yab-with vocal.
a) Intense agonism			
b) Red-white-blue display			
32. Confident-walk	Y	Ya	Yab
a) Supplantation encounters			
b) Red-white-blue display			
33. Walked-away-from-in-crouched-manner	Y	Ya	Ya
a) Supplantation encounters			
34. Tail erect	Y	N	N
a) Red-white-blue display			
b) Intergroup encounters			
35. Orienting-posterior-quarters-toward	Y	N	Ya
a) Red-white-blue display			
36. Encircling	Y	N	Ya
a) Red-white-blue display			
37. Rising-up-on-hindlimbs	Y	N	N
a) Red-white-blue display			
38. Looked-over-shoulder-toward	Y	N	Ya
a) Red-white-blue display			
39. Hopping-backwards	Y	N	Ya
a) Red-white-blue display			
40. Shaking-head-laterally	Y	N	Ya-as Headflagging during Broadside.
a) Red-white-blue display			
41. Grabbing-hips	Y	Yb	Yab
a) Homosexual behavior			
b) Heterosexual behavior			
42. Muzzle-perineum	Y	Yb	Yabc
a) Homosexual behavior			
b) Heterosexual behavior			
c) Intergroup encounters			
43. Hand-on-back	Y	N	Ya
a) Homosexual behavior			

Table 5-2 continued.

	AMBOSELI	ST. KITTS	NATAL
44. Presenting	*Y*	*Ya*	*Ya*
a) Heterosexual behavior			
45. Harassing	*Y*	*Ya*	*Ya*
a) Heterosexual behavior			
46. Play	*Y*	*Yabc*	*Yabc*
a) Not apparent			
b) Intergroup encounters			
c) Grooming prelude			
47. Sucking	*Y*	*Ya*	*Ya*
a) Infant social interactions			
48. Weaning	*Y*	*Ya*	*Ya*
a) Infant social interactions			
49. Hugging of infant	*Y*	*Ya*	*Ya*
a) Infant social interactions			
50. Head-flagging	*Y*	*N*	*Ya*
a) Perception of a foreign group			
51. Branch shaking	*Y*	*Ya*	*Ya*
a) Intense, intergroup agonistic encounter			
52. Entwining of tails	*Y*	*Ya*	*N*
a) Not apparent			
53. Straddling	*Y*	*N*	*Ya*
a) Not apparent			
54. Penile-display	*Y*	*Ya*	*N*
a) Not apparent			

Not recorded as communicative at Amboseli but seen as such at St.Kitts and discussed in this study is the *Yawn*.

In summary this study revealed 48 of the 54 gestures, while St. Kitts had only 41 (not 44 as stated by McGuire).

5.2. THE SOCIAL INTERACTIONS OF MALE VERVETS.

5.2.1. Frequencies. The nature and frequency of all male intratroop interactions are recorded in Table 5-3. The data come only from focal-animal samples and include both the Cage and Burman Bush males.

These data will not be analysed here because of the differences in the numbers of vervets falling into each age-sex category and, while certain trends are clear, it really provides the data base for some of the analyses that follow.

i. `Aggression' is a blanket term for supplanting, threatening and chasing. Of these the first was the most common.

ii. `Amicable behaviour' conflates non-agonistic encounters such as grooming and approach-and-sit.

iii. `Homage', as used here, refers to all agonistic encounters initiated by subordinates and directed at more dominant animals. It incorporates Struhsaker's `false chase' (1967b) and is discussed at length below.

iv. `Play' is a subset of (ii) above but is considered separately becauses of its greater motor intensity and its special social relevance.

v. `Sex' indicates all encounters that were obviously sexual in nature, i.e. if mounting did not occur the subject would at least have initiated a sustained olfactory investigation of a female's ano-genital region. Male-male sexual activity was scored when one male was mounted by another without there having been agonism between them immediately prior to the encounter.

		CLASS OF SOCIAL PARTNER				
		MALE	FEMALE	JUVENILE	INFANT	TOTAL
	CONTEXT					
1.	AGGRO. GIVEN	54	42	16	14	126
2.	AMICABLE BEH.	33	159	79	28	299
3.	PLAY	3	1	40	0	44
4.	HOMAGE	14	0	0	0	14
5.	AGGRO. RECEIVED	44	21	5	2	72
6.	SEXUAL	3	53	5	0	61
	TOTAL	151	276	145	44	616

TABLE 5-3: The distribution of male interactions among social categories and age-sex classes.

5.2.2. Male dominance hierarchies.

Hierarchies were obtained by mapping all incidents of aggression between males (Table 5-4). While the frequencies are small, it is evident that the hierarchies are linear, the exception being due to the change in attitude to TE just prior to his departure. The Burman Bush hierarchy is split in accordance with the dominance shift that occurred in 1977. Subsequent analyses tend to deal with an `alpha-subordinate' male comparison as a way in which, with small samples, points can be made most clearly. However, it was also apparent during the study that there was something qualitatively distinctive about the top-ranking male. This will be considered further in the discussion.

5.3. GENITAL SIGNALS.

5.3.1. Colour.

Adult male vervets in Natal have the conspicuous powder-blue scrotum and crimson penis recorded elsewhere for males of the C.a. pygerrythrus group (Fig. 5-11). In contrast to Wickler's assertion (1967) scrotal colour was not seen to vary seasonally, nor did subordinate males appear to have paler genitalia. Natal vervet males also had the same orange-red circumanal region as males elsewhere.

Subadult males had paler genital colouration (Fig. 5-12)

WINNER	LOSER		
	TE	TOG	TY
TE	-	7	9
TOG		-	0
TY			-

a. Burman Bush: 1976-1977

	TOG	GEO	TE	POI	PER
TOG	-	9	8	3	6
GEO		-	1	4	3
TE		2	-	0	1
POI				-	0
PER			1		-

b. Burman Bush: 1977-1978.

	ALF	TOM
ALF	-	6
TOM		-

c. The Cage.

Table 5-4: Male dominance hierarchies.

Figure 5 - 11 : The genitalia of an adult male. The penis is extended.

although a faint blue undertone could be detected in even infant males. Colour intensification took place at puberty (circa 3.5-4yrs.).

Adult females had red clitori and blue vulvar margins (Fig. 5-13), but these were much paler than the corresponding colours in males and than those depicted for females by Wickler (1967). Examination of photographs of one female revealed no distinctive seasonal differences in colour.

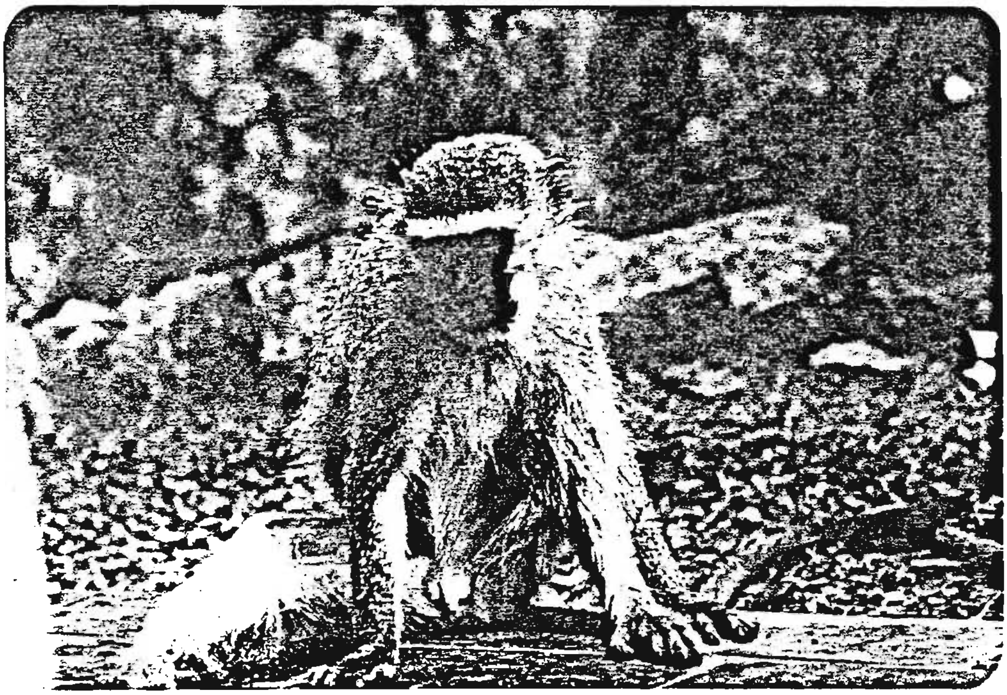
5.3.2. Male genital signals

The striking differences in colour suggest that the penis and the scrotum may constitute signalling subsystems. They are therefore considered separately.

5.3.2.1. The Scrotum.

The unretracted scrotum is pendulous and was visible most of the time. It was made even more conspicuous during motion by the sideways movement of the tail which, in passing between the scrotum and the viewer, resulted in a `flashing' of the colour (Fig. 5-14). During `jerking erections' the scrotum bobbed up and down, this acting in much the same way.

1. Retraction. As one consequence of the powerful muscles attached to it the scrotum is capable of retraction. When this occurs the testes are adducted into the inguinal canal and the scrotal sac is removed from view (Fig. 5-15). The following



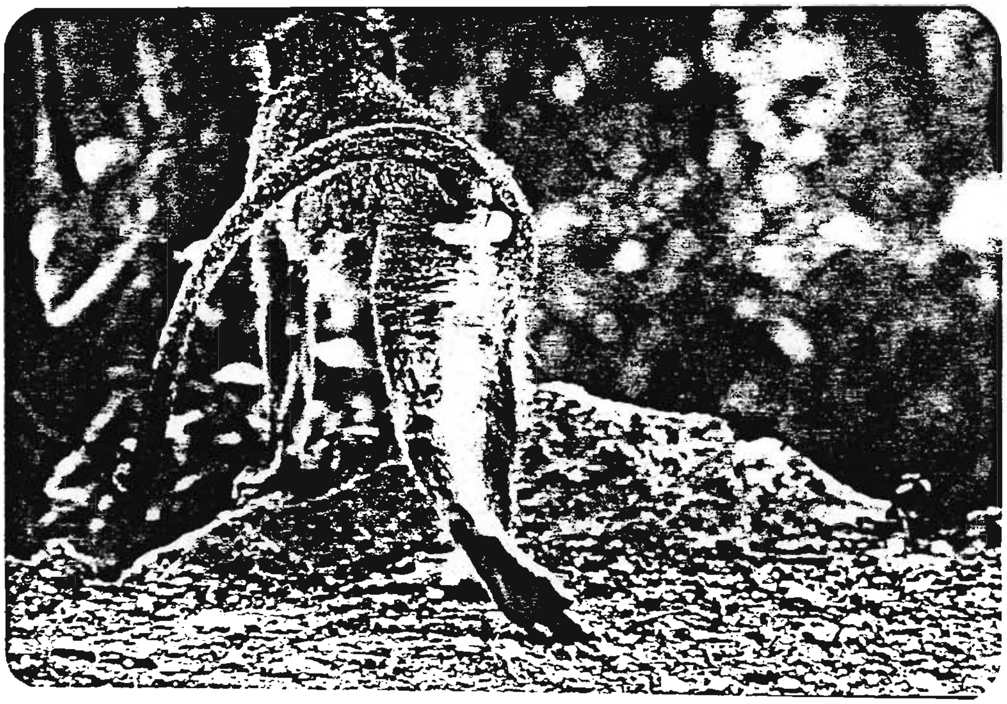
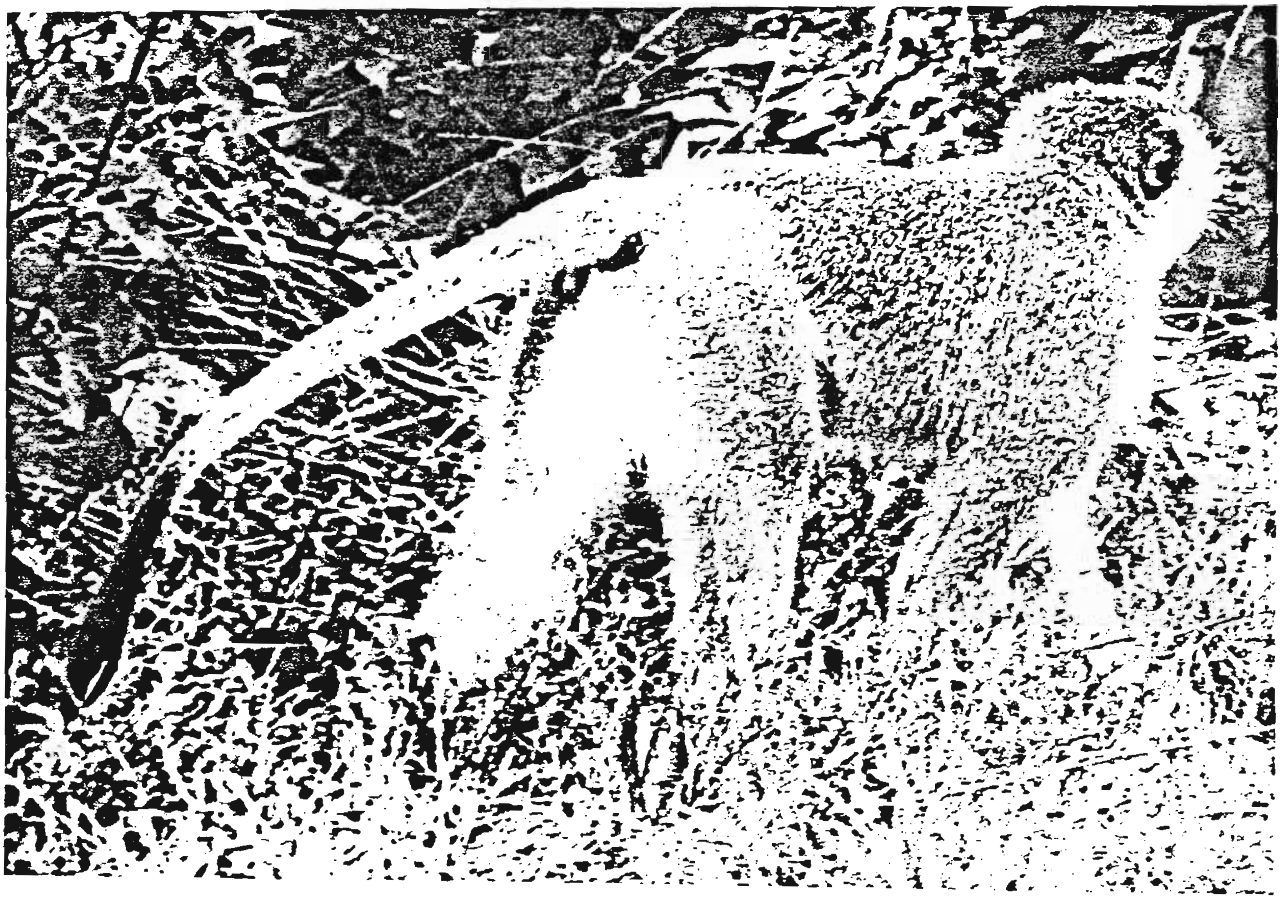


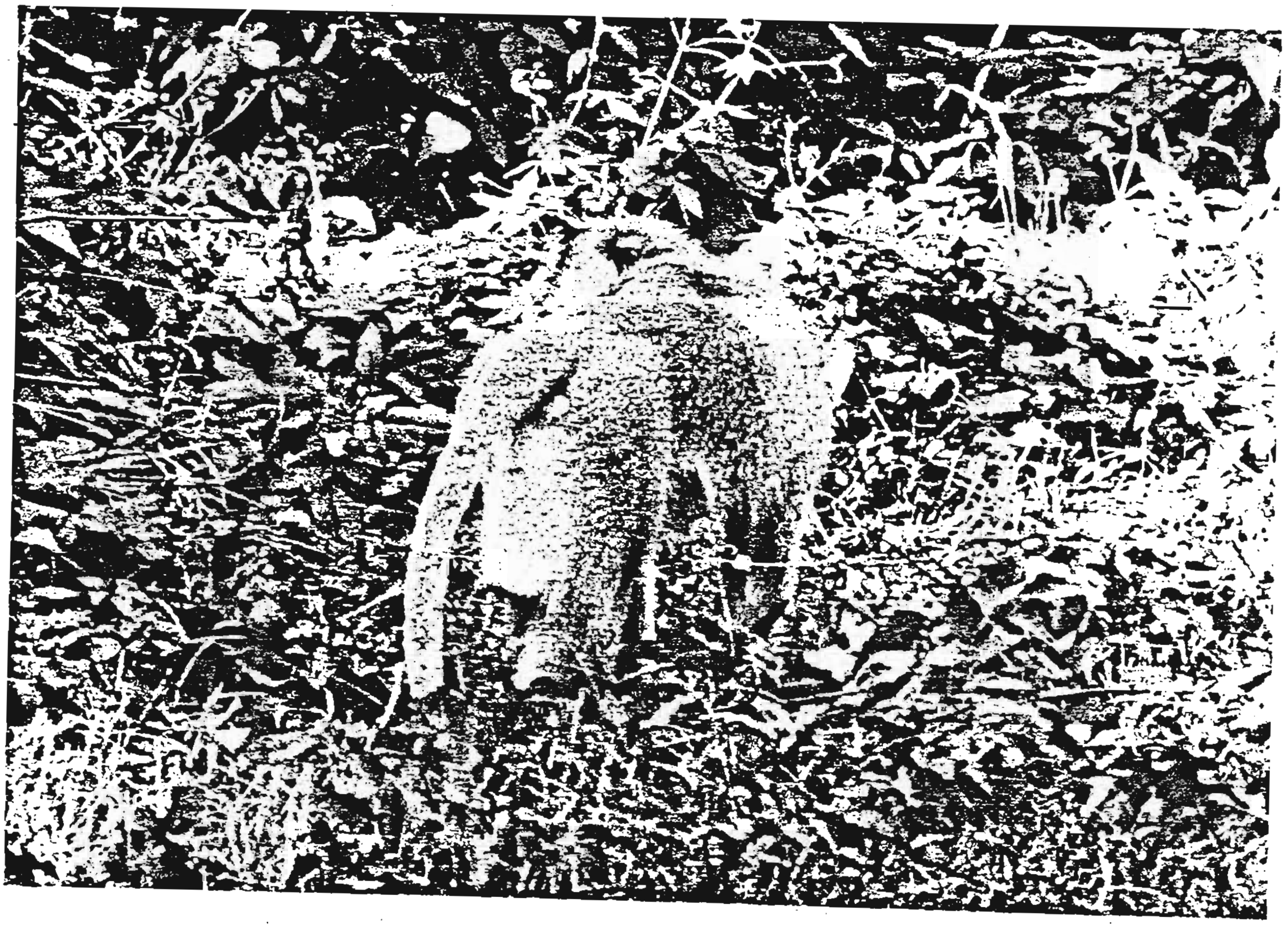
Figure 5–12 : Two views of the genitalia of a subadult male, showing them as relatively inconspicuous.

Figure 5-13 : The genitalia of an adult female, illustrating the relative lack of colour.

Figure 5-14: Lateral tail movement during locomotion 'flashes' the scrotum by alternately covering and exposing it.

Figure 5-15: Testis adduction after a fight. (a) shows the male immediately following the incident and (b) three minutes later.





analyses deal with these retractions.

2. Status. All adult, and some subadult, males were seen to retract their scrota (Table 5-5). The data for each animal come only from its own focal-sample and represent a lower limit of occurrence as, occasionally, the subject's position or posture prevented positive identification of retraction.

Among the adults, subordinate males retracted their scrota more frequently than alphas did (Cage and Burman Bush combined: Chi-square = 15.83, df = 1; $p<0.001$). This is shown graphically in Fig. 5-16. Non-adults performed the behaviour only as they approached puberty.

3. Concomitants of retraction. When seeing retraction, it was also noted whether or not the subject was interacting with other animals. If so, the identity of the partner and the type of interaction were recorded. When there was no observable direct interaction, the events to which the subject was visually attending, and in which it appeared to be interested (as evidenced by rapid glancing, headcraning etc.) were recorded (Table 5-6).

Homage - an act of subordination - needs to be considered more fully at this point. During encounters classified as such, the initiator ran the risk of `annoying' the recipient by running towards him while uttering loud, submissive vocalizations. As it is of some importance its analysis is based on 27 instances seen as a consequence of group or concurrent sampling (at Burman Bush) as well as on the 8 recorded from focal samples. The former do

SUBJECTS	No. SCROTAL RETRACTIONS	No. PENILE EXTENSIONS	No. HOURS OBSERVED.
TOG (A)	5	77	5.1
TE (A)	1	15	1.6
ALF (A)	2	8	2.85
TOG	4	14	1.6
TE	12	19	2.55
TY	1	12	1.5
GEO	12	46	4.7
PER	13	17	1.8
POI	12	7	1.9
TOM	3	11	2.85
TOTAL	65	226	26.45

a. Adult Males.

GTL	0	5	6.4
GMR	3	17	4.15
U	0	4	2.85
CM	1	0	2.85
DISC	0	0	2.85
CROSS	0	8	2.85
TOTAL	4	34	21.95

b. Subadult males.

Table 5·5 : Frequencies with which adult and subadult males, at the Cage and Burman Bush, retracted their scrota or exhibited penile extensions.

	Class of social partner				
Context	Male	Female	Juvenile	Infant	Total
Aggression given	2	1	0	0	3
Groom	1	0	1	0	2
Play	0	0	3	0	3
Homage	8	0	0	0	8
Aggression received	29	3	0	0	32
Total	40	4	4	0	48

(b) Non-interactive contexts

Context	Subordinate males	Alpha males
Other males fight	3	0
Jump from tree	1	2
Appearance of dogs	2	2
Sudden noise	2	0
Surprised by juvenile	0	1
Infants play near	0	1
Unknown	1	2
Total	9	8

Table 5-6: Contexts of scrotal retractions. Alpha males were not seen to retract the scrotum during direct encounters with other vervets.

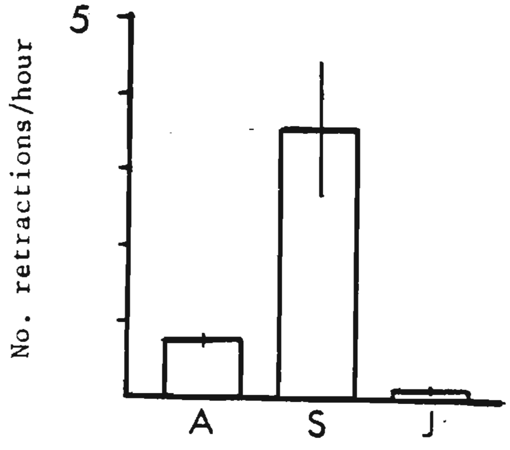


Figure 5-16: The number of scrotal retractions per hour seen in alpha males (A), subordinate males (S) and juvenile males (J). Standard errors are expressed as vertical lines.

not appear, on description, to differ in any significant way from the latter. Those from the focal-samples do not include ones received by the focal-animal. Two forms of the behaviour were distinguished.

i. Type I: On 16 of the 35 occasions, the initiator chased after an animal that had either been engaged in agonism with a third party (N=11 - 9 of whom were adult females) or had threatened him (N=2). Once the behaviour was directed towards a male in the process of mounting a female, while the cause was unknown in two.

