OBSERVATIONS ON THE BEHAVIOUR OF VERVET MONKEYS *CERCOPITHECUS AETHIOPS*

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THE SCOPE AND OBJECT OF THE INVESTIGATIONS

The observations described in this paper were made on a captive troop of vervet monkeys, the study being part of a wider one aimed at providing a direct comparison, in ethological and ecological terms, between the two species of *Cercopithecus* monkey found in southern Africa. The species involved are the vervet *C. aethiops* and the samango or blue monkey *C. mitis*. The first part of the project is concerned with studies on captive troops of both species; the second, with field investigations, particularly in those areas where the two species are found together.

These monkey studies form one branch of the writer's research on past African environments, with a view to providing new data on palaeo-ecological and climatic changes in southern Africa; the other branch, dealing with palaeontological and geological evidence, is being run concurrently and is supported by the Wenner-Gren Foundation for Anthropological Research in New York.

Of the numerous species of *Cercopithecus* monkeys found throughout Africa, only two, *aethiops* and *mitis*, show any marked tendency to an adaptive shift from forest to woodland and savannah. Of them, *aethiops* has a far greater tolerance to environmental differences than has *mitis* and, in Central Africa is found throughout, from high-rainfall forest to semi-arid woodland, with particular preference for riverine vegetation. It is the most terrestrial species of the genus, occupying an intermediate position between the other representatives and the patas monkey *Erythrocebus*, from further north in Africa. By contrast, *C. mitis* is less terrestrial and more closely restricted to evergreen forest, although in parts of Nyasaland it occurs in dense Brachystegia woodland. Apart from *aethiops* it is the only *Cercopithecus* monkey with an extended southerly distribution, being found