This 'false chase' (Struhsaker, 1967b) is distinguished from a true one in that the initiator vocalized submissively (see below) and never made contact with the recipient who often just walked off and never showed any signs of distress (Fig. 5-17). The false chase also differed from the 'scream chase' - sometimes given to males by females - in that the latter's pace is faster and the vocalizations are different. There may also be facial threat associated with it and coalitions of females are a common consequence of it.

ii. Type II: On 19 occasions a male walked or ran towards a stationary recipient , either spontaneously (without prior contact) or, once, after having been threatened. The initiator always moved in a low, crouching manner while vocalizing. No amicable interactions followed this.

While all adult males except ALF and TY were seen to perform both homage and the false chase, the recipient was <u>always</u> an alpha male. During 33 encounters the subordinate male's scrotum was retracted while the recipient's was not. The remaining two in each could not be ascertained and were scored as opposing the norm (Table 5-7). The resultant test is therefore conservative but highly significant (Chi-square = 29.02; df = 1; $p<0.001$) with the participants differing in their scrotal state during such interactions.

Homage only twice resulted in the receipt of aggression from the alpha male who usually sat or continued to walk/run while the initiator moved off.

Using the data in Tables 5-3 and 5-6 (see Fig. 5-18 for a graphical representation of the way in which scrotal retraction stands in relation to categories of interactions) some conclusions may be drawn for adult males:

i. Subordinate males are more likely to retract their scrota for social reasons than are alpha males (Chi-square - corrected for continuity - = 22.37; df = 1; $p<0.001$). The latter were, in fact, never seen to do so as a consequence of interactions with other vervets.

ii. Retraction is more likely during interactions with adult males than with any other age-sex class (Table 5-8. Infants excluded from the analysis).

iii. By ranking the social contexts of interactions associated with retractions according to the increasing likelihood that the subject's behaviour will be submissive or fearful (reading down

	RETRACTED	NOT RETRACTED
RECIPIENT	2	33
INITIATOR	33	2

Table 5-7: The state of the scrotum during homage.

	SCROTAL STATE	
CLASS OF PARTNER	RETRACTED	NOT RETRACTED
MALE	40	107
FEMALE	4	272
JUVENILE	4	141

Table 5-8: The distribution of interactions with different age/sex classes with which a scrotal retraction is/is not associated. Chi-square = 88.46; 2 d.f.; $p<0.001$.

	SCROTAL STATE	
AGGRESSOR	RETRACTED	NOT RETRACTED
MALE	29	15
FEMALE	3	18

Table 5-9: The scrotal response of males when receiving aggression from either males or females.

Table 5-6) it is found that retraction frequency increases, relative to the distribution of interactions lacking them, with the estimated frequency of fearful behaviour (Kolmogorov-Smirnov Two Sample Test; $p<0.001$).

iv. It can be seen from Table 5-9 that males are much more likley to respond to aggression with retraction if the aggressor is male (Chi-square = 15.13; df = 1; $p<0.001$).

4. Vocalizations. Of the 48 incidents of retraction due to direct social interaction, 26 were accompanied by auditory signals. These were either lipsmacks, vocalizations falling somewhere along the 'woof-wa' continuum (Struhsaker, 1967), or combinations of these. From Fig. 5-19 it can be seen that sounds only accompanied the reception of aggression or homage. Within the former category, they were only present during male-male encounters and, additionally, were absent from some of the less vigourous supplantations. Nevertheless, when they occurred they were conspicuously audible. Recipients of such sounds were themselves generally silent. In two instances, in encounters between subordinate males, both participants lipsmacked.

The use of sounds during homage is particularly interesting. Of the 35 extracted cases all but two involved vocalizations by the initiator, while the recipients were always silent.

When the sounds are ordered according to increasing intensity (volume) (reading down Table 5-10) and homage is divided into its two subcategories it can be demonstrated that

VOCALIZATION.	TYPE I.	TYPE II.
1. Silent	1	1
2. Lipsmack	0	4
3. Lipsmack/Woof	1	7
4. Woof	7	6
5. 'Saw'	5	0
6. Saw/Waa	1	0
7. Waa	1	1

Table 5-10: A comparison of the frequency with which specific vocalizations accompany the two types of Homage.

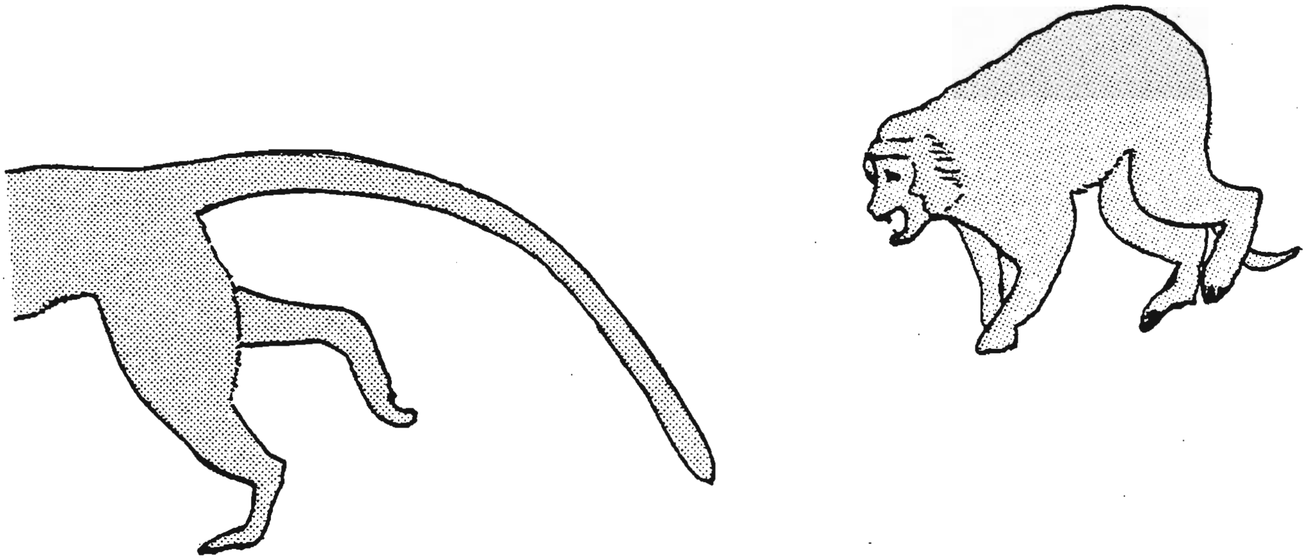
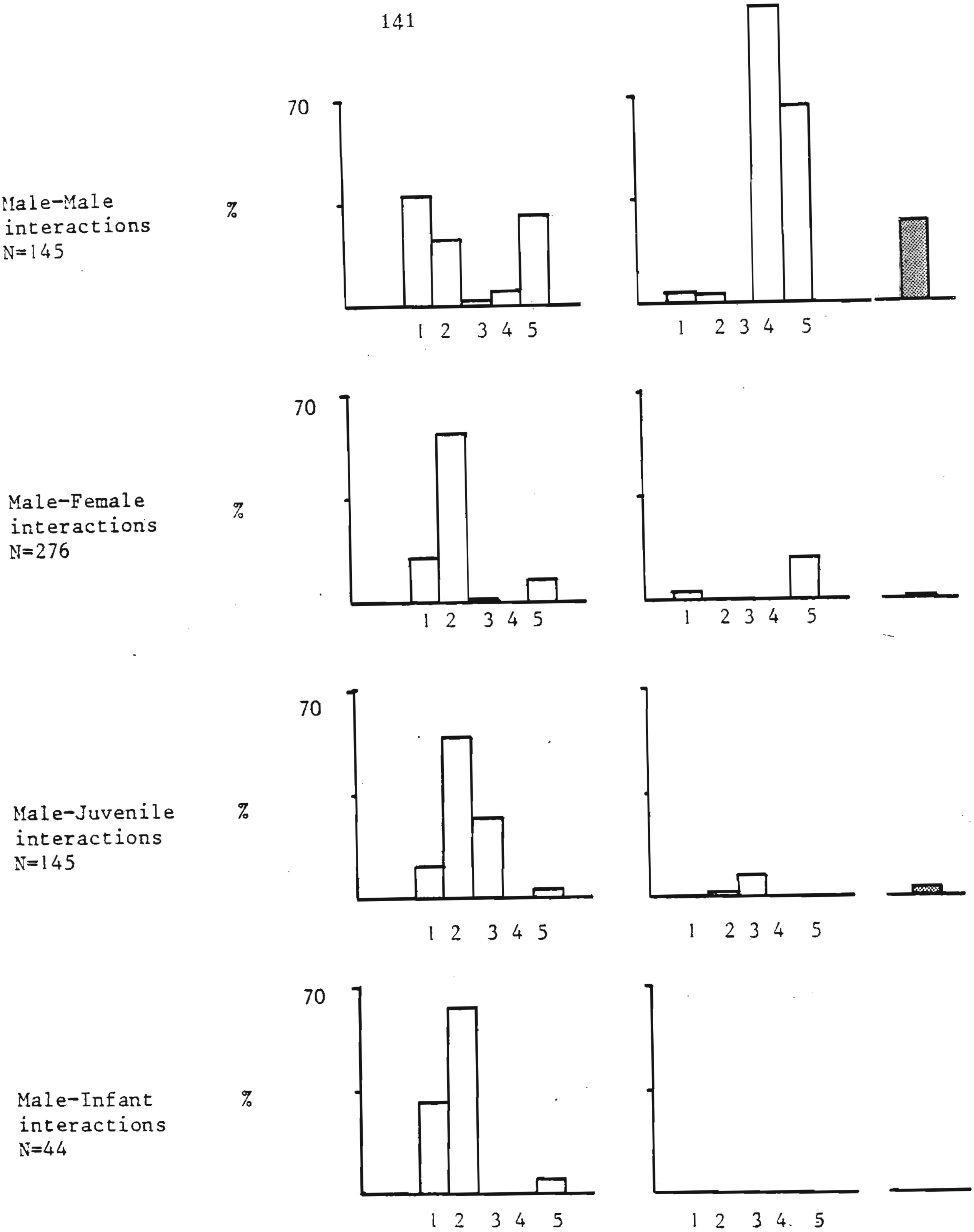


Figure 5-17 : A false chase. Drawn from a B+W photograph it shows the posture of the chasing male and the facial expression associated with the 'Waa' scream. Note the differences in the way that the tail is carried.



a. Contribution of each category to the total

b. % with which each category is accompanied by an extension

c. $\bar{X}$ % with ext

Figure 5-18: The contribution of different types of social encounters to the interactions between males and various age-sex categories, and the degree to which each is accompanied by scrotal retractior The categories (1-5) are taken from Table 5-3. Sex is not listed although it is used in the derivation of the percentages. In this figure homage refers only to that given to other males.

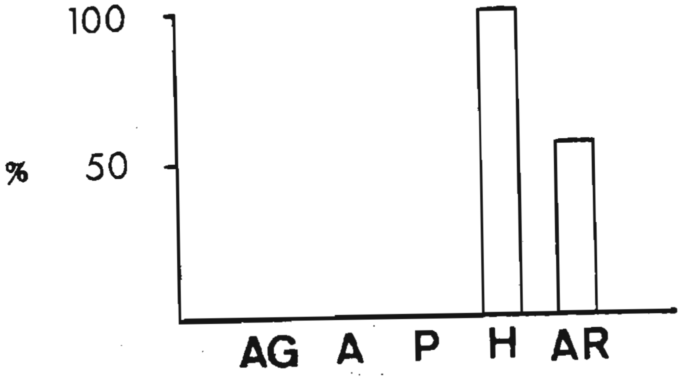


Figure 5-19: The degree to which different social interaction categories are accompanied by vocalizations. The categories come from Table 5-3 and sex is excluded.

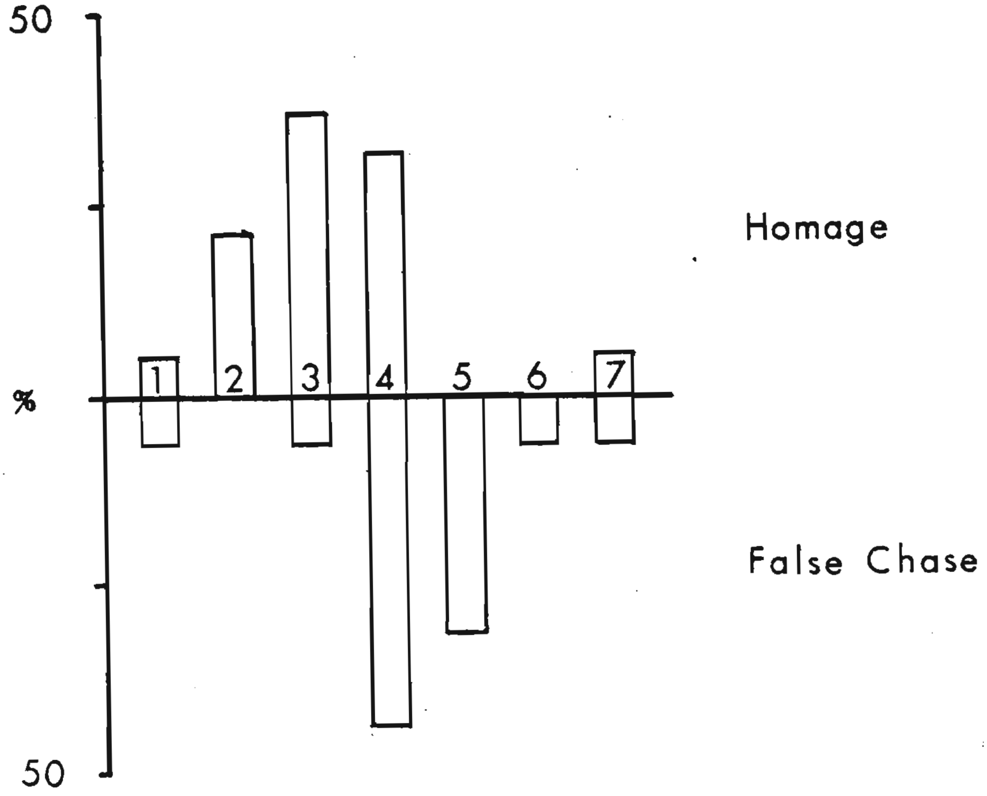


Figure 5-20: A comparison of the distributions of different vocalizations accompanying the two types of Homage. "Homage" in the graph refers to Type II. The vocalizations are numbered as in Table 5-10.

these are associated with sounds at different ends of the intensity continuum (Kolmogorov-Smirnov Two Sample Test; $p<0.05$). From Fig. 5-20 it is evident that false chases are accompanied by more intensely submissive vocalizations than are other acts of homage. These rely more on softer sounds and on the lipsmack, which is usually seen as being designed for close-range pacification. This finding provides interesting support for that view and underwrites the validity of separating homage into two subclasses.

The only sounds accompanying non-social retractions were the `chutters' with which strange dogs were greeted. This is a fear/alarm vocalization (Cheney and Seyfarth, 1981).

5. Potential Recipients. Who is it who receives the information that scrotal retraction has taken place? To answer this it is necessary to know what postures were adopted during retraction (Table 5-11).

It is clear that all postures in the repertoire were not evenly used. The scrotum is really only visible to any attending party when the animal is standing, sitting 4-leg up, walking or running. In that 4-leg postures, especially where the subject is hunched, are by far the most frequently employed (Chi-square = 20.4; df = 1; $p<0.001$. Categories collapsed), it is generally only the participant who, in being close by and facing the subject, has any chance of receiving the information.

RUN FROM	4
RUN TO	4
WRESTLE	3
WALK	7
STAND	1
HINDLEG SIT	2
4-LEG SIT	2
4-LEG HUNCH/ BACK-OFF	24
4-LEG UP	1

Table 5-11: Postures adopted while the scrotum was retracted.

TAIL	10
HINDLEGS	8
TRUNK	1
ARMS/HANDS	4
NECK/HEAD	1

Table 5-12: The location of wounds (N = 24) on males at Burman Bush.

The hunched posture associated with many of the agonistic encounters was important to its adopter for several reasons. It decreased apparent body size and thereby emphasized submissiveness; it was protective of the ventral surface; assisted in hiding the testes and concealing the scrotum from view. In being associated with a `backing off' it allowed the opponent to be kept in sight during departure. Leaving the vicinity in this way might also be wise for a male with Darwinian fitness in mind. Table 5-12 shows the location on the body of wounds received by males at Burman Bush over a 12 month period.

Tail and hindlegs, when considered together, were damaged more frequently than the rest of the body combined, despite differences in surface area (Chi-square = 6.0; df = 1; $p<0.02$). It is very likely that this distribution is a consequence of the animal running away. In respect of this it is interesting that no male ever emphasized scrotal retraction to the participant by means of a `present'. Subadult males, at least, were capable of performing appeasement presents but did so only very rarely (once at the Cage and once at Burman Bush).

<u>6.</u> <u>Aftermath.</u> As already mentioned earlier, encounters did not develop further. the dominant animal characteristically moved off while the retractor remained stationary (this was once the interaction was over). Grooming developed once and two interactions ended with threat being redirected to me.

5.3.2.2. The Penis.

The penis is normally retracted and not visible except, perhaps, as a small ring of red against a background of scrotal blue. Analysis is primarily concerned, therefore, with penile extensions.

1. Extensions. The penis may be rapidly extended, by variable lengths, remaining either flaccid (Fig. 5-11) or developing into an erection. This, in turn, may either be stationary or jerk rhythmically in the sagittal plane.

When flaccidly extended, the penis, in a standing male, is directed down towards the ground, hanging below the scrotum. This is due to the action of the testes, whose weight pulls the shaft entrance down and thereby ensures that the extension is as visible from the rear as the scrotum is. In a sitting male the penis is only visible from the front - if the posture allows - and hangs down over the scrotum.

Extensions were recorded as being `slight', `medium', or `long'. The latter were the most commonly used of all extension/erection types, constituting 61.7% of the total (N = 226). The following analyses, unless specifically stated, do not distinguish between either the length of the extension or the type of erection. `Extension' is used generically.

Status/Age. All adult and four subadult males displayed extensions (Table 5- 5). Alpha males performed it more frequently than did subordinates (Chi-square = 42.73; df = 1; p<0.001). This result should be treated with caution as it is due largely to the disproportionately high rate of use by TOG (Fig. 5-21).

Table 5-13: Concomitants of Penis Extensions (N=226) due either to a. Direct interaction with other animals or b. non-interactional encounters.

	CLASS OF SOCIAL PARTNER				
CONTEXT	MALE	FEMALE	JUVENILE	INFANT	TOTAL
AGGRO. GIVEN	34	11	4	0	49
AMICABLE BEH.	4	8	6	1	19
PLAY	0	0	7	0	7
HOMAGE (received)	4	0	0	0	4
AGGRO. RECEIVED	3	0	1	0	4
SEX	3	39	2	0	44
TOTAL	48	58	20	1	127

a. Direct interactions.

BEHAVIOUR OF EXTERNAL MALE:	34
ARRIVAL OF OTHER TROOP:	11
ARRIVAL OF HUMANS:	22
OTHER MALES FIGHT:	3
OTHERS FIGHT:	1
OBSERVING FEMALES:	2
MALE GIVES TREE DISPLAY:	1
ARRIVAL OF DOGS:	2
UNKNOWN:	13
TOTAL	99

b. Non-interactive.

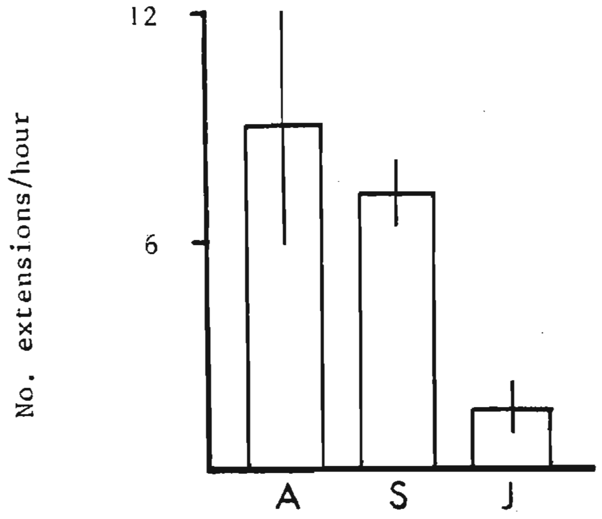


Figure 5-21: The number of penile extensions per hour seen given by alpha males (A), subordinate males (S) and juvenile males (J). Standard errors are expressed as vertical lines.

On the other hand the changes in use associated with TOG and TE's status shifts are both in the right direction.

It is possible that juvenile adult males did develop extensions which, as with scrotal retractions, were not seen because of the lack of genital colour (Fig. 5-12). While this is in itself interesting from a signalling viewpoint, the excellent observation conditions made it unlikely that many were missed.

2. Concomitants of Penile Extensions. These are listed in Table 5-13. Fig. 5-22 shows graphically how extensions stand in relation to types of interaction.

i. It is clear from Table 5-14 that males both direct their sexual activity towards the appropriate partners and that extensions accompanied sexual activity more often than not (Binomial Test; $z = -3.29$; $p<0.001$). Only five of these encounters led to immediate mounting by the male.

Once sex is left aside the following further conclusions can be drawn:

ii. Extensions are more likely to be present when aggression is given than during all other interactions combined (Chi-square = 47.57; df = 1; $p<0.001$. Expected values were computed using the distribution of all recorded interactions among the categories).

iii. Males made significantly more use of extensions when directing aggression towards other males than towards females (Table 5-15).

SEX PARTNERS	PENILE STATE EXTENDED	NOT EXTENDED
MALE	0	0
FEMALE	39	14
JUVENILES	2	3

Table 5-14: Sexual partners and the penile state associated with sexual activity.

AGGRO. GIVEN TO	PENILE STATE EXTENDED	NOT EXTENDED
MALES	34	20
FEMALES	11	31

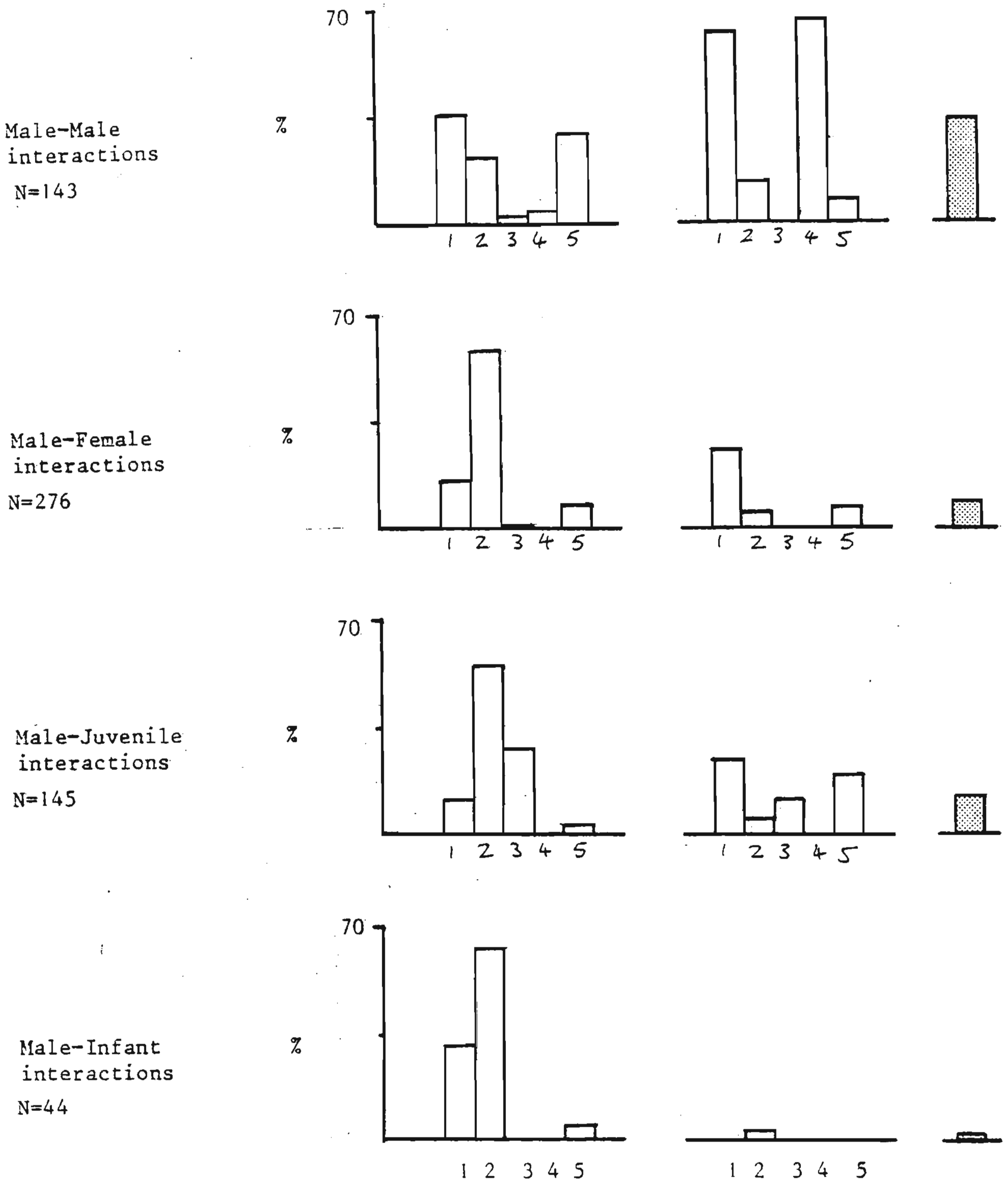
Table 5-15: The allocation of extensions during aggressive encounters. Chi-square = 12.85; df =1; $p<0.001$).

iv. While extensions did not, accompany a higher proportion of male-male amicable encounters than such interactions between males and females (Chi-square = 2.41; df = 1; $p>0.1$), a significantly greater number of amicable encounters took place without extensions at all (Table 5-16).

From Fig. 5-22, in summary, it can be seen that extensions are more likely to develop during interactions with males and that this is in some measure due to the greater likelihood that male-male encounters will be agonistic. At the same time extensions are not a characteristic of male-female agonism.

3. Extra-group events. The largest single number of extensions arose out of interactions involving non-group members, either other vervets or human visitors. Table 5-17 lists these instances against the probability that they would induce extensions. Binomial tests were applied. While the differences are all significant, it is only in the first that the probability is greater than one would expect.

A large number of extensions developed when the male was paying close attention to the behaviour of extra-group males. These ranged from walking across territory boundaries to the initiation of intra-troop aggression. It was not possible to assess why the male should respond this way some times and not others. For this reason the condition could only be tested on the basis of the proportions of occasions where the subject was actively paying attention to a non-group male.



a. Contribution of each category to the total.

b. Percentage of each category that is accompanied by an extension.

c. $\bar{X}$ % with ext.

Figure 5-22: The contribution of different types of social encounters to the interactions between males and various age-sex categories, and the degree to which each is accompanied by penile extensions. The categories (1-5) are taken from Table 5-3. Sex is not listed although it is used in the calculations. In this figure, homage refers only to that received from other males.

PARTICIPANTS	PENILE STATE EXTENDED	 NOT EXTENDED
MALES	4	29
FEMALES	8	151
JUV/INF	7	100

Table 5-16: Penile state during amicable encounters. Chi-square = 227.8; df = 1; $p<0.001$ (tested with categories collapsed).

CONTEXT	PENILE STATE EXTENDED	 NOT EXTENDED
BEHAV. OF EXTRA-GROUP MALES $p<0.001$	34	2
ARRIVAL OF OTHER TROOP $p<0.01$	11	30
ARRIVAL OF HUMANS $p<0.05$	12	25

Table 5-17: Scrotal state during certain interactions with non-group members.

Arousal in these circumstances was clearly not due to direct interaction but seemed occasioned by the sudden appearance of relative strangers, in addition to the conspicuous behaviour of strange males. Not all dogs, for example, were responded to with fear and extensions. Some, regularly exercised in the area, were well known to the troop and their presence was ignored.

4. Vocalizations. These were not recorded as accompanying encounters where extensions were present. Recipients of aggression vocalized as described in the section on retractions.

5. Potential Recipients.

Table 5-18 displays the distribution of postures (this includes locomotion) adopted while the penis is extended. A distinction is drawn between those seen during sexual encounters and those attendant on other interactions. The data are not independent - more than one posture was often used during a period of extension - and is not amenable to a statistical assessment of distribution. However, the distributions are plotted in Fig. 5-23 . This allows some assessment of the degree to which any signal might be specifically directed towards the current partner.

i. Sexual Encounters. The range of postures was more restricted than in other encounters; walking - usually following the female - was the modal pattern, and only the mount was exclusive to this category.

POSTURE	TYPE OF INTERACTION. SEXUAL	NON SEXUAL
1. LIE DOWN	0	4
2. 4-LEG HUNCH	0	5
3. 4-LEG	11	42
4. 4-LEG UP/SPLAYLEG	4	43
5. HINDLEG SIT	0	6
6. STAND	7	8
7. BIPEDAL STAND	0	3
8. MOUNT	5	0
9. BROADSIDE	0	14
10. RED-WHITE-BLUE DISPLAY	0	4
11. TREE DISPLAY	0	8
12. WALK	23	61
13. PLAY	0	7
14. RUN TO	0	23
15. RUN OFF	0	3
TOTAL	50	231

Table 5-18 : Postures, both static and dynamic, adopted during periods of extension. Data comes from male focal-samples.

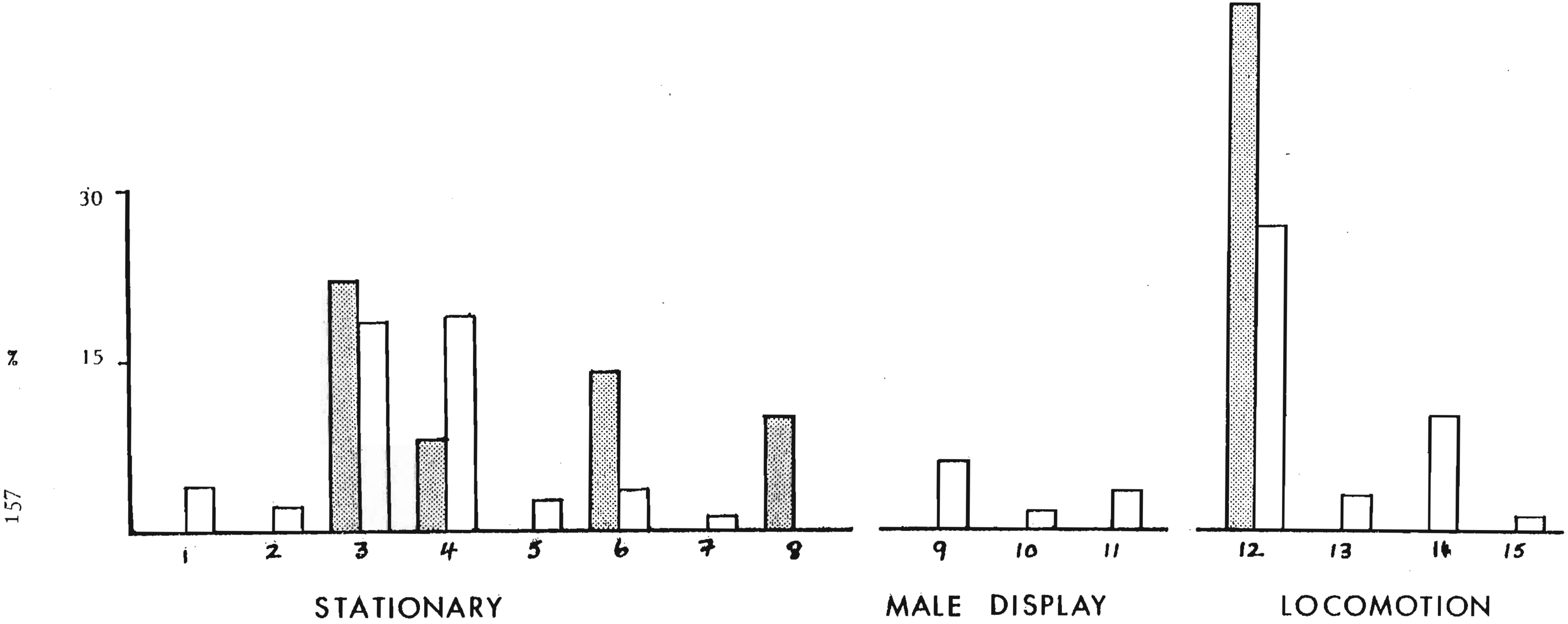


Figure 5-23: Penile extensions: A comparison of the postures used during sexual encounters (hatched bars) and non-sexual social interactions. The numbers refer to specific postures and are those used in Table 5-18.

Only when the animal was sitting was it conceivable that the partner alone could see the extension and there did not appear to be any specific `display' of genitals to female recipients of sexual behaviour. Except for walking all postures were static.

ii. Other Social encounters. A much greater variety of postures appeared here, including three `complexes' never seen in the absence of extensions and which must, therefore, be considered further.

a. The Broadside.

A `broadside' was an unmistakeable, maintained, posture achieved by walking or running up to another animal and then turning to stand at 90 to it. In doing this, and often also moving a little past the recipient, the subject's scrotum and penis were clearly displayed (Fig. 5-24 . See also Fig. 5-25). Recipients always looked towards the genitalia at some stage during the encounter.

A total of 24 were seen (14 in focal-samples); of these three were not directed at close-range but appeared to be prompted by the sudden appearance of another troop in the distance. In these cases the male ran to the troop boundary, turned and stood at right angles to the advancing troop while `headflagging'. Headflagging is a rapid turning of the head from side-to-side and, while it may well be ritualized (see Kingdon, 1980), it also served to allow the male to keep both troops in sight. At the same time the `flashing' of the headband it

Figure 5-24: The broadside.

Figure 5-29: A sexual present given by an adult female.

produced made the male even more conspicuous. The Broadside, with the exception of the example shown in Fig. 5-25 , always appeared as a behaviour on its own, and not as part of something else.

a. When given within a troop it was always given to a lower-ranking adult male (N=9) whose response, typically, was to back off, perhaps vocalizing, and for the performer to move off. A recipient was once seen to come up and smell the performer's genitalia after having looked at them.

b. When given to an external male (N=11) the response was generally different, being reciprocated twice, ignored six times and resulting in submissiveness in only three instances. When not behaving submissively the recipient always developed a penis extension of his own. The distance of display to external males was generally greater than to males of the same troop.

c. When given to an advancing troop (N=3) the was no observable consequence as was the case when given to an external female (N=1).

Interestingly, on the one occasion it was seen to be given by a subadult male (GMR) to an adult (POI) he got cuffed and threatened for his troubles.

This sex difference in recipients, even when tested conservatively (there were more females than males and therefore associated expected values should be higher) was significant (Binomial Test; $p<0.001$). Struhsaker (1967b) recorded a `sideward-display' but this was seen to be given in conjunction with facial threat and it is more likely that this study's broadside is one of the variants of his Red-White-and- Blue display.

b. The Red-White-and-Blue Display.

Struhsaker's description of a Red-White-and-Blue Display included both walking back and forth in front of the recipient as well as encircling him. The former may have been an elaborate version of the broadside but was never seen in Natal. The latter was however, and the term Red-White-and-Blue display (hereafter RWB) is used, in this analysis, to refer to it specifically.

In performing an RWB a male would move up to the recipient and then `confidently' walk around him (Figs. 5-25 and 5-26). Although in the illustrations the display ends in grooming and a broadside these were atypical. Of the 12 displays recorded (4 in focal-samples):

a. All were to adult males of the same troop. Something similar in form was given to a female but differed in that the male was attempting an olfactory investigation of her anogenital region and, in pursuing this, kept his head close to the ground.

b. Two were incomplete in that the performer moved off before completing a 360 turn.

c. The performer had a medium-to-long flaccid extension 10 times and a jerking erection once.

d. The response was usually one of subordination, with the recipient sitting hunched, vocalizing and giving rapid glances to the performer. His testes were definitely adducted during 10 of the displays. The display then ended with the recipient backing off and the performer walking off. In going off like this the genitals remained in the recipient's field of view after the display had ended.

e. When both protagonists were low-ranking (N=2) the recipient also had an extension and the display ended with a request for grooming.

As far as the RWB serves to display the genitals of the more dominant male its mechanics are interesting. By being approached closely and circled, the recipient - to keep the displayer in sight and his genitals out of harm's way - is forced to turn as well. The necessity to avoid making sudden moves and the hunched posture assumed slows down the recipient's rate of turn relative to that of the displayer. This lag therefore results in the sender's genitals remaining in the recipient's visual field throughout the display. The performer's tail, which could otherwise obscure his genitals, is carried curved throughout.

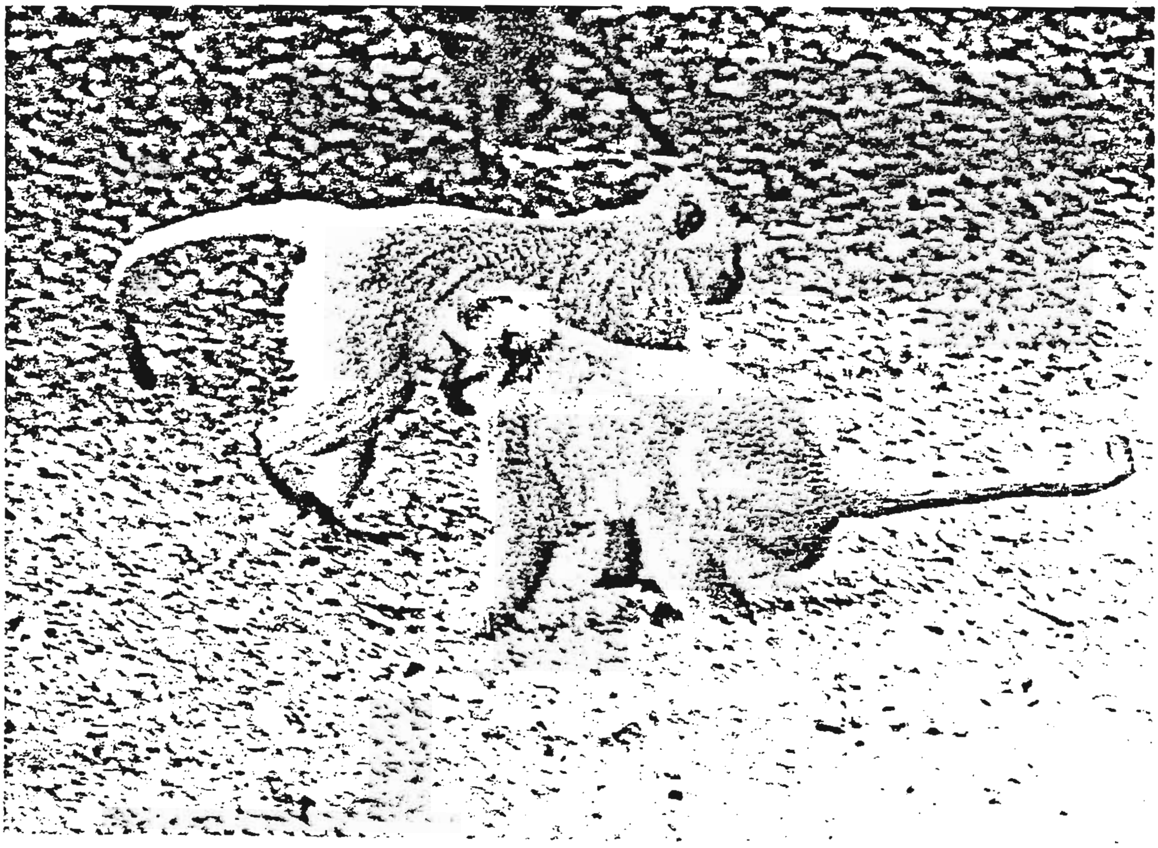
The display as seen in Natal closely resembles Struhsaker's description although Natal males never placed their hands on the recipient's head, nor did they carry their tails vertically erect. Struhsaker's `penile display' (a male holds the recipient and bipedals close to him) was not seen.

Although juvenile males were capable of extensions and erections they were never seen to perform even a rudimentary

On the following two pages:

Figure 5-25 : A Red-White-and-Blue display in which the displayer circles the recipient in a clockwise direction. The display concludes with a broadside.

a



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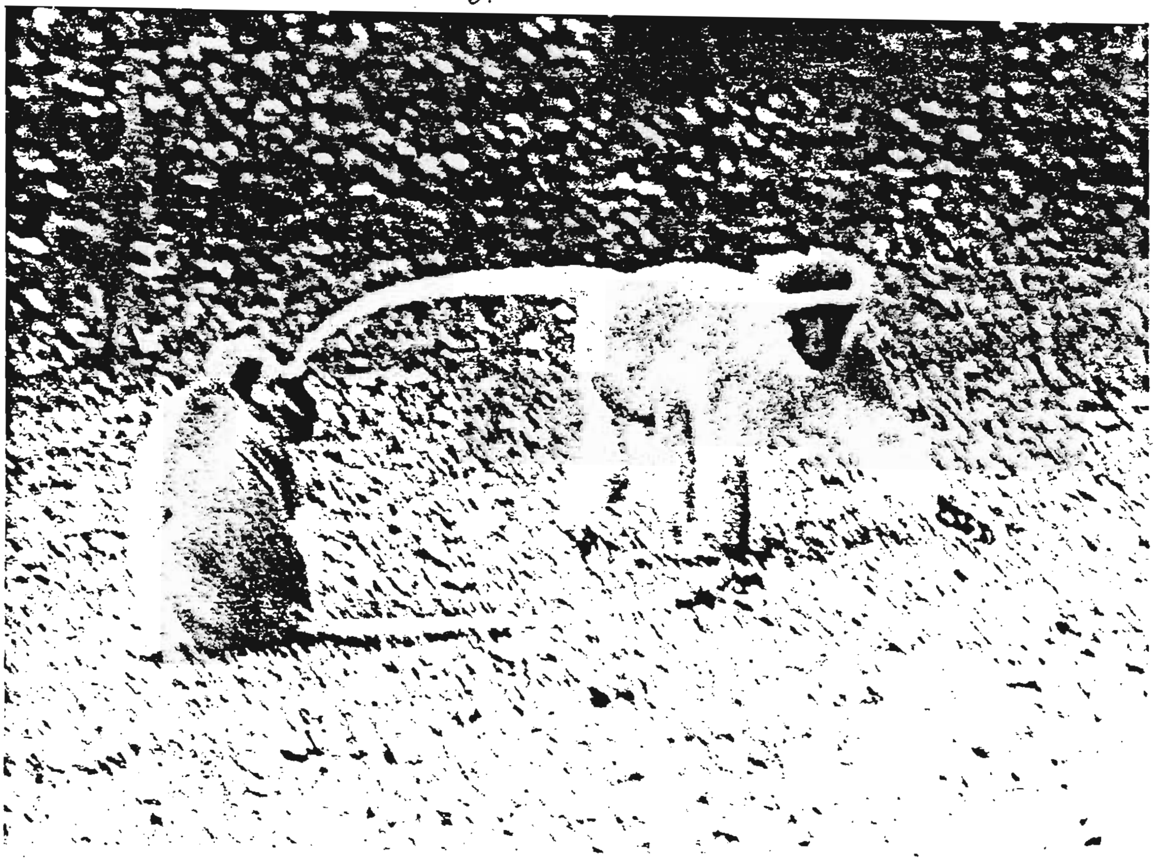

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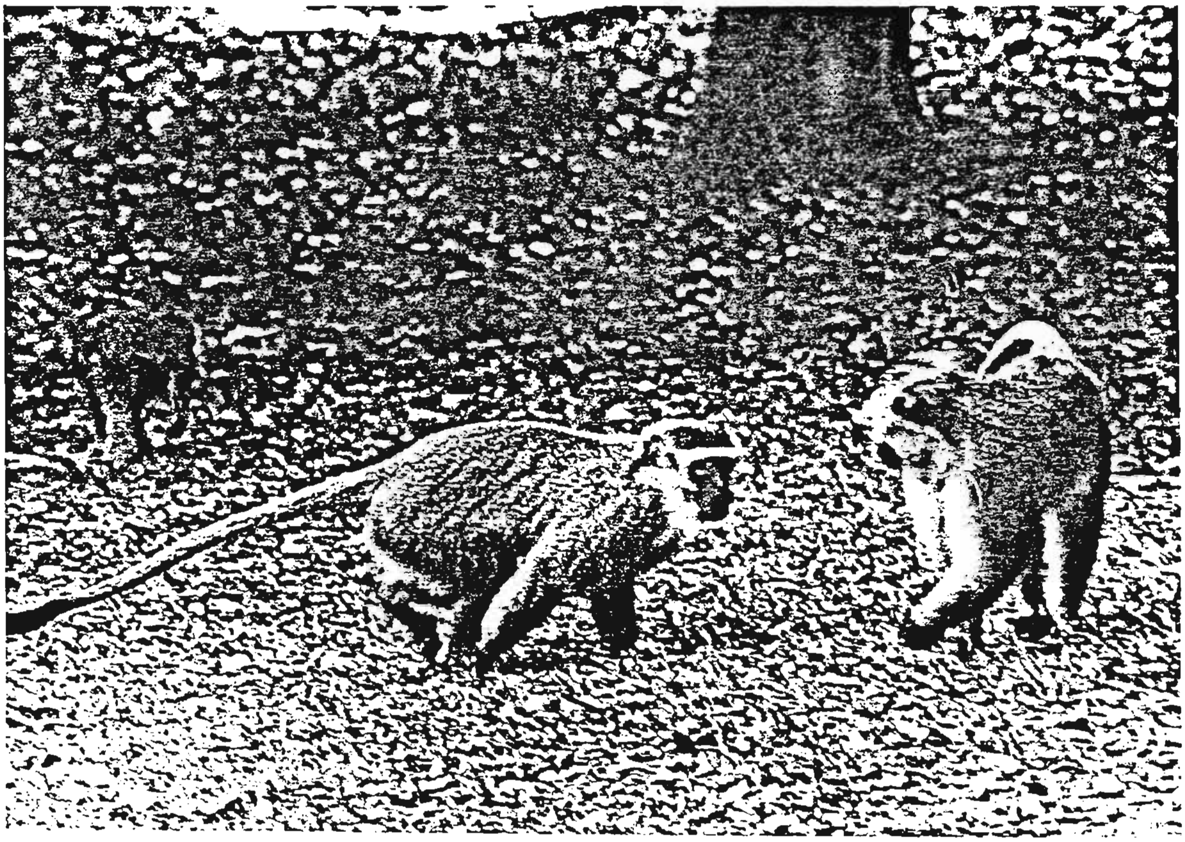

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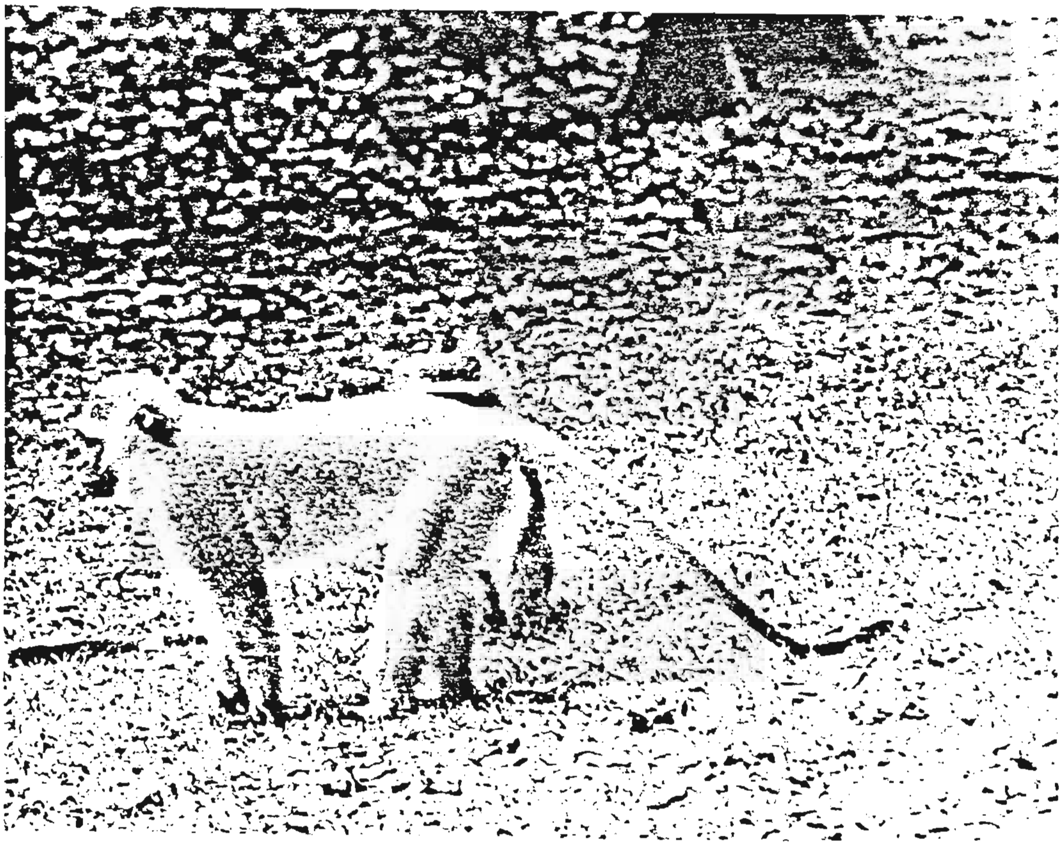


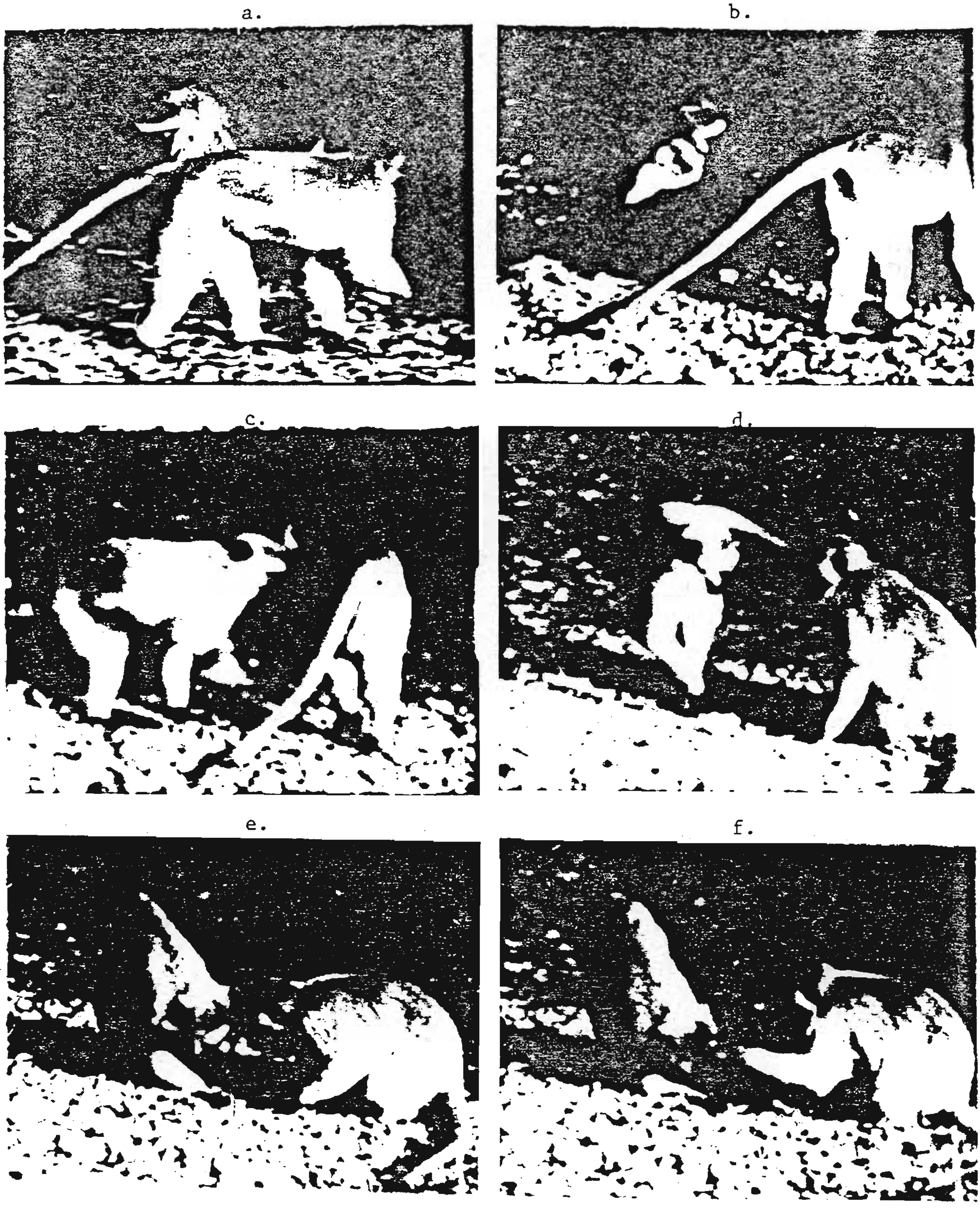


Figure 5-26: The Red-White-and-Blue display. The displayer is seen walking around the recipient from left to right and then successfully soliciting for grooming.

version of either the broadside or the RWB.

c. The Tree Display.

Like many other species, the vervets sometimes performed a display that, because it took place arboreally, is referred to as the `tree display' (Struhsaker's `branch shaking'). The phrase is also applied to similar displays at the Cage, where vertical and horizontal wooden supports replaced trees.

It was performed only by males and involved, in essence, bounding and leaping, with tail curved and body tense, through the upper reaches of a tree. The performer sometimes paused briefly to shake the branch on which it was standing and twice actually concluded the display by leaping out of the top of the tree and landing on branches some 10 or 12 feet below.

It was a display of high intensity and the combination of visual and auditory output made it very conspicuous. As it could not be missed all instances (N=21) are assessed.

a. It was performed more by the alpha males than by the subordinates. (Table 5-19).

b. It was caused more frequently by the behaviour of external animals (N=20) than by behaviour within the troop (Binomial Test; $p<0.001$). More specifically, external males were responsible (N=16) for most of the displays. They would follow confident walking in the territory of the performer (on the roof at the Cage), the sudden initiation of intra-troop aggression, or

aggression directed to the performer himself. On two occasions the performer had slowly walked up to an external male without otherwise interacting before returning and initiating the display. The single display due to an intra-troop encounter was performed by TE after he had given a false chase to TOG.
c. 12 of the displays led to the reception of very noisy aggressive chases from coalitions of females (N=11) or infants. Not once did the chased male adduct his testes because of this (see Fig. 5-27) even when, as happened to GEO, he was pursued by a group of 15 adult and juvenile females. Five of these chases led, in turn, to false chases from subordinate males.

One surprising thing about the display was the ease and suddenness with which the male could stop and shift into another behaviour, such as autogrooming or foraging, giving the appearance that the male's emotional investment in the display did not match its manifest intensity.

In 18 other cases all taken from troop samples at Burman Bush, males and females were involved in intense aggression that seemed similar to that seen during the Tree Display. They differed in that the aggression was not preceded by a Tree Display, although the male, once chased, often took to crashing away through trees. It was started by what appeared to be a `pointed' walk towards a female who then responded with a scream-chase.

It was again performed significantly more by an alpha male

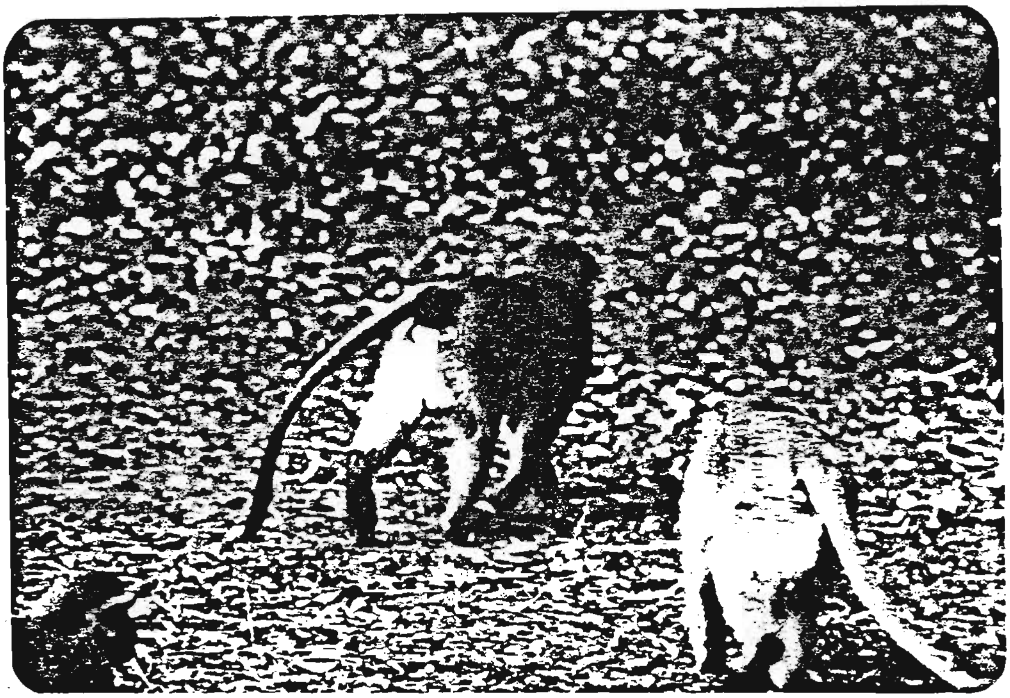


Figure 5-27: The alpha male walks off as a female initiates a scream chase. He has not adducted his testes and has an extension.

than by any subordinate (16:2. Chi-square = 39; df = 1; $p<0.001$).

The cause of these wasn't always detectable although external males had been involved at least 6 times and general intertroop aggression 8 times.

Recipients were always female and the male again moved off without adducting his testes. In a few cases he stopped and confronted the females with a threat . The tension evaporated rapidly, though, and the male then just turned and moved off. Sometimes, however, the female did not respond quickly enough to the advancing male and, consequently, was physically attacked - either bowled over or grabbed and bitten - before responding with a scream-chase. 14 of these episodes resulted in the formation of female coalitions and three led to false chases from single subordinate males.

There was no noticeable response from the other troop to this, except that, reciprocally, a male there would sometimes initiate a Tree Display of his own.

Returning to the postures generally, there is one other group - the 4-leg up and splayleg - that are also mentioned in the literature as being specifically adopted to display the genitals advantageously (Wickler, 1967, Bolwig, 1978). These are shown in Figs. 5-7 and 5-8. In the splayleg, the thighs are spread and the legs either bent at the knee or straightened out. Visually the angle of the legs acts to draw attention to the genitals, which are situated at their intersection. In the 4-leg up sit all four limbs are lifted off the substrate on which the ischial callosities have been placed. This position allows the genitals to be seen from both the side and the front, except where the view is obstructed by the surface against which the legs have been placed.

To test Wickler's hypothesis that the males do assume these `sentinel' positions in order to act as optical markers of the troop position, the frequency with which they accompanied an extension caused by non-group members (vervets and humans) was compared to the frequency of adoption due to intragroup activity (Table 5-20. Sexual behaviour is excluded).

While the allocation of postures to categories generally violates independence, it is possible to test any particular posture insofar as it was only ever recorded once during each period of extension. It is concluded that the 4-leg up/splayleg group was used more frequently against externals (Chi-square = 27.27; df = 1; $p<0.001$). Nevertheless, it was clearly observed that these positions were <u>not</u> assumed spontaneously in the event of extensions but were given in response to the behaviour of externals.

One way of showing this is to compare the frequency of use of postures when there is no extension with those when there is

	FREQUENCY OF DISPLAY	
PERFORMER	OBSERVED	EXPECTED
ALPHA	17	6.3
SUBORDINATE	4	14.7

Table 5-19: The frequency with which different status males performed the Tree Display. Chi-square = 26.9; df = 1; p<0.001.

CONTEXT	ADOPTED	NOT ADOPTED
INTRAGROUP	14	69
EXTRAGROUP	29	18

Table 5-20: The frequencies with which the 4-leg up and splayleg postures accompany extensions during intra- and extragroup encounters.

(Table 5-21 . See Table 5-34 in the Yawn section for the distribution of postures when no genital signals or yawns were being given. Unfortunately, splayleg is included in the `hindleg' category, and so only the 4-leg up posture is compared). The test indicates that it was more frequent during periods of extension (Chi-square = 15.56; df = 1; $p<0.001$) and that, as shown above, extensions themselves were not adopted spontaneously. The implications are that this posture is specialized for genital display but specific to encounters that induce extensions in the signaller. Nevertheless, spontaneous use of the posture is more frequent for males (11/188) than for females (6/298 samples) as tested at Burman Bush (Chi-square = 4.87; df = 1; $p<0.05$).

Yet another reason for arguing that the 4-leg up/splayleg postures are adapted for genital signalling is their association with the `jerking erection'. While this section has been based on undifferentiated extensions, the fact that the jerking erection adds motion to an otherwise static penile display suggests that it may serve to maximize signal power/efficiency. It can only do this if it is displayed optimally and the postures under consideration can, in the absence of the use of any sustained bipedal posture, be asumed to be the best for this. This is confirmed by the data in Table 5- 22 In this way the most conspicuous of the extensions and the postures least likely to hinder their visibility were associated and evoked by events happening at a distance where signal clarity is essential.

PENILE STATE	OBSERVED	EXPECTED
NOT EXTENDED	11	23.5
EXTENDED	30	17.5

Table 5-21 : The use of the 4-leg up posture during periods of non-extension (N=188 focal-samples) and periods when the penis is extended (N=140 extensions).

PENILE STATE	OBSERVED	EXPECTED
JERKING ERECTION	14	5.4
OTHER EXTENSIONS	33	41.6

Table 5-22: The frequency with which 4-leg up/splayleg were associated with jerking erections (N=26) and other extensions (N=200). Chi-square = 15.47; df = 1; $p<0.001$.

In conclusion, there is clear evidence that postural complexes specialized to display the genitals, or which are exclusively linked to extensions, exist. However, while these may even be specifically directed towards a particular recipient, they do not preclude others from obtaining any visual information transmitted via the genitals.

6. Aftermath. As regards intratroop aggression, recipients responded submissively to the behaviours that accompanied extensions. External males showed no such response to extensions, either ignoring the signaller or initiating aggression within their own troop.

After these encounters the signallers were sometimes the recipients of amicable behaviour from females and, much less frequently, from males. Interestingly of the 11 recorded friendly interactions with females that followed male aggression, 7 involved the alpha female.

7. Interest in Male Genitals.

During observations, animals were sometimes seen to focus their attention on adult male genitalia despite not being recipients of male displays. Table 5-23 lists all incidents seen at Burman Bush.

The data suggest that juvenile and adult males were more likely to pay close attention to male genitals than were females.

BEHAVIOUR	MALE	FEMALE	JUV. MALE	JUV. FEMALE	INF.
CLOSE LOOK	0	0	2	0	9
LOOK/SMELL	4	1	2	0	1
LOOK/GRAB	4	1	4	0	5
TOTAL	8	2	8	0	15

a. How animals responded to male genitals.

SCROTUM	6	1	5	0	4
PENIS	2	1	3	0	11

b. To what part of the genitals the attention was directed.

Table 5-23. The frequency with which different age-sex classes showed an interest in male genitals. Extracted from Burman Bush data.

It also seems that these males directed more of their attention to the scrotum than infants did.

Most of these encounters were low-key with the recipient paying little attention to the curious, although an infant was once bitten after grabbing a male's penis.

Four encounters were more spectacular and therefore particularly interesting:

i. The following is an extract from a transcript:

"WML comes and sits by GEO - puts hand under his tail, grabs his penis and then presents to him, looking over her shoulder. He develops jerking erection......She repeated this twice more but got no further response".

ii. On three occasions, without prior interaction, adult males were seen to run up to a more dominant male and grab or cup his scrotum in their hands. Here is one transcription:

"...runs some distance to TE - stops - quickly reaches out and pulls TE's scrotum. TE starts and then moves towards PER who sits hunched. TE has developed an extension as has PER. TE goes off."

8. The Relationship Between Penis and Scrotum.

This relationship will be dealt with in the discussion. It is relevant, though, to stress here that of the four possible combinations, one was common (no extension, no retraction) and

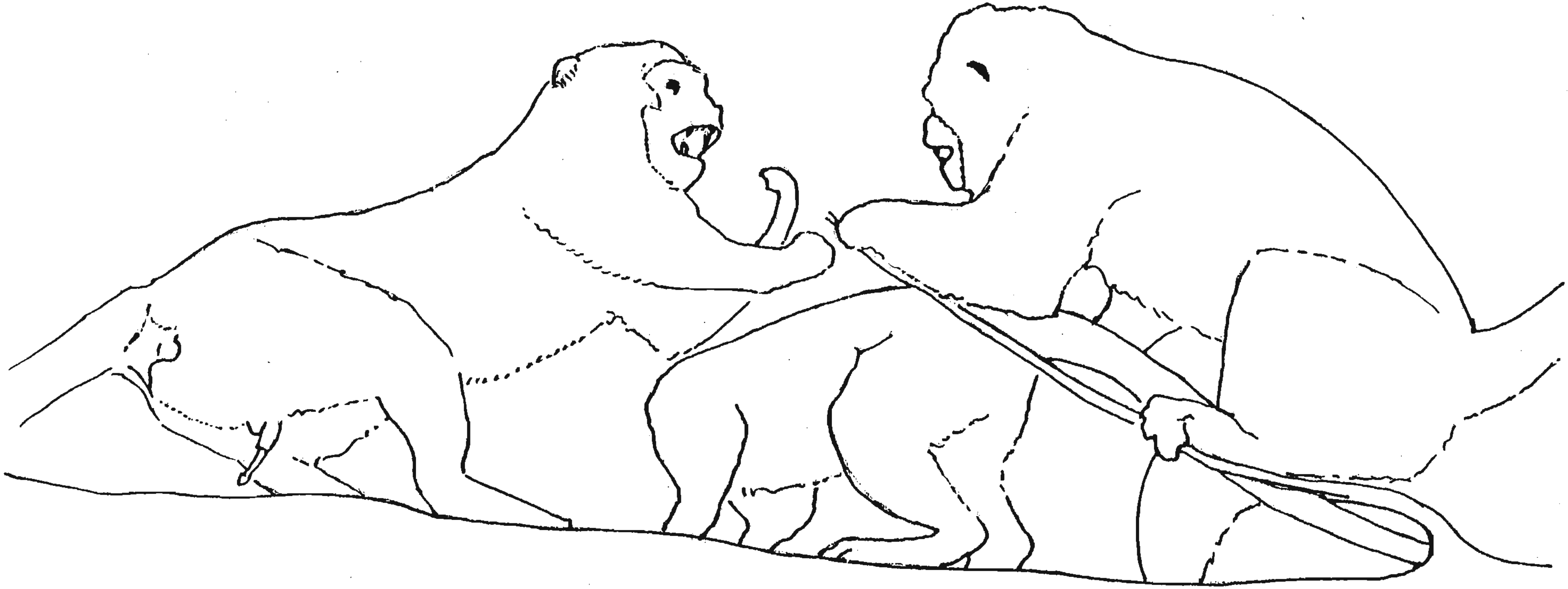


Figure 5-28: Drawn from a B+W photograph this figure shows adducted testes and an extended penis, present during intense aggression between adult males.

one was very infrequent (extension, retraction). The former represents the genitals' resting state while the latter was only seen during fights (Fig. 5-28), where the extension had been present prior to combat.

9. Other Study sites.

The same trends were evident at Stainbank and Burman Bush. The unhabituated males at Stainbank developed 10 jerking erections in response to my presence during the first half of the study period and only five during the second half, this despite the fact that the number of contacts had increased. The use of scrotal retractive capability during fearful encounters was also demonstrated in a more natural setting when a male did this while chasing off a raptor of unknown species.

5.3.3. Females.

The only display of the female anogenital region was seen in a sexual context when the hindquarters were `presented' to a male who either mounted or ignored it. It was not a prerequisite for mating which could as easily be initiated by a male (see Ch. 4).

The female usually presented by walking up to, and standing in front of, a male. She then slightly splayed her front legs, looked over her shoulder towards the male, flexed her knees a little and swung her hindquarters towards him. If he was not looking, as is the case in Fig. 5-29, this served to atract his attention. One infrequently seen variant had her walking a pace or two away from the male, looking over her shoulder, and merely lowering her haunches without swinging them. The tail was never held above the back. Older juvenile females were also seen to perform these motor patterns, Recipients almost always responded with an olfactory invstigation.

Males, especially during the breeding season, were sometimes seen to look intently at the perineal region of a passing female and develop extensions on the strength of this alone. It may be possible that the colouration enhanced the region's salience.

5.4. YAWNS.

5.4.1.Definitions.

As with Hadidian's (1980) macaques, the vervet yawn is a fluid, gaping movement of the mouth, which may last up to five seconds from initiation to completion. Two phases were recognised.

The half-yawn. The mouth partially opens and the lips tighten as the cheeks compress over the teeth. The mouth forms a small oval that shields both teeth and gums and is then rapidly opened without the upper incisors or canines being exposed. At this point the eyes may close (Fig. 5-30).

The full-yawn. As with the half-yawn except that, once the mouth is wide open, the head is thrown back and the lips are retracted and the canines and incisors become visible. (Fig. 5-31).

Figure 5-30 : The half-yawn.

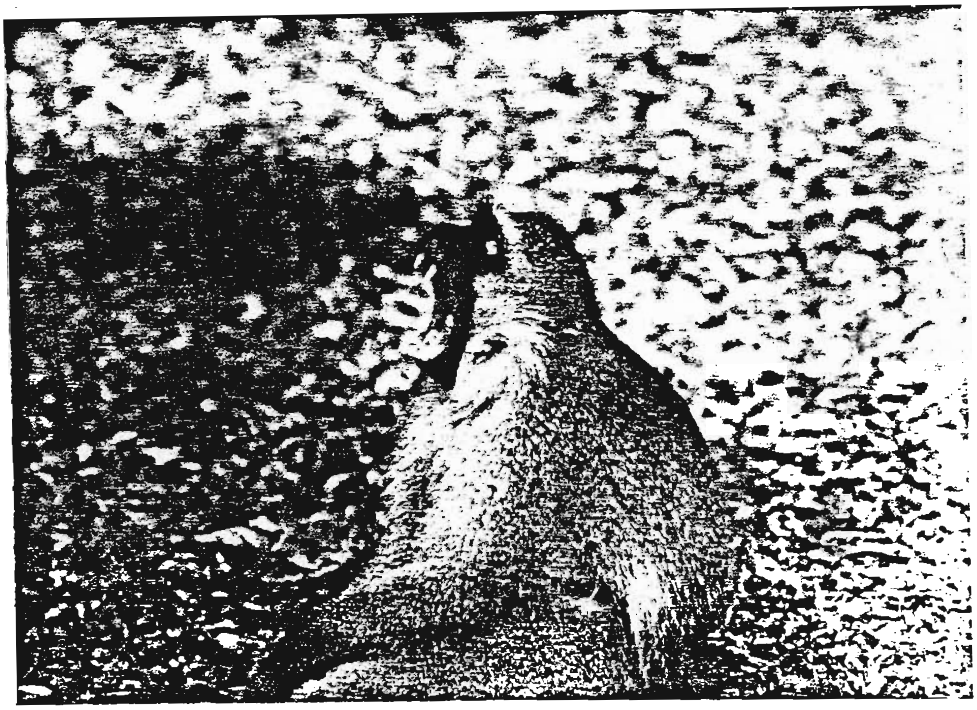


Figure 5-31 : The full-yawn given by an adult male.

There are no vocalizations associated with either of the yawn types although, at close range, the inhalation and exhalation of air may be audible.

Since the primary reason for an interest in yawns is the possibility that they serve to display the canines most of the following analyses are based only on full-yawns (hereafter yawns).

5.4.2. Age-sex related yawning frequencies. Table 5-24 lists the frequencies with which subjects yawned. Extrapolated rates are depicted in Figs.5-32 and 5-33. After the birth of her first infant, YBL was sampled as an adult female. All statistical tests are two-tailed with $p=0.05$ as the designated level of significance.

i. At both the Cage and Burman Bush, adult males yawned more frequently than the other age-sex classes combined (Cage: $U = 0$; $p<0.05$; Burman Bush: $U = 1$; $P<0.02$. Infants were excluded from the analysis). Adult female frequency did not differ from those of non-adults (Cage: $U = 5$; NS; Burman Bush: $U = 6$; NS).

ii. The above trends were repeated for half-yawns.

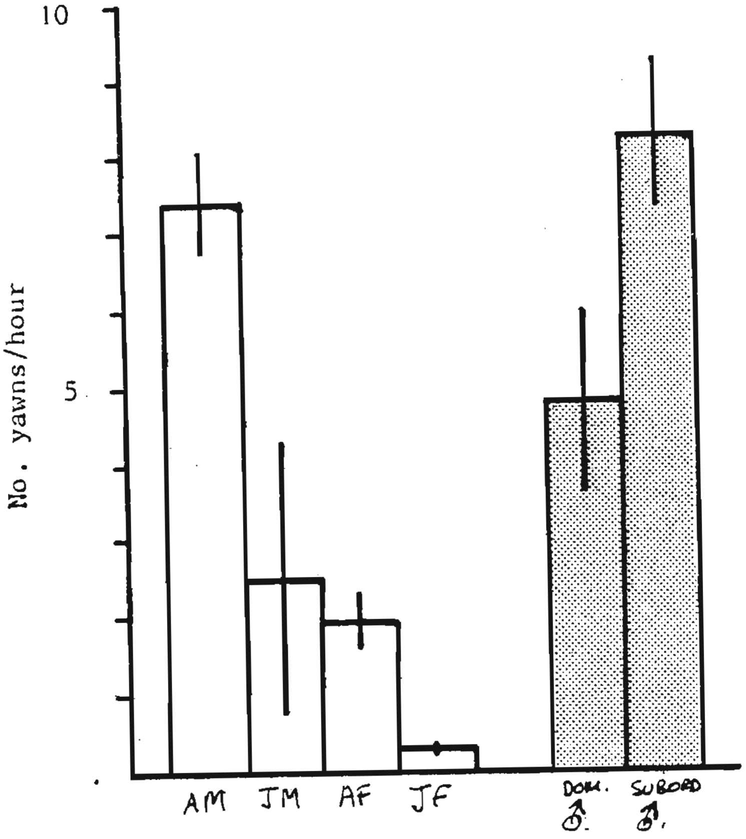
iii. At both localities, adult males yawned at the same rate (Burman Bush: Chi-square = 8.9; 5 d.f.; $p>0.1$; Cage: Chi-square = 2.189; 1 d.f.; $p>0.1$), as did females at Burman Bush (Chi-square = 10.94; 5 d.f.; $p>0.05$). Yawn frequencies of the Cage females were too small for testing.

SUBJECT	HALF-YAWN	FULL-YAWN	No. HOURS OBSERVED.
ALF	5	23	2.85
TOM	8	14	"
<u>a. Adult males.</u>			
U	6	5	"
DISC	2	9	"
CROSS	0	5	"
OM	1	0	"
<u>b. Juveniles.</u>			
OBL	10	4	"
BOLT	1	1	"
TEE	1	4	"
SQ	1	2	"
VEE	0	3	"
<u>c. Adult Females.</u>			
LB	0	0	2.5
TT	0	1	"
DS	2	0	"
<u>d. Infants.</u>			
TOTALS	37	71	36.85

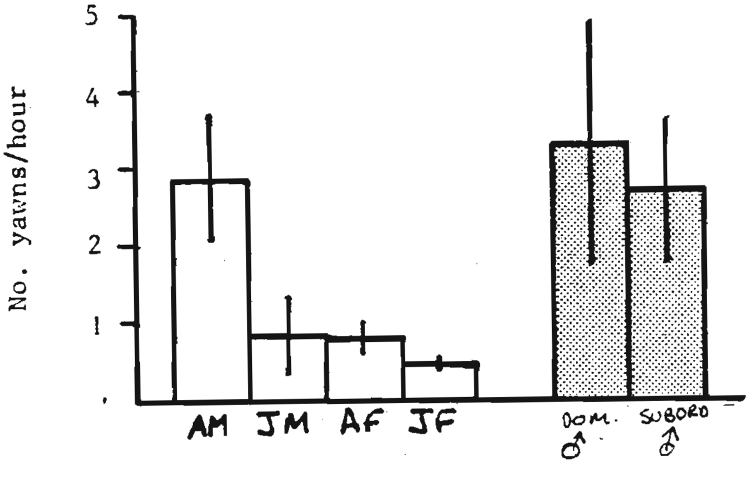
Table 5-24a: Frequencies of yawning for different age-sex classes at the Cage.

SUBJECT	HALF-YAWN	FULL-YAWN	No. HOURS OBSERVED.
TOG (A)	5	33	5.1
TE (A)	9	5	1.6
TOG	5	20	1.6
TE	11	12	2.55
GEO	0	38	4.7
POI	2	17	1.8
PER	2	13	1.9
TY	10	12	1.5
a. Adult males.			
GMR	6	19	4.15
GTL	1	3	6.4
GBR	2	2	5.45
b. Juveniles.			
OTR	5	12	6.15
LBN	9	23	6.1
WML	1	10	6.5
WTR	1	9	4.85
BS	3	2	1.8
YBL	1	4	3.45
c. Adult Females.			
INFANTS	0	1	2.05
TOTALS	75	236	70.65

Table 5-24b Frequencies of yawning for different age-sex classes at Burman Bush.

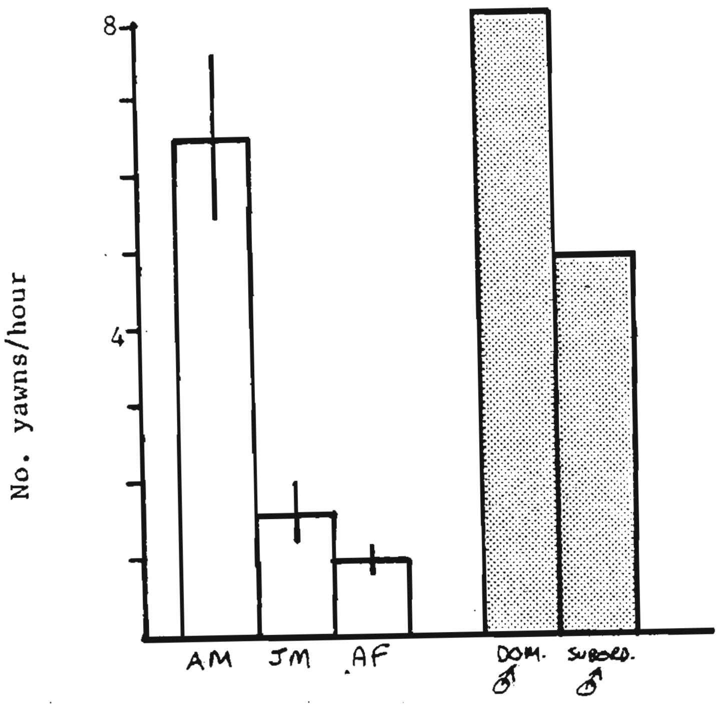


a. Full-yawns

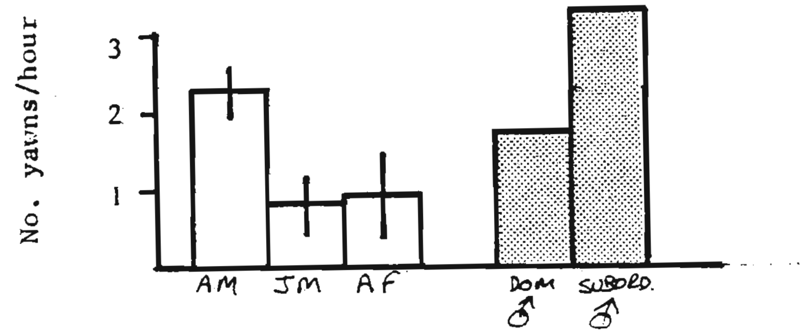


b. Half-yawns.

Figure 5-32: The rate at which different age-sex classes and different status males yawned at Burman Bush. AM = Adult male; AF = Adult female; J = juvenile. No infants were included in the analysis. Standard errors are given as vertical bars.



a. Full-yawns.



b. Half-yawns.

Figure 5-33: The rate at which different age-sex classes and different status males yawned at the Cage. Standard errors in the estimation of the mean are given as vertical bars. Infants were excluded from the analysis.

5.4.3. Dominance. Although adult males were a homogeneous group with respect to yawn rate it was found that, at Burman Bush, when divided on the basis of dominance, subordinate males yawned more frequently than alpha males ($U = 0$; $p<0.05$). At the Cage, as already stated, the two males did not differ. Interestingly, the trend there was in the opposite direction.

5.4.4. The distribution of adult male and female yawns. A preliminary means of assessing whether males yawn more than females for directly communicatory rather than energetic (i.e. they are more tired) reasons, is to hypothesize that their gross distributions will differ. This is to ask whether, if only males yawn to communicate, an observer will be able to act on the information conveyed in the yawn without having to rely on contextual cues. Three distributions will be considered below: because of the quality of the data base, analysis of the first two will utilize information from Burman Bush only.

1. Diurnal variation. If, for the moment, females are regarded as yawning primarily for fatigue-related reasons, then the diurnal distributions of their yawns should relate to energy expenditure. In contrast, males should perform a significant number of yawns independently of their state of wakefulness, or despite it.

The diurnal distributions are given in Table 5-25 and depicted in Fig. 5-34 . To prevent inflation of N (Siegel, 1956), observed frequencies (O) were corrected to take into account the differing number of observation hours per subject. This was done by:

$$(0) = \frac{\text{row total} \times \text{rate/hour (per sex)}}{\text{male rate + female rate}}$$

The resultant Chi-square (1.83; 11 d.f.; p>0.2) indicates that there is no difference in the diurnal distribution of male and female yawns.

2. Monthly variation. Again, if they are facing different pressures, either physiological or social, during the year, then this should be reflected in the rate with which males and females yawn. For instance, pregnancy and birth may stress females physiologically (see Altmann, 1980), while an influx of males may precipitate the use of `tension' yawns by males. These events do not happen at the same time of the year (see Ch. 4).

However, the monthly distribution of male and female yawns did not differ (Table 5-26; Fig. 5-35) and the prediction could not be supported (Chi-square = 15.07; 11 d.f.; p>0.1). This was so even when the analysis was restricted to months of peak intertroop movement (April, May, June) and birth (October, November, December) and tested in a 2×2 matrix (Chi-square = 1.52; 1 d.f.; p>0.2).

3. Yawning bouts. Yawns were not always performed singly and as many as four were sometimes seen to be delivered in quick

Time of day:	6	7	8	9	10	11	12	13	14	15	16	17	TOTAL
MALE YAWNS:	3	25	23	12	7	12	3	9	31	15	9	1	150
No. HOURS:	.75	2.1	2.65	1.5	1.45	1.65	1.0	1.2	2.75	2.55	2.3	0.6	20.75
FEMALE YAWNS:	2	6	4	6	6	5	1	5	5	12	5	3	60
No. HOURS:	.75	3.1	2.6	2.7	1.65	2.4	1.55	1.7	3.85	4.3	3.25	1.0	28.85

Table 5-25: Diurnal distribution of full-yawns at Burman Bush.

Month:	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
MALE YAWNS:	3	17	7	9	34	36	3	6	7	11	4	13	150
No. HOURS :	.95	1.35	1.9	1.8	3.95	3.95	.7	1.35	.7	1.15	1.3	1.65	20.75
FEMALE YAWNS:	1	8	4	6	14	4	2	4	2	5	7	3	60
No. HOURS:	1.6	1.7	3.0	3.2	4.9	5.2	.8	1.45	1.25	1.3	1.9	2.55	28.85

Table 5-26 : Seasonal distribution of full-yawns at Burman Bush.

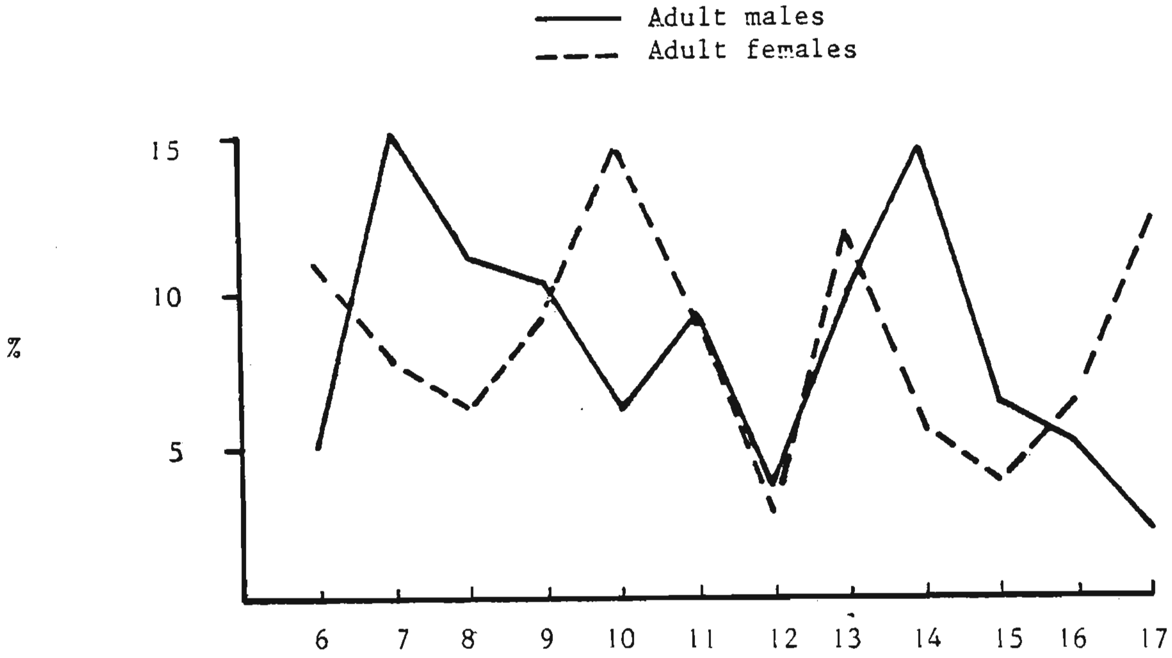


Figure 5-34: The diurnal distribution of the full-yawns of adult males and females, each expressed as a percentage of its total.

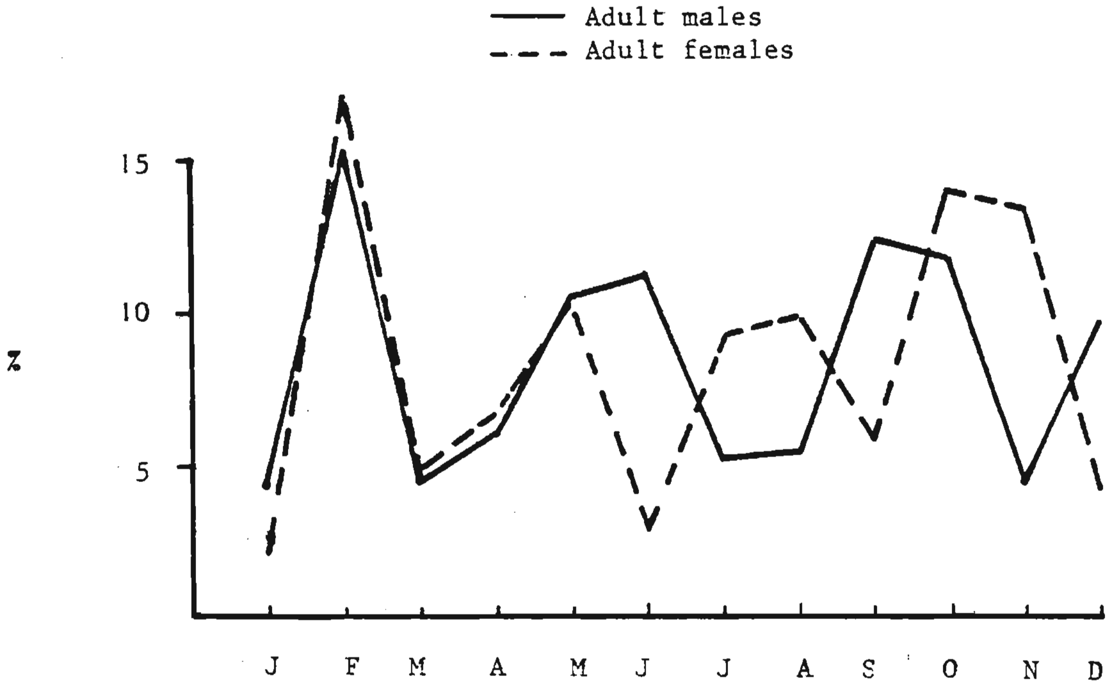


Figure 5-35: The monthly distribution of the full-yawns of adult males and females, each expressed as a percentage of its total.

succession (Table 5-27). Bout length is defined as the number of yawns performed without a change in the gross behavioural state that was occupied at the time that the first yawn was given. Only once was a run of yawns judged to have been delivered in two separate bouts.

To test whether male and female bout length distributions differed in their dispersal the dispersal statistic <u>d</u> was computed (Post, 1981). This is defined as:

$$d = \sum_{i=1}^{k} \frac{(N_i - \bar{N})^2}{\bar{N}}$$

where $N_1, N_2 \ldots, N_k$ are the lengths of the k observed bouts and $\bar{N} = \Sigma N_i / k$.

The <u>d</u> statistic is distributed as a Chi-square variate with k-1 degrees of freedom, under the null hypothesis that the observed bout lengths are sample observations of a Poisson variable.

From the results (Fig. 5-36) it must be concluded that neither male nor female bout length distributions differ from the Poisson model. They do also not differ from each other (Kolmogorov-Smirnov Two Sample Test; p>0.1).

<u>5.4.5.</u> <u>The analysis of context.</u> It is clear that any communicatory relevance that yawns might have are not independent of the context in which they occur. Context is used here to refer to the "events or entities that accompany or surround" yawning (Smith, 1977). The information that yawns make available can be translated into `meaning', only if they correlate with

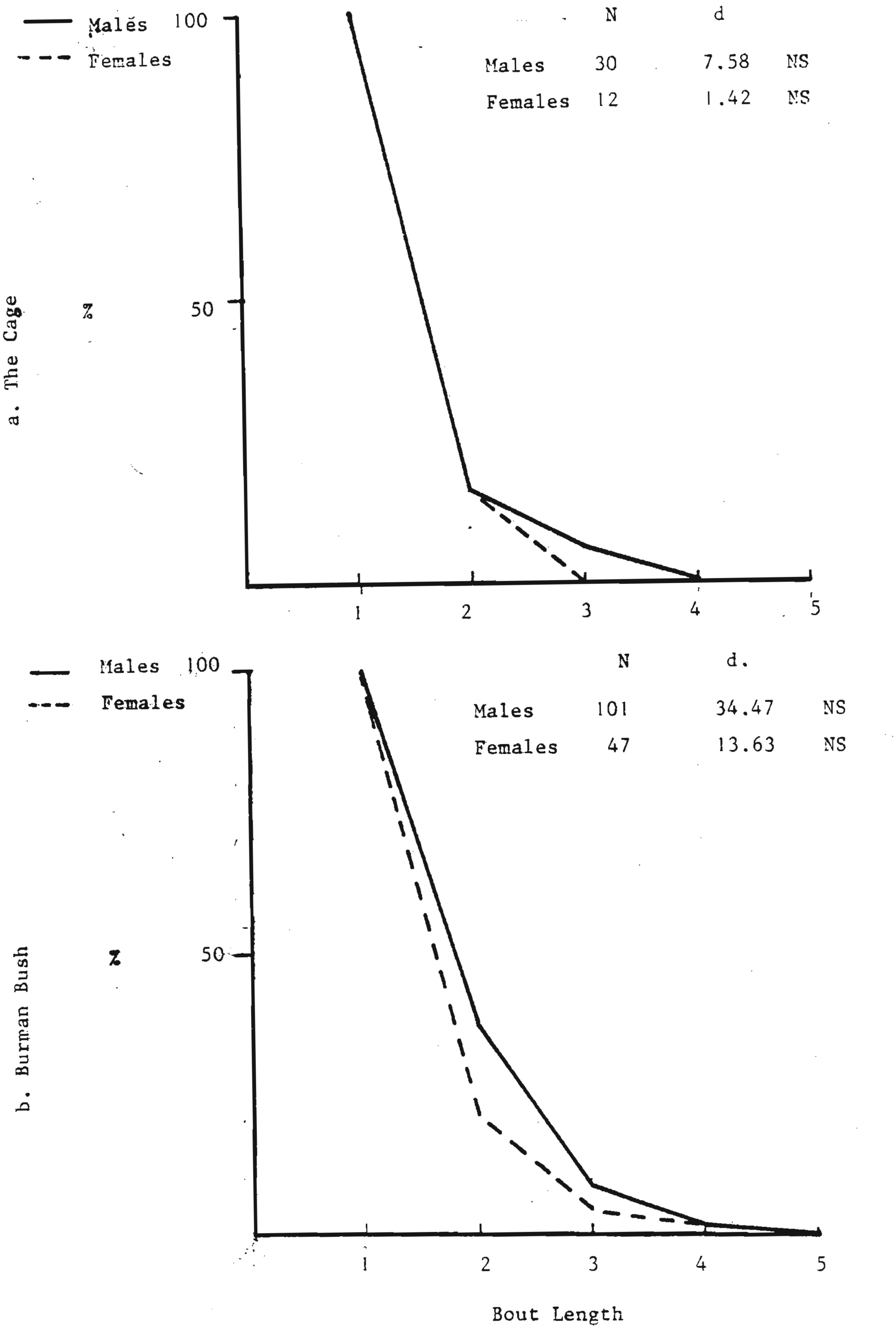


Figure 5-36: Survivorship curves of male and female yawn bout lengths. Given is the size of each sample (N), the value of _d_, and the degree of significance reached.

definable kinds of activity (Smith, 1968; 1977).

Prior work has specified at least two distinct yawns, those induced by fatigue and those related to immediate social events, this analysis proceeds by defining the two operationally and allocating all adult yawns appropriately.

Fatigue-yawns are given by an animal who, prior to the yawn, appeared to be relaxed or sleeping; was either alone or engaged in low-level activity (e.g. grooming); and who had given no recent indications of being either alert or tense (such as would be suggested by rapid glancing or vocalizing). Additionally, such an animal's behaviour will remain essentially unchanged for at least 10 seconds afterwards. All other yawns were regarded as being due to social events.

It is obvious that any such procedure has basic flaws, not least in its underlying assumption that such divisions will allow a reasonable interpretation of the vervets' social constructions. While it is ultimately impossible to be certain that a "relaxed" monkey is not yawning in response to events that we do not see or perceive, but to which recipients can respond appropriately, it is necessary that this approach serve as a first approximation.

As this thesis is also concerned with genital signals and the possibility that they too may be indicators of `tension', the presence or absence of penile extensions or scrotal retractions were expressly not used as defining characteristics.

BOUT LENGTH	CAGE MALES	B.B. MALES	CAGE FEMALES	B.B. FEMALES
1	25	63	10	37
2	3	29	2	8
3	2	7	0	1
4	0	2	0	1
TOTALS	30	101	12	47

Table 5-27.The frequency of occurrence of yawn bout lengths.

SUBJECTS	FATIGUE-INDUCED	SOCIAL	UNKNOWN
CAGE MALES	12	16	2
B.B. MALES	35	61	5
CAGE FEMALES	9	3	0
B.B. FEMALES	33	11	3

Table 5-28: Allocation of yawns on the basis of context.

1. Sex differences. Male and females did not appear to have yawned for the same reasons (Table 5-28). As the Cage and Burman Bush figures vary in the same direction, a single analysis was performed, with all 'unknown' yawn bouts allocated so as to minimize the sex differences. The result is still highly significant (Chi-square = 14.99; 1 d.f.; $P<0.001$). The fact that males also perform more fatigue yawns than females do (Chi-square = 5.89; 1 d.f.; $p<0.02$) suggests that some category confusion is attendant on this way of determining yawn types.

2. The effect of dominance. Alpha and subordinate males performed social yawns at the same rate (Chi-square = 2.54; 1 d.f.; $p>0.1$).

5.4.6. Concomitants of social yawns. The circumstances in which social yawns were performed are listed in Table 5-29.

a. Male yawns appeared to be overwhelmingly associated with either the occurrence of intratroop aggression or the behaviour of external animals. Within the aggression category yawns accompanied the reception of aggression more frequently than expected (Table 5-30).

b. While male yawns were more likely to have been induced by the behaviour of other males, probably because of their greater representation in agonistic encounters, female yawns, at least at Burman Bush, gave some slight evidence of being due to the behaviour of other females.

5.4.7. The timing of yawns. Yawns related to social events may be given during those events or after they have ended. Using

CONTEXT:	B.B. MALES	CAGE MALES	B.B. FEMALES	CAGE FEMALES
ALERT	7	1	2	1
PRESENCE OF HUMANS/DOGS	11	2	2	0
PLAY	0	0	1	0
SEXUAL	2	0	0	0
OTHERS FIGHT	2	1	0	0
BEHAV. OF OTHER TROOP	12	9	0	0
INTERTROOP AGGRO.	1	0	3	0
AGGRO. GIVEN	4	1	2	0
AGGRO. RECEIVED	14	0	1	1
PROXIMITY OF OTHER MALES	8	2	0	1
TOTALS	61	16	11	3

Table 5-29: The contexts in which yawns were seen to be given.

CONTEXT:	MALE	FEMALE	JUVENILES	INFANTS
AGGRO. GIVEN	3	2		
SOCIAL				
PLAY				
HOMAGE				
AGGRO. RECEIVED	12	2		
SEX		2		
TOTALS	15	6	0	0

	YAWN	NO YAWN
AGGRO. GIVEN :	5	121
AGGRO. RECEIVED:	14	58

Chi-square = 12.59; 1 d.f.; $p < 0.01$.

Table 5-30 : The intratroop interactions at B.B. with which male social yawns were associated and a comparison of the degree to which they accompanied aggression.

male data from Burman Bush (Table 5-31) it can be seen that the timing of yawns is dependent on the nature of the event. When agonism was specific - either given or received - yawns occurred afterwards, but when the encounters were passive - as when humans, dogs or more dominant males were present - the yawns were given before circumstances changed.

5.4.8. Response of 'recipients'. In the main, the conspecifics involved in these encounters were not close (>3m) to the subject at the time that he yawned. In most instances the recipients, i.e. anyone who could see the display, showed no overt response. In nine of the bouts at Burman Bush the recipients (here = those associated with the event that had produced the yawn, and all males) were physically close to the subject. Their recorded responses were:

a. Sits, observes - yawns as well.
b. Goes off.
c. Sits, develops penile extension.
d. Initiates mutual grooming.
e. (External male) goes off.
f. (External male) comes and displaces yawner.
g. Comes and displaces.
h. No overt response (2).

At the Cage the external male showed no overt response to those yawns elicited by his arrival.

On two occasions interesting responses were seen by low-ranking animals in close proximity to the yawner. One, a male, adducted his testes and the other, a female, hurriedly looked away and then turned away. On the other hand, a female was seen to yawn directly into the face of a male without affecting his behaviour in the slightest. It must be concluded that there is no striking change in a recipient's behaviour following the reception of a yawn.

5.4.9. Direction of yawns. In the literature, yawns are described as either `directed' or `non-directed'. In the vervets studied here, the animals nearly always yawned in the direction they were facing, although the head could be turned as much as 45 to the side. This means, especially in close-range encounters where the yawner always faced in the direction from which trouble might have come, that the yawn - both as a stylised movement and as a display of teeth - was always visible to the recipient. Since the canines stood out sharply against the background, even when viewed from the side, facing to the side while yawning is unlikely to have reduced their potential potency as a signal.

5.4.10. Behaviour of males after yawning. Table 5-32 lists the behaviour of subjects after they had yawned. It is clear that they are most likely to do nothing immediately afterwards but, if they do, they will choose equally among the active alternatives (Chi-square = 7.61; 3 d.f.; $p>0.05$). The behaviour chosen probably reflects more specifically the type of interaction that had preceded the yawn, although there was latitude even here.

5.4.11. Bout length. Using the formula given above, social and fatigue yawns were compared to see whether their bout lengths differed in dispersal (Table 5-33). Neither distribution

CONTEXT	DURING	AFTER
ALERT	5	2
BEHAV. OF OTHER SPP.	11	0
SEX	1	1
3rd. PARTIES INTERACT	2	0
BEHAV. OTHER TROOP	11	1
INTERTROOP	0	1
GIVE AGGRO.	1	3
RECEIVE AGGRO.	0	14
PROX. MALES	7	1
TOTALS	25	36

Table 5-31 : Time of occurrence of yawns.

POSITIVE SOCIAL BEHAV.	10
GO OFF	10
SIT STILL	33
GIVE AGGRO.	7
HOMAGE	1
TOTAL	61

Table 5-32 : Post yawn behaviour of males.

BOUT LENGTH	SOCIAL	FATIGUE
1	37	26
2	17	12
3	6	1
4	1	1
TOTALS	61	40

Table 5-33 : A comparison of the distribution of the bout lengths of social and fatigue-induced yawns for males at Burman Bush.

POSTURES	SOCIAL	FATIGUE	NON-YAWN
STAND	5	1	86
HINDLEG SIT	13	2	35
4-LEG SIT	29	21	45
4-LEG UP SIT	13	11	11
LIE	1	5	11
TOTALS	61	40	188

Table 5-34: The frequency with which different postures were used with different yawn types. Also given are the distribution of postures taken randomly from male samples at Burman Bush.

differed from the Poison model (Social: d = 21.48; 60 d.f.; NS; Fatigue: d = 12.46; 39 d.f.; NS), nor did they differ from each other (Kolmogorov-Smirnov Two-Sample Test; NS).

5.4.12. Posture. Social and fatigue yawns at Burman Bush were also compared along this dimension (Table 5-34). They were not distributed equally among the categories (Chi-square = 11.13; 3 d.f.; $P<0.02$ with `stand' and `hindleg' categories combined). From the data it appears that, when used, energetically more costly postures (stand and hindleg- sit), are more likely to be associated with social yawns. An observer could use this to infer that a yawn was social but there remains a large degree of overlap and posture alone would be of little use in assigning yawns to categories.

5.5. INTER-TROOP MOVEMENT.

While the phenomenon of inter-troop movement is well established, the current theoretical climate and interest in sexual selection and parental investment (Crook, 1972; Trivers, 1972) require that, for an increased understanding of population and social dynamics, more detailed analyses be made. In addition this elaboration is necessary if we are to begin to understand the determinants of the behaviour in the individual.

Specifically, data concerning the age-sex class of the migrants, proximal reasons for departure, the timing of the event, and the direction of movement are needed. We also need to know what the consequences are, both for the migrants and the troops involved.

With information of this type it will be possible to begin to assess the social use of signals within the framework of individuals´ life-history tactics.

5.5.1. MALE MOVEMENT

1. Frequency.

During the study period 12 males were seen to change troops; 4 of these migrated more than once, producing a total of 18 migrations in 4 years. Eight moved once, 2 moved twice, 2 moved 3 times and none stayed in the same troop throughout. No lone males were seen although this could be due to the nature of the habitat as they are occasionally found in areas where farming has spread troops out (Gooch, pers. comm.; Barnes, pers. comm.). No all-male groups were ever seen.

2. Age of migrants.

Of the 12 migrants, 5 were young adults (4.5-5.5 years) and it likely that, for them, movement was from the natal troop. Of the rest, 6 were mature males and 1 was old (as judged from his general appearance and the worn condition of his canines). No infants or juveniles moved, although 3 infants and 1 juvenile of unknown sex accompanied their mothers when Upper Troop split (see below).

3. Season of movement.

The males were recognisable as individuals and it was possible to note precisely when they moved between troops. The distribution of migrations through the year is illustrated in Fig.5.37 . It can be seen that there was a marked increase in the rate of movement during the months April, May and June. When the observations are partitioned so that they are amenable to analysis, it is shown that movement was not evenly distributed over the year, but occurred significantly more frequently during April to June (chi-square = 18.38; with a two-tailed test $p<0.001$. Expected frequencies were obtained by assuming equal monthly likelihood).

4.Direction of movement.

Twelve of the 18 migrations were from one of the three troops to another, while 5 were departures from the burman Bush community to troops outside. In one case, a male of unknown origin moved into Third Troop. It is interesting to note that, of those who changed troops more than once, only 1 male returned to a troop in which he had been earlier. Both males who were seen to move 3 times moved out of the area only after they had spent time in all three troops. This suggests that they moved into the nearest previously unvisited troop. One of the males who travelled beyond Burman Bush was spotted a few months later in a troop living on University property; his move having necessitated the successful negotiation of 8 km. of suburban Durban. Subsequent observations on him in this new troop revealed that he had become the dominant male.

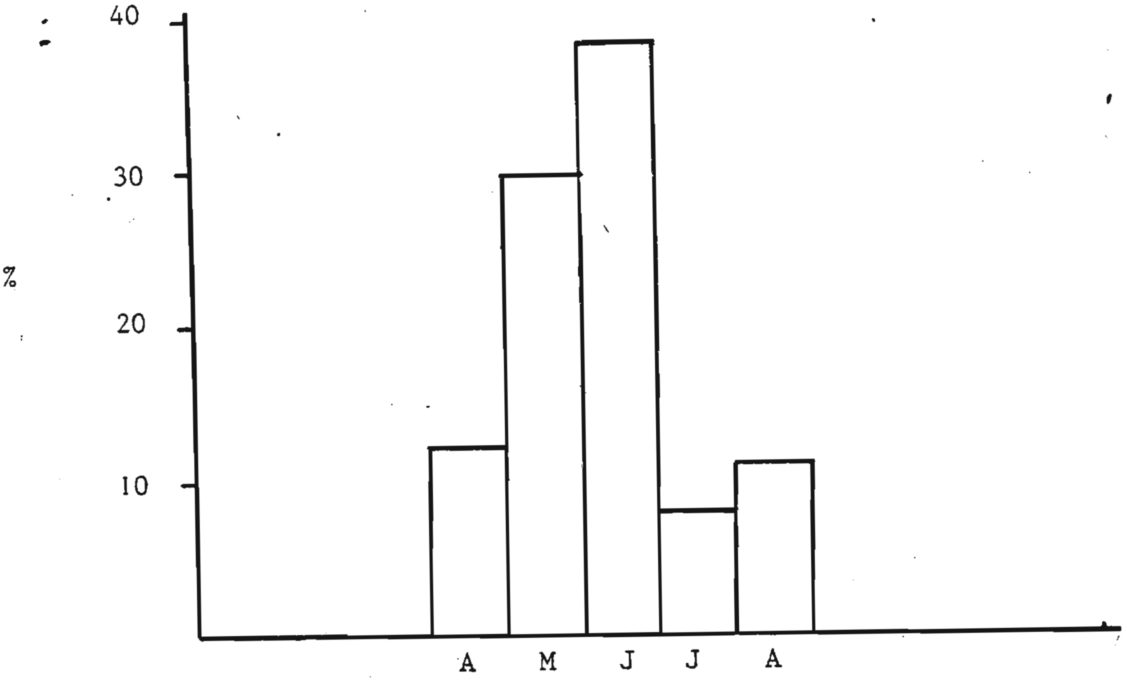


FIG. 4·5 . Annual distribution of heterosexual mounts (as a percentage of the total) seen at Burman Bush. (N = 46).

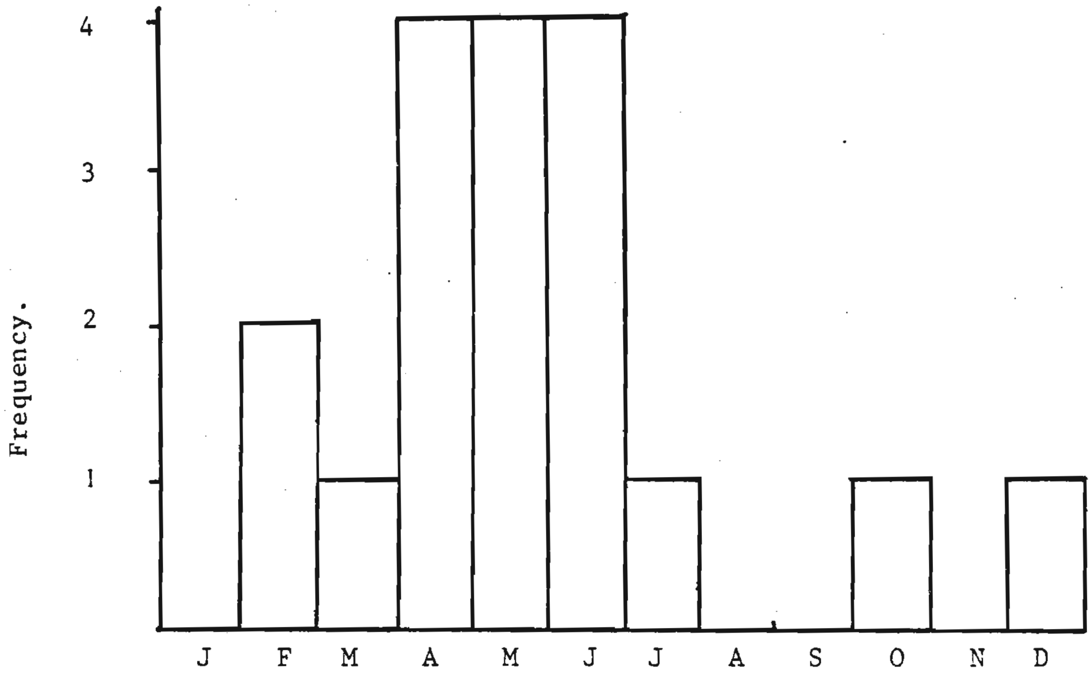


FIG.5-37. Annual distribution of male inter-troop movements.

The number of sexually mature females did not appear to unduly affect the direction of male movement. Of the 18 migrations, 6 were into troops with more adult females than the previous troops, 6 were into troops with fewer and one was into a troop with the same number. Numbers could not be gauged for the remaining 5.

5.Status.

All migrant were subordinate animals. No alpha-males moved until after they had declined in rank.

6.Precipitating factors.

To ascertain the reasons for the departure of a male from a troop of which he appears to be a relatively stable member, it is necessary to see what changes occur, generally, in relationships during the pre-departure period. The immediate reason was perhaps most obvious in those cases where a dominant male was defeated. Only once was the defeat not followed by the rapid departure of the loser (N=5). The victor did much to hasten the departure by continually harassing the loser. Dominance changes occurred both in and out of the breeding season. Since, however, many subordinate males left without a prior decrease in status and, moreover, tended to do so during the breeding season it is relevant to see what changes occurred at this time of the year.

i. Aggression. There was an increase in the quantity and
5-39 intensity of aggression during the breeding season. Fig.5-38

	Sample size	No. of wounds
Adult males	6	24
Adult females	11	15
Juveniles	9	7
Infants	10	0

TABLE 5-36·The distribution of wounds among age-sex classes.
5-36

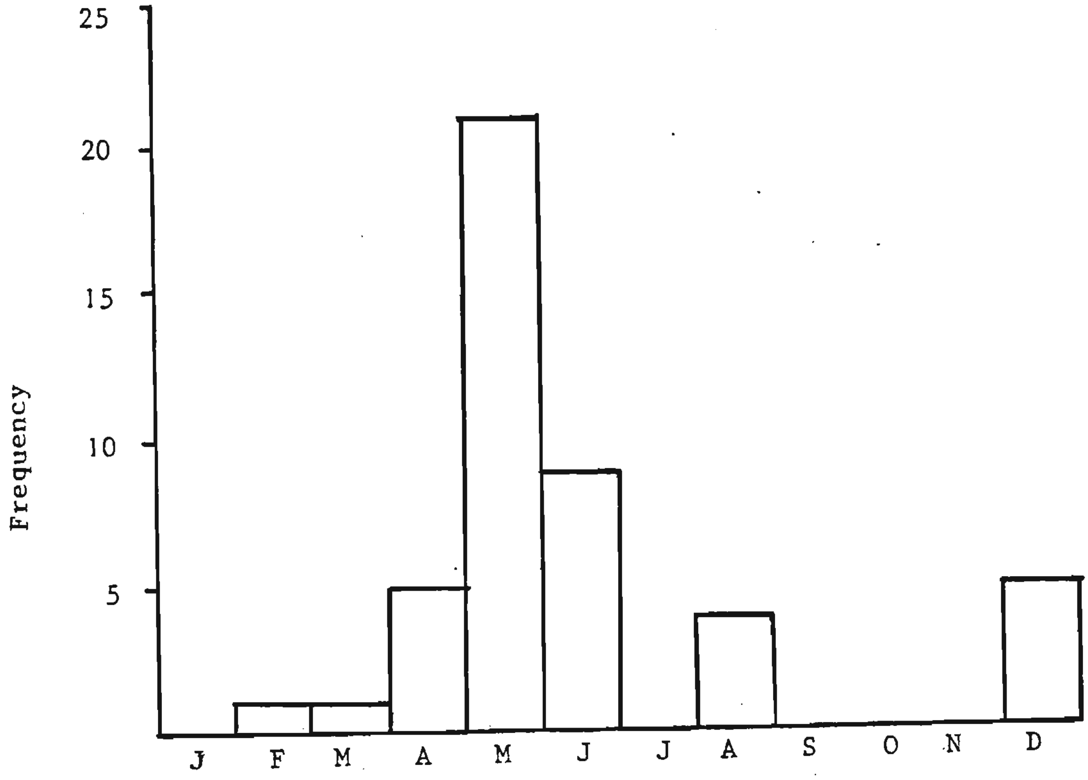


FIG.5-38. Annual distribution of fresh wounds.
5-39

shows the frequency with which fresh wounds were sighted during a single 12 month period (July, 1977 - June, 1978). Again more wounding occurred between April and June, inclusive, than during the rest of the year (chi-square, two-tailed; p<0.001).

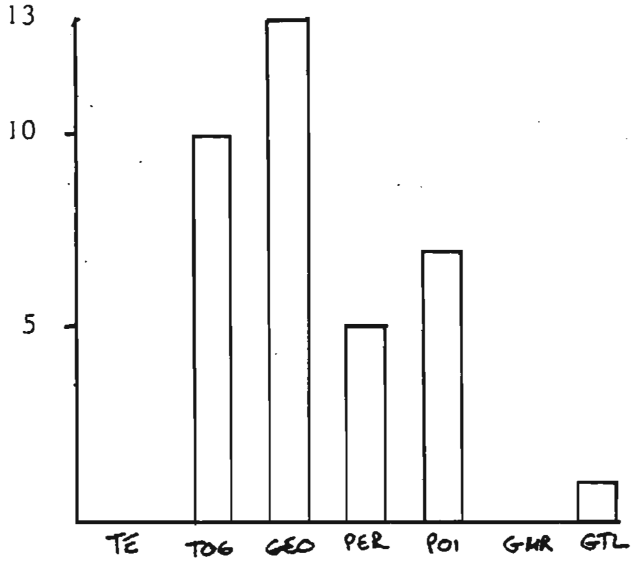
In a sense fresh wounds, rather than simply the frequency of agonistic encounters, are the best indicators of the intensity of aggression, since they imply a change in the nature of the agonism (Hausfater, 1975). Examination of the wounds revealed that they were unlikely to have been accidentally inflicted and were most likely to have been caused by fighting. Table 5-36 lists the distribution of wounds by age-sex category. Adult males received more wounds than adult females (chi-square, pairwise comparison, two-tailed; p<0.01) and non-adults were wounded less frequently than expected.

New arrivals bore 67% of the injuries seen on males and were, in fact, free of wounds when they moved into the troop. This suggests that they were not moving into a less hostile environment. The distribution of wounds also implies that serious fighting was confined to those who were the protagonists in sexual activity.

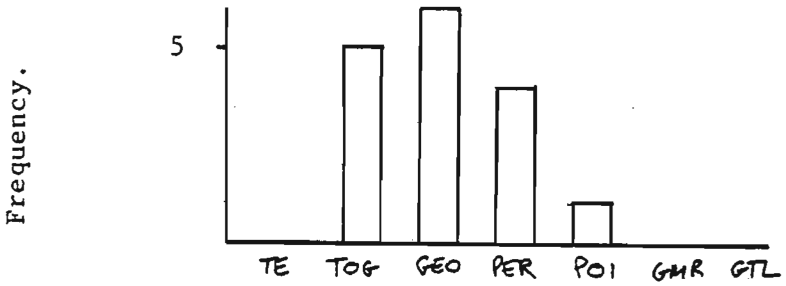
ii. Sexual activity. While established males (TOG and GEO) mounted females more frequently than newly-arrived males (PER and POI) over the same period of time this difference did not reach significance (Chi-square; p>0.05). Both of these groups performed far better than either the defeated male (TE) or subadult males (GMR and GTL) who were, on the basis of their inter-troop activity, sexually-active (Fig.5-39).

There is little evidence that high-ranking females mate preferentially with the dominant male (although it is not known whether they mate with him when they are most likely to conceive) although their spatial association with him may deter new males from interacting. On one occasion NN came and presented to PER who immediately looked towards TOG and moved off.

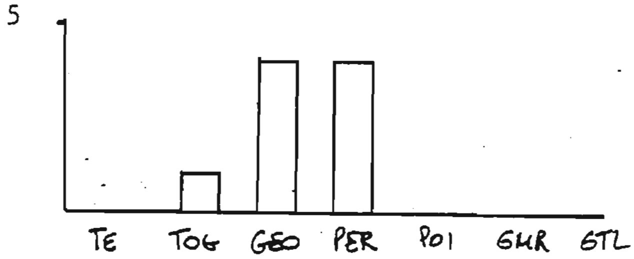
iii. Direction of attention. In addition to the suggestion that sex, or rather the lack of it, and aggression were the reasons for which males left, there is another factor that may have been significant. This has to do with the way in which male vervets view the world and would account for the readiness with which young males left their natal troops, as well as why departure did not appear to be the traumatic event we would expect it to be. It was noticed that subadult males showed fewer interactions with females and infants than did non-adult females and, more specifically, that they tended to become more `outward-directed´ as they grew older. The 2 sub-adult males in Upper Troop, who were as yet receiving little aggression from the adult males, began to voluntarily take more and more interest in other troops during inter-troop contact. They were often separated by some distance from their own troop as a consequence of their interactions with other troops, and when the latter were visible would orientate towards them. During close contact they were seen to play with external juveniles and even solicit for grooming from the other troops´ females. On one such occasion, a subadult male (GMR) became so engrossed in his interaction with



a. Heterosexual mounts.



b. Number of (a) that include thrusting.



c. Number of presents by females.

FIG. 5-39: Mating activity of males at Burman Bush.

Lower Troop that he failed to notice that Upper Troop had moved off. This was never seen to happen to anyone else and the distress it induced was reflected in GMR´s subsequent exhibition of typical lost responses such as frantic searching and the use of the "rrr" vocalization (this being normally only used by infants separated from their mothers). GMR was, in fact, later run over by a car and killed while crossing a road to rejoin Upper Troop, which was departing.

TY´s departure also showed signs of not having been due to coercion. He had moved into Upper Troop with TOG a year prior to TOG´s ascension to alpha-status, but while they had always been closely associated he left after TOG rose in dominance, even though he was not made the recipient of any increased aggression. TOG was, at the time, more concerned with suppressing TE who chose not to leave for another year despite such prompting.

7.Moving Behaviour.

Since the 4 troops live in close proximity it is understandable that inter-troop movement occurred rapidly. Males at Burman Bush do not enter a twilight zone where troop allegiance is ambiguous. Nevertheless lone males do occur where troop density is lower (see above) and, certainly, the male who moved into the university troop is unlikely to have travelled that distance in a single day. Even though actual transfer occurred suddenly the new males did travel at some distance from other members of the adopted troop for a few days. In the 3 instances where a pair of males transferred at the same time they initially stayed close and moved about the new territory together. It was noticed that once males had transferred they tended to participate strongly in aggressive encounters against their old troops. This `hyper-aggression´ decreased over time and stood out in strong contrast against the behaviour of male members of longer standing. Interestingly, TE continued to associate amicably with Upper Troop after he had eventually moved into Lower Troop. He would separate off and join them when the 2 troops were close, even initiating play with Upper Troop juveniles, something he was not seen to do in the new troop.

8.The Importance of Inter-Troop Contact.

As they shared a common boundary which ran along a favoured tourist feeding spot, Upper and Lower Troops interacted with each other far more than either did with Third Troop. Consequently, although the number of interactions was artificially high, and although close-range encounters were more common than in unprovisioned troops (Lucas, pers. comm.; pers. observ.), the situation still provided an excellent opportunity to observe the nature of such periods of contact. They were, in summary, mostly characterized by aggressive competition for food but both play and inter-troop sexual activity were seen. Such interaction could have served to introduce prospective migrants to other troops and perhaps have influenced the choice of direction.

9. The Stay in the New Troop.

i. The response of the new troop. Immigrants were the recipients of harassment from the established males: far more, in fact, than they had been seen to be receiving in the old troop. This harassment decreased over time, although new males who did not immediately effect a take-over remained wary and strove to stay clear of the dominant male. It may be that the initial intensity had been sufficient to establish dominance emphatically, thereby creating a climate in which the new males were sufficiently subdued to allow the established males to return to other activities. Not once, however, was a male chased out of a group because of the aggression directed at him.

Juveniles and females promoted the first non-aggressive contact with the immigrants through play and sexual activity respectively. The males responded readily to these advances and soon initiated interactions themselves. In a sense, the transfer often merely interrupted relationships that had begun prior to movement. This was, however, most probably due to the circumstances that exist at Burman Bush and has not been recorded at other study sites (Lucas, pers. comm.). It is important to note that even the most dominant female in Upper Troop was seen on several occasions to sexually present to new males within a week of their arrival.

ii. Duration of Sojourn. The length of stay was calculated by estimating the number of migrations per adult-male day (Dittus, 1975). With 18 migrations and 17,520 male days (12 males over 4

years), males may be assumed to move between troops approximately every 2.68 years (every 2.87yrs. for multiple-transfer adult males). The longest association actually recorded was 26 months (ongoing at the end of the study) and the shortest, 2 months. It must be emphasized that not a single adult male, of all those recorded in 1974, was with the same troop in 1978.
iii. Duration of Alpha-Male Status. Several of the migrants succeeded in becoming dominant in the new troop. 5, all mature, achieved this on arrival, and 2, 1 young and 1 mature, did so after waiting a year. All dominance changes were preceded and accompanied by heightened aggression between the reigning male and the pretender.

The actual duration of tenure could be measured in 3 cases and were 8 months, 24 months and 30 months. 2 males were known to have become dominant in at least 2 troops but there were no data pertaining to the other mature males. 5 of the 7 status changes occurred during the breeding season.

5.2.2 5.2.2. FEMALE MOVEMENT.

The only known migration of females occurred in 1974 when 3 adult females, their infants and 1 juvenile left Upper Troop to form Third Troop. They were accompanied by a male who had been low-ranking prior to his departure. Unfortunately this event occurred at a time when no regular observations were being made and no data are available on the dynamics of the event. Consequently it is not known whether the females followed the male or whether he, in fact, seized his opportunity and followed them.

Since the males are relatively uninfluential in the daily lives of females it seems plausible to suggest that the females who left were peripheral and did so in response to competition, engendered by a shortage of some resource, with more dominant females. A lack of food is one possibility; before the split the troop was as large as it would be in 1978 but the quantity and quality of tourist provisionization was poorer.

CHAPTER 6

DISCUSSION AND CONCLUSIONS

1. COMPARISON OF ETHOGRAMS.

Of the communicatory gestures and communicatory contexts seen at Amboseli, 88.8% and 85.2% respectively were recorded in Natal. The figures calculated for St. Kitts were 76% and 63.6% (see Table 5-2). This alignment of the Natal and Kenyan populations is not unexpected, given their common subspecific affiliation. What differences exist are minor and mostly concerned with the attribution of context, as well as some variation in the form of the RWB display. It is concluded that future work on the *C.a. pygerythrus* subspecies can validly utilize the information presented here and in Struhsaker (1967b).

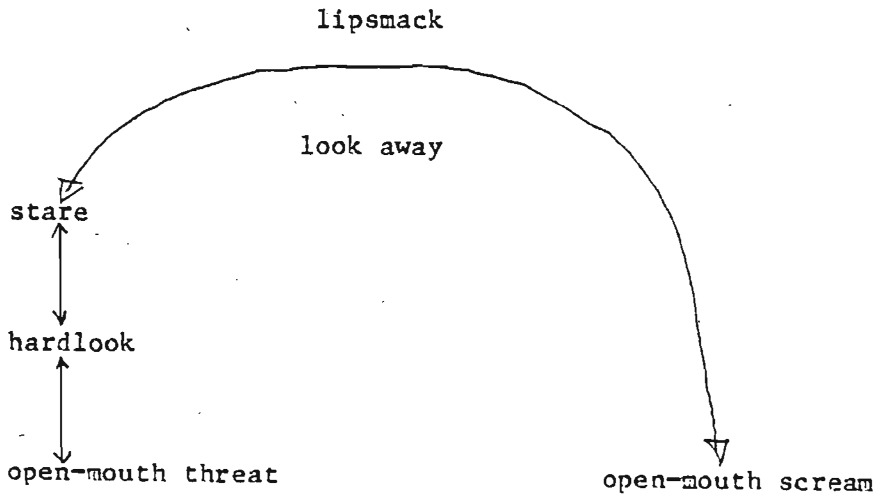
What these catalogues provide with respect to other subspecies is less concrete; the apparent discrepencies in the *C.a.sabeus* suspecies stem largely from patterns related to the RWB display complex. This absence has recently been confirmed in a field study of *sabeus* in Senegal (Harrison, pers. comm.), indicating that the loss is not associated with any dimunition of the gene pool on St. Kitts. The other differences stem from an assumed absence of certain contexts on St. Kitts, but this is hardly surprising, given the reported viewing conditions on the islands. Work, in this study, on the vervets at Stainbank revealed no new patterns, neither did it provide as comprehensive a list as that seen on habituated groups elsewhere in an equivalent time.

One residual difficulty with the comparison of existing ethograms has already been aired by Reynolds (1976). The argument is that the act of labelling does not in itself confer objectivity to categorization, and that comparisons of such categorizations do not, subsequently, have an adequate base. While Reynolds is correct about the underlying intuitiveness of the schema, which should make us hesitant about declaring populations to be different, it is also quite clear that access to descriptions made it possible to see that differently named behaviours were equivalent. That it was also possible for Reynolds to do this for rhesus suggests that the critique serves yet again simply as a caution against not describing patterns adequately. As examples, Struhsaker's "exposure of eyelids" (15) was seen in Natal but not listed separately of the facial expressions it accompanied, and my "broadside" is subsumed into his description of a headflag. One thing that Reynolds does not consider is that a worker may get a better perception of behaviours from reading different descriptions that differ slightly than he might from reading ones that are uniform. The differences in dissection are insightful in their own right.

2. FACIAL EXPRESSION AND HABITAT.

The expressions used by Natal vervets were also recorded by Struhsaker (1967b) and Rowell (1971), although the gradation of threat in this study, established on the basis of mouth position and movement, is finer. While there was some variability in the form of expressions they did appear to constitute MAPS (Barlow, 1977), clustering at fixed points along the continuum (Stringer, 1973).

The continuum of expressions seen in agonistic encounters is given below:



attack face (not assumed to be a visual signal).

When compared to Shirek-Ellefson's diagram (Ch.2) some differences are evident:

i. Lipsmack is not regarded as part of the continuum as it lacks physical similarity to the other signals, and is used primarily in close-range encounters where its function appears more placatory than directly submissive. However, it is included because of its functional association with the continuum and because it does occur at one end of a signal chain that ends in a open-mouth scream (see Table 5-10). It must be presumed that it bore the same relation to submissive expresssions in <u>M. fasiscularis</u>.

ii. There was no reason to exclude the open-mouth threat from the continuum; movement patterns associated with it were also seen with the hardlook as were the contexts in which it was given. It is possible that Shirek-Ellefson saw the open-mouth as a precursor of biting and therefore motivationally distinct. This was not so for vervets where the `attack face´ (ie a bite) had no expressive role extrinsic to its physical effect and was given deliberately, without a prior warning threat.

iii. The vervet repertoire is smaller than that of macaques. Moreover, the deficit is specifically due to a decrease in the range of fearful expressions.

Provided that there are advantages to maintaining it at all, the adaptation of the facial signalling system to `noisy´ habitats can take place in two ways.

Firstly, the head itself can be rendered more conspicuous so that it is easier to locate. An examination of forest species shows that this has happened independently in different phyla.

the vervet head, with its black face framed by a white headband and cheeektufts, is typical of the adaptations seen (Kingdon, 1980). It is repeated for the common langur (*P. entellus*), the liontailed macaque (*M. silenus*), *Co. guereza*, the forest baboons (*Mandrillus* spp.) and even the lar gibbon (*H. lar*). In addition to such framing, the faces of forest species are darker (compare the liontail macaque to the rhesus), so that unpigmented circumocular areas - revealed when signalling - stand out more distinctly, making head and gaze direction unambiguous.

Secondly, the clarity of the signal continuum itself can be improved by decreasing the number of signals that appear along it. Vervets are similar to other forest species (Bernstein, 1968; Poirier, 1970) in that their repertoire is smaller than those reported for baboons and macaques (Hall and DeVore, 1965; Hinde and Rowell, 1962; Bertrand, 1969).

Furthermore, with the exception of the talapoin (Wolfheim and Rowell, 1972), forest or arboreal monkey repertoires are reduced by the restriction of fearful expressions to a scream-grimace (Poirier, 1970; Struhsaker, 1967b; this study. Chalmers, 1968b, does not record any form of grimace for *Ce. albigena*). It can be hypothesized that submissive signals, essential if aggression is not to escalate, must be quickly and accurately conveyed to the aggressor. Slight changes in mouth position, common in macaques (Angst, 1974) and baboons (pers. observ.), are unlikely to be seen in less open habitats. By coupling the expression to a loud vocalization, the sender ensures that the message is attended to (Marler, 1965). The coupling of sound and vision will allow the message to be transmitted even if only the vocalization is received by the aggressor. Since the encounters are close-range the constraints imposed by time lag do not apply (Wickler, 1978). While this results in an increase in signal intensity, it is not known whether there is an accompanying increase in the intensity of the underlying motivation.

The corollary of any reduction in ambiguity, however, is that it is achieved at the loss of flexibility. It has not yet been shown how this is reflected in the quality of social relationships, but Chivers (1976) has suggested that the siamang, despite a small expressive repertoire and a black face that further diminishes the quality of signal transmission, is still capable of subtle and complex coordination and information transfer.

A major objection to be raised against such an environmental explanation is that effects due to taxonomic affiliation might be more important (Struhsaker, 1969, emphasizes the influence of phylogenetic factors on social organization). An alternative explanation for the vervet system would then be that it had evolved from pure forest stock with relatively simple social organizations. Colour would be present because of its prior importance for the locating of individuals in very dark habitat (Hailman, 1977) and for species identification (Kingdon, 1980). This view has obvious credence: patas monkeys, evolved from guenon stock (Kingdon, 1971; Napier and Napier, 1967), have moved into a terrestrial savannah niche while retaining a one-male social organization (Struhsaker, 1969; Wrangham, 1980), striking colour contrasts and a small repertoire of visual displays (Hall et al., 1965). At the same time *M. fasiscularis* is a small, arboreal macaque with a fully developed repertoire and a multimale social organization.

Since it is rare to find congenerics inhabiting grossly different habitats it is difficult to compare the repertoires of closely-related species occupying different habitat zones. The obvious comparison - between *Mandrillus* and *Papio* or *M. silenus* and other macaques - has yet to be done. While there appears to be no way, at present, of settling the issue of derivation, it remains clear that the vervet has an expressive repertoire adaptive to its environmental conditions.

3. INTERTROOP MOVEMENT.

At Burman Bush vervet inter-troop movement is a male phenomenon that is significantly correlated with sexual activity ($r=0.7756$; $p<0.01$). This has been seen in other species with discrete breeding seasons (Lindburg, 1969; Sugiyama, 1976; Drickamer, 1975). An assessment of the possible proximal and ultimate causes of migration is relevant to an understanding of these trends.

(1). The ultimate cause, or survival value, may be that: (a) Males are subjected to a test of fitness as extra-group animals may be forced into ecologically poorer zones (Sugiyama et al., 1965; Gartlan, 1974) or exposed to a greater risk of predation (Frame and Frame, 1976). The death of a procrastinating GMR under a car serves as an urban illustration of this. (b) A troop gains knowledge from an immigrant who may, for example, come from a troop eating a food not recognised as such by the new group. Cultural transmission has been shown to be important in the exploitation of introduced food sources (Kawai, 1965). (c) Migration improves the reproductive success of the participants and promotes exogamy. Constant migration and the rate at which it occurs offers males a means whereby their genes can be spread among different groups, thereby avoiding the deleterious effects of excessive endogamy (Itani, 1972). Table 6-1 shows, for different species, the duration of *adult* male attachment to one troop and compares this with the age at which females reach sexual maturity.

Species	Duration of male stay	Age of females	Source
C.aethiops	2.87	+2.5	This study
M.sinica	4.21	+4.5	Dittus, 1975, 1977
M.mulatta	~2.5	4.0	Meikle + Vessey, 1981
M.fuscata	+4.5	3.5	Sugiyama, 1976; Itani et al, 1963
P.senex	~3.0	3.5	Rudran, 1973
P.entellus	2.3	3.5	Hrdy, 1977
C.guereza	~4.0	4.0	Struhsaker + Leland, 1979; Oates, 1977

Table 6-1. A comparison of the mean duration of stay in one troop by adult males and the age at which females reach sexual maturity.

The important point about this data is that males are unlikely to be present after their female offspring have reached maturity, even though the mechanism of change may vary from the violence of the take-over of *Presbytis* groups to the peaceful departure of Japanese macaques (Rudran, 1973; Sugiyama, 1976).

That males rarely return to their natal groups, or groups where they have lived previously, further decreases the possibility of incest. Packer (1979a) feels that, because 27% of his baboons had remained in troops after their daughters there had matured, there is little evidence that repeated transfer is due to the promotion of exogamy. It isn't known how long they remained or how frequently they mated with their offspring. Until there is more evidence it is still possible that baboons do behave in accordance with the exogamy hypothesis. Of greater interest is the finding by Taub (1980) that male or female Barbary macaques (M. sylvanus) rarely leave the natal troop. This apparent exception to a general rule makes further investigation essential.

The evidence is limited for vervets, but dominant males are observed in most species to associate and mate with the high ranking females more than subordinate males are. We would then expect that the resultant offspring would stand, when resouce availability is such that prior access is advantageous, a proportionately better chance of survival. This has actually been demonstrated for vervets in a water-limited habitat (Wrangham, 1980a). In adddition the dominant male also has improved access to other females simply because the other males maintain their distance from him (see Bernstein, 1976). Consequently, it would pay a newly-arrived male to mate when and where he can, but to leave if he does not become sufficiently high-ranking within a certain period of time. Similarly, as seen by TE's lack of success, it is to the advantage of recently-defeated males to leave. The success of this strategy can be gauged by the fact that adult males, peripheral in one troop, became dominant in another, while 2 defeated males regained alpha status as a consequence of movement.

(2) The proposal of various possibilities regarding the survival value of migration allows the consideration of possible mechanisms whereby it may be effected.

(i) Could the mechanism stem directly from the ultimate cause? That is: (a) A male has some direct urge to test his fitness, with the inevitable possibility of failure. It is hard to see how this could evolve but easier to imagine the evolution of a female tendency to mate with new males, i.e. those that have survived a troop change. Females could, with some justification assume that such males have demonstrated their fitness. The model here is one of a male drawn to a new troop because the females there are more compliant than those in his old troop. Burman Bush females did mate readily with newcomers (Fig.5·39; see also Packer, 1979a). (b) A male may join a new troop out of curiosity , as part of broadening his experience and is accepted because his extra knowledge or novel behaviour is attractive. The first part of this seems plausible since vervet males do spend much time watching other troops before moving but there is no evidence of following or copying new males. (c) A male may be averse to mating with close relatives, or they may reject him, so that when their number increases he looks elsewhere for mates. Movements are correlated with sexual activity and subadult males appear to have little opportunity to mate (Fig. 5-39). Sade (1968) reports an inhibition of son-mother mating in rhesus. In vervets, the interest shown in other troops by even immature males was never matched by females and might well reflect a lack of interest in the natal troop that increases as individuals become better known. This seemingly casual attitude to troop allegiance is apparent in other species (Hausfater, 1975; Mohnot, 1978; Vessey, 1971) and such `boredom´ may explain why males in their prime, and capable enough of becoming dominant in other troops, should relinquish their status so regularly and without intense struggle. If a tendency to `boredom´ could be established as a valid component of the males´ psychological make-up it would be feasible to promote this as the mechanism underlying incest avoidance. The alternative view, that the process has no emotional substrate and the males depart as soon as the cost of migration is exceeded by the cost of decreased mating opportunities, does not account for all the variance. The fact that females must also `lose interest´ in males further implies that a psychological level of explanation is relevant.

(ii). Can aggression be regarded as the cause? It may be said that a male is chased out of a troop by defeat (if he had been the alpha-male), by new harassment or by a new response to it (if subadult). Rates of aggression and movement are strongly correlated ($r=0.72$; $p<0.01$) but there are factors that prevent a ready acceptance of this proposal. Firstly, adult females also receive severe wounds (Table 5-36) but are not prompted to leave.

Secondly, migrants receive most of their wounds soon after arriving in the new troop but stay on. Males that do not become dominant are liable to aggression each mating season and yet spend more than one season in the same troop. Thirdly, TY was seen to move after TE´s rise to alpha-status despite the fact that this change did not appear to drastically alter their relationship. Nevertheless he left suddenly and was soon involved in intertroop activities against his old troop.

These examples suggest that aggression is likely to hasten the departure of a male that is ready to leave but does not present the primary reason for doing so. This can be illustrated by the attitude of young males who are migrating from the natal troop. While they do receive the antagonistic attention of the alpha-male they manifest a prior and inordinate interest in other troops, with the reluctance to move that one would expect as a consequence of peer and familial ties not being evident. This conclusion, that aggression is a goad but not the main cause, is shared by Gartlan (1974) for Erythrocebus patas and Bouliere et al. (1970) for Cercopithecus campbelli and since these species, unlike vervets, live in uni-male troops, it implies that the underlying mechanism may have wider generality. However, since wounding was correlated with mating activity ($r=0.79$; $p=0.001$) we should, perhaps view both migration and the increase in aggression as consequences of breeding activity (Drickamer, 1975; Hall, 1966).

(iii). Is restricted access to females the cause? For various reasons a male might have only limited access to sexually receptive females and so move in the hope of improved opportunities. That breeding seasons are causally related to migration appears a reasonable supposition. It accounts for the seasonality of migration , the age and status of the migrants and the fact that they attempt strenuously to copulate with the females in the new troop despite opposition from the resident males. That the females are more sexually-amenable is shown by the comparison between the mating activity of new males and subadult and defeated males. It can be presumed that new males were in the position of the latter prior to moving. Movement for increased mating opportunity also helps explain why males, instead of leading permanently solitary lives after their departure, gravitate towards other troops. Naturally other factors may promote this, but in Japanese macaques at least, movement into a troop by generally solitary males takes place during the breeding season and signifies access to females as a motivation (Sugiyama, 1976). The same conclusions have been reached for other species by Lindburg (1969) and Harcourt et al. (1976).

(iv). Is restricted access to food a reason? This more ecologically oriented proposal requires that subordinate males, as opposed to other troop members, are being prevented from acquiring sufficient food. Dittus (1977) has demonstrated that behaviourally imposed feeding efficiencies do exist but that, in *M. sinica*, juvenile females fare worst in the efficiency rating but do not leave the troop. Moreover, the Burman Bush population is expanding at a rate (Table 4-2) comparible to those of other provisioned monkey troops whose males also migrate (Drickamer, 1974; Dittus, 1977). There is an abundance of tourist food and movement mostly occurs just after the rainy season when natural food is plentiful.

CONCLUSIONS.

The available evidence does point towards the evolution of migration as a mating strategy for vervet males which is prompted by a improved access to sexually-receptive females. This also results in the decreased likelihood of endogamy and may be facilitated by the psychological attributes affecting male attachment to a troop.

Females, on the other hand, were not seen to transfer to other groups and there are presumably strong advantages accruing to them from remaining within a community cemented by long-term bonds (Wrangham, 1981). They go to lengths to protect this integrity and their intertroop activity is directed against other females while other males are generally ignored. By encouraging strange males, either passively through not threatening them, or actively by soliciting, they can maintain group cohesion and still benefit from the influx of new genes.

4. SECONDARY SEXUAL CHARACTERS AND COEXISTENCE IN MALE VERVETS.

1. The Scrotum. The normal, abducted state of the scrotum allows identification of a particular class of animal - the adult male - and as such may allow appropriate relationships to be established. It is held that this is especially important in male-female relationships and that the emphasizing colouration has evolved for that reason. However, one consequence of any intersexual signal is that it must also enable competitors to recognise and react to one another. Since males are the competitors in vervet society, the scrotum serves as a signifier to both sexes. The importance of this for males may be best indicated by consideration of the fact that testis adduction is a concomitant of scrotal retraction.

The ability of male cercopithecoidea to adduct their testes into the inguinal canal has been documented previously (Hill, 1966) and its occurrence in tree shrews *Tupaia glis* (Kawamichi and Kawamichi, 1979) points to its being a long-established primate trait.

While the muscular ability that allows the scrotal surface to be adjusted is usually seen as an aid to thermoregulation (Waites, 1970) data given in this thesis and elsewhere suggest that scrotal retraction is also a concomitant of `emotional´ states (Hill, 1966) such as fear (see Wickler, 1967).

Any animal wishing to optimize the spread of his genes depends on the correct functioning of his reproductive system and it is held that the evolution of the scrotal state in mammals is one response to this need (Cowles, 1958; Bedford, 1978). Nevertheless, while the location of the testes outside the abdomen may have conferred important advantages , it has also greatly increased their vulnerability to damage, either through dangers inherent in the environment or through intraspecific aggression. Given the risk, either the benefits of this testis position significantly outweigh the attendant problems, or the scrotal mammals have evolved means whereby the exernal genitalia can be protected. The data presented in this thesis provide support for the latter in vervets. While a male was once seen to to retract his scrotum rapidly when coming to sit on a cold substrate, there is little evidence that these powerful muscular contractions exist primarily to assist thermoregulation; this being more efficiently achieved through fine adjustments of the scrotal surface. Adductions should therefore be seen rather as a specific response to incidents, both social and non-social, construed by the performer to be dangerous.

Male vervets in this study obviously saw danger as a consequence of the social rather than the physical environment (Table 5-6). That their perception had credence is indicated by the distribution of the wounds that they received (Table 5-12). However, when compared to the distribution of female wounds (Figure 6-1) it is clear that there is no difference (Kolmogorov-Smirnov Two-Sample Test; $p>0.1$). What this signifies is that the distribution is probably due to the nature of the habitat and does not reflect a specific strategy of male attackers. Environmental 'noise' has devalued submissive posturing (vervets do not make use of social presents as savannah baboons do - this study; Wickler, 1967): it is wiser to move off from trouble rather than give a gesture that may not be seen. However, moving off exposes the hindquarters to the attacker. That no damaged scrota were seen must therefore be due both to the efficacy of testis-adduction as a protective measure and to the 'down-and-out' tail carriage characteristic of subordinate males.

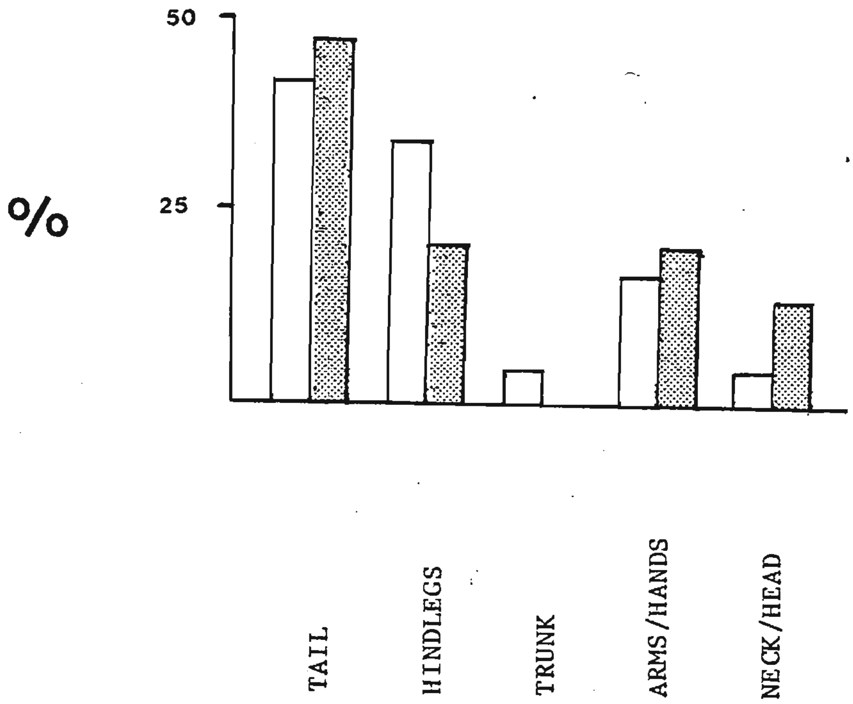


Figure 6-1: The distribution of male wounds (N=24) and female wounds (shaded bars; N=15), expressed as percentages.

An intriguing speculation arising from this concerns the possible effect of increased temperature on the sperm production and storage capability of the testis, which is finely heat-sensitive (VanDemark and Free, 1970). Although data exist that would question any effect to the slight elevations of temperature that must accompany adduction in the vervet (R. Short, pers. comm.), the behavioural regulation of testicular temperature in relation to status has never been investigated. The current sociobiological concern with paternity and its `guesstimation' (May and Robertson, 1980) increases the importance of such an investigation, especially in species like the vervet where consort relationships are not formed. It may be that an alpha male gains advantage beyond that which could be estimated from the frequency or timing of his copulations with oestrus females, through his ability to lower the sperm count of other males. Temperature may not be sufficient to do this, but the effect of agonism and harassment by dominant animals also has the effect of lowering the circulating levels of plasma testosterone and producing endocrine profiles characteristic of animals under stress (Keverne, 1980). This results in lower fecundity (Keverne, 1980) as well as in aggressivity (see Rose et al., 1971).

Given that other males must be tolerated, it is clear, in theory at least, that an alpha male has at his disposal a strategy whereby he can reduce the degree of competition. By harassing new arrivals he may well actively create males that suit him. This may therefore be the price subordinates must pay in order to stay in the troop and, if so, will explain why they actively display submission with homage, which can do little to reduce stress. This further suggests that removal of the signifier (the blue colour) has as its message "I am frightened of you" and as its meaning (what the message signifies for the recipient - Smith, 1977) "That male is currently undergoing stress". The signal value of retraction therefore lies in its ability to indicate to the alpha male that the relational 'rules' are being adhered to. Homage is the way in which subordinates can emphasize this.

.2. <u>The Penis</u>. The penis is normally not visible and its extension correlates with either the giving of aggression to males or sighting of and interaction with extra-group males. Associated with its extension are some stylized motor patterns (RWB display, broadside, tree display and the 4-leg up/splayleg complex) that have been demonstrated to display the penis to the recipient in the most efficient manner. Most of these are directed to males but, as an aftermath, the tree dislay often results in females chasing males who retain their extensions (Fig. 5-27).

In being directly correlated with the giving of aggression extensions signify the likelihood that interactions will take particular, agonistic courses. This is especially true of those extensions adopted in the absence of direct interactions. Recipients of these signals may therefore predict the consequences of immediate interaction. The possibility of bluff on the part of the sender, with respect to his ability to escalate interactions, is small, given the wounding that subordinate animals were seen to receive. The system must therefore function, from the point of view of the signaller, to regulate the behaviour of animals whose presence in the troop is either in his interests or beyond his control.

3. The genital signalling system. While scrotal and penile signals subserve opposite goals, they have depended on a common system - external genitalia - for their evolution and must consequently also be considered as components of a common system.

In evolving, both have relied on preadaptations; the process of testis adduction and the linkage of penile extensions to sex (with testosterone underlying both sexual and aggressive processes). The coevolution of colours to emphasize the signals is a necessity demanded by the habitat (with independent development of the same colouration by Mandrillus) and constrained by the limitations of mammalian physiology.

Within these constraints, the guenons appear to have developed colouration that best counteracts the effects of the habitat. Once the eye is light adapted, colour perception is possible as long as the light stays above a certain threshold (Hailman, 1977). With green being a colour to avoid in a forested habitat either blue or red becomes the best choice. The vascularization of the penis will have provided the base colour (seen in baboons and chimpanzees where the genitalia are otherwise undifferentiated). Red also has the property, at least for human trichromats, of appearing especially salient. That is, humans `confuse´ redness with brightness (P. Silver, pers. comm.). Once red is chosen the prediction is that scrotal colour would be highly contrasted. Green is the subjective opposite of red and within the nervous system the most common class of colour coding cells are tuned oppositely to red and green (DeValois and DeValois, 1975; Mollon, 1982). Given that green is a strong environmental feature, blue becomes the best alternative as it also excites the red/green opponent cells. Observation during this study confirmed Jouventin´s finding (1975) that the genitals were highly visible under poor light conditions.

This trend towards optimal colouration answers, in part, Darwin´s (1876; p 18) assertion that "no case interested and perplexed me so much as the brightly-coloured hinder ends and adjoining parts of certain monkeys". He proposed that such colouration was an example of sexual selection, serving to attract females during courtship. From this discussion it seems better to regard the colour as serving to enhance signals that were already present and which still occur in species that do not have chromatically differentiated genitalia (eg rhesus macaque; _Ce. galeritus_). Nevertheless, it is sexual selection that will have favoured the acquisition of the signalling system itself. However, it is important to note that the pressure arises out of both intra- and intersexual factors. The data show that neither the scrotum or the penis are presented in any way that would suggest that they function to facilitate mating in the short term, but serve instead to identify a class of animal to which other animals, of both sexes, will respond appropriately.

This leads onto Wickler's hypothesis (1967 - and endorsed by Clutton-Brock and Harvey, 1976) that the signals mimic female colouration so as to instill in recipients emotions antithetic to aggression. The data do not uphold this view (see also Crook, 1972) and indicate that continued observation is important in the development of theory. In retrospect his theory, derived from work on mimicry in cichlids, has proved to be reductionistic. Instead, the alternative, that of explaining female colour in terms of the male system, proves more fruitful. Stuhsaker and Leland (1979) have pointed out that sexual swellings are largely a characteristic of multimale species and cite as examples the presence or absence of swellings in colobines. The same is true of the guenons although instead of swellings, the vervet female has mimicked the colouration of males, capitalizing on the probability that adult males are especially sensitive to it. What advantages accrue to females with genital emphasizers is not yet known. The prediction here is that female genital colour in vervets will serve the same function as sexual swelling in other species, although their evolutionary routes have been different.

Lastly, it is important to emphasize that the colouration and the signals with which they were associated did not function in the classical way described for `releasers', where presentation of the stimulus produces a fixed and circumscribed response. This may well be true in the ancestral one-male species where the resident male could have used the appearance of scrotal colour to expel adolescent males from the group or could have responded aggressively to the appearance of any strange conspecific bearing it. Data on extant unimale species that do <u>not</u> form all-male aggregations would be valuable in this regard. In vervets, however, such a limited response, given the presumed advantage of surplus males, could not persist. What has happened seems to be that the fixed response has been toned down so that males now only have an inordinate interest in the colouration (see the interest of juvenile males in the genitalia - Table 5-23) which can be exploited by others. It is likely that the deliberate displays of the penis, for example, function to `teach´ the recipient the meaning of the signal, thereby incorporating contextual information to such a degree that a simple system is transformed to allow complex interpretation. Gartlan (1975) argues that the presence of genital colouration and the interest shown in it by males serve to mediate the formation of all-male groups. I believe instead, that, in line with the data presented here, the use of the system approximates that of the vervets with the important difference that, in the presence of females, males are intolerant of one another. Signalling at a distance must then carry the message that approach will definitely be followed by attack. The conclusion that learning is central to the utilization of the signal has not been drawn before and should be investigated in other multimale species such as the mandrill.

4. <u>Yawns</u>. The data indicate that the yawns given by vervet

males do satisfy Altmann's (1967) criteria for tension yawns. They are given in social circumstances, largely by adult males whose canine teeth are thereby exposed. Moreover they are largely given in response to the behaviour of other males and can therefore be regarded as having been acted on by the forces of intrasexual selection. However it must be concluded with Hadidian (1980) that the meaning of the signals remains unclear. Vervets did not deliver yawns in the way that Packer's baboons did. Nor could the display serve to indicate superior status (Gautier and Gautier, 1977) or function as a threat (Hall and DeVore, 1965; Chalmers, 1968b). It was a frequent response given to events that were often clearly tension-inducing. Recipients could then clearly attribute an emotional condition to the yawner, provided that the context was known, but would not easily predict his subsequent behaviour (Table 5-32). Two speculations are possible: that it 'dampens' any aggressive behaviour in the recipient or that it actually serves to inhibit sudden movement in the yawner himself, thereby calming him. There is no evidence for these and it would have to be sought through physiological measurement of arousal. The final possibility is that yawns are not used in a direct communicatory sense at all and that males yawn frequently simply because they are placed in tense situations much more often than other age-sex categories are. There is some substance to this given the amount of agonism between males and the effect that even the presence of other males has on behaviour. The canines, while not necessarily required primarily for communication, are still very useful as weapons (Saayman, 1971; personal observation) and may have developed for this reason alone.

5. Characteristics of multimale systems. As is to be expected, given the relative paucity of data, the first analysis of the structure of primate societies (Crook and Gartlan, 1966) appear to have been oversimplistic (Eisenberg et al., 1972; Clutton-Brock, 1974). One way in which this was so concerned the classification of systems on the basis of male membership. 'Unimale' species, rather than constituting a single grade, were shown to be structurally distinct from one another (see Kummer, 1968; Hall, 1965; Dunbar and Dunbar, 1975). While this is accepted now, the same conclusions for multimale systems is less overtly acknowledged.

The first step to a refinement of classification was taken by Eisenberg et al (1972) who introduced an intemediary category. This "age-graded" configuration has been been shown (Chapter 4) not to apply to vervets, for whom it was posited. Neither does it hold for M. talapoin (Rowell, 1973; Rowell and Dixson, 1975), P. entellus (Hrdy, 1977) or E. patas (Gartlan, 1975).

Examination of multimale systems (in female-bonded societies) reveals that males can associate in a number of ways:

i. Loose extra-group aggregations seen in terrestrial and semi-arboreal species and presumed to arise out of predation pressure acting on individuals excluded from one-male groups (patas and langurs). Dominance shifts are achieved by take-over of a group of females and the subsequent breakdown of the weak cohesion of the male aggregation (see Gartlan, 1975). Infanticide is a characteristic of such take-overs.

ii. All-male subgroups permanently associated with females, but generally separate until the breeding season when agonism among males increases and subgroup stability breaks down (talapoin).
iii. "True" multimale systems characterized by complex, reciprocal interactions between males (see Packer, 1977), and where status is stable only in the short-term (baboons and macaques). Infants are neither killed nor ignored but are used to mediate relationships among males.

6. Evolution of the vervet system. Data presented in this thesis and elsewhere (Cheney, 1981) indicate that male vervets do not undergo a non-group phase during the process of transfer, unless the groups are inordinately spaced-out, when lone animals are sometimes seen.

Observation of male vervets within heterosexual troops reveals that they do not interact in the way that males from true multimale species do (reciprocal altruism, exploitation of infants). Interactions are most frequently agonistic. Furthermore, strong evidence from this study, McGuire (1974) and Gartlan (1968) suggests that one male is particularly prominent in vigilance, intergroup activity and in the reception of submissive gestures. The hypothesis put forward here is that, while the coexistence of males in breeding groups is not predictable on phylogenetic grounds (Struhsaker, 1969), the way in which it has been achieved is. One-male harems where take-over is violent are the norm for guenons and their allies (Struhsaker, 1977; Bourliere et al.; 1970; Gartlan, 1975), with extra-group males either moving about singly or, as is the case with patas, in loose aggregations. These aggregations, in being a response to greater predation, are likely to have been a factor in vervet evolution. What appears to have happened, then, is that the extra-group component of males has become contiguous to the one-male group, leaving the dominant male behaving in much the same way that his patas or C. mitis counterparts do. What has been produced is a multimale configuration that is not simply age-graded but structurally less complex than true multimale social systems.

6.1. Precipitating factors. For any particular male, total access to sexually-mature females provides him with the best means of increasing his genetic contribution to the population, relative to his competitors. For this reason, males would, in an evolutionary sense, need good reasons for even risking loss of paternity.

It has been traditionally assumed that predation pressure has been responsible for multimale groupings in primates (Kummer, 1971; Crook, 1972) with the presence of competitors being traded off against increased survival of offspring due to increased vigilance and/or defence against predators. While there is some evidence to support this, it still remains to be demonstrated more precisely (Deag, 1977). However, if a harem male is capable of intense vigilance (see Hall, 1965) it remains difficult to understand why he tolerates other males, especially if these do not assist in defense (seen in the response of males to the trapping of infant vervets where only the alpha male ever attacked us).

It is also not easy to predict why females should tolerate surplus males. Wrangham (1980) lists vervets as the one exception to the rule that territorial species have only one male associated with each group of related females.

The only animals for whom inclusion makes eminent sense are the surplus males themselves. Outside of the group they are subject to higher predation, poorer nutrition and no mating opportunities (Frame and Frame, 1976; Gartlan, 1975). They stand to gain on several fronts if the resident male exhibits an increased tolerance of their presence.

6.2. Consequences. While there may be some doubt as to the reasons for the vervet multimale system, the consequences of this are clearer. As suggested by Wrangham (1980), if surplus males are inevitable it may well pay females to mate with all of them, thereby reducing certainty of paternity and, with it, the likelihood of infanticide. The development of female genital colouration becomes a response to this need in that it serves to attract males. Data was also presented confirming that females did present to more than just the alpha male.

From this, and the fact that male migration is related to mating opportunities, it is evident that the resident dominant male experiences a constant influx of competitors whose presence he cannot ultimately prevent. Work on other species (Hausfater, 1975; Packer, 1979a,) leads to the suggestion that he may nevertheless develop strategies that both limit the extent of the competition and exploit whatever benefits the presence of other males brings.

Subordinate males, at the same time, may be expected to develop and utilize skills that prevent them from being expelled.

It has been the contention of this discussion that the development and enhancement of secondary sexual structures, by being correlated with particular activities, mediate such strategies. As far as males are concerned, these are:

i. Strategies of the dominant male. The display of genitals to extra-group males may well influence their choice of troop (the chasing of males has been shown to have this effect in baboons - Packer, 1979a). If they still arrive and cannot be made to leave by the application of force, then the male may act so as to limit their success.

ii. Strategies of subordinate males. Subordinate males benefit by inclusion for more than one reason and should be expected to resist attempts to remove them. Displaying submission is one way in which this can be achieved.

Further research should investigate more comprehensively the relationship between males by means of a more detailed and quantitative sociological analysis which takes seasonal changes into account. At the same the differential strategies of vigilance should be assessed. Are males more vigilant than other vervets? Are subordinate animals more vigilant than alpha males?

Answers to these questions, coupled with a better understanding of predation pressures, will indicate more clearly factors favouring the inclusion of surplus males. Other areas that should be thoroughly explored are the vervet mating system where good quantitative data are needed and the foraging strategies and dietary requirements of males and females. The data thus collected will be central to an understanding of the degree of competition and cooperation shaping vervet society.

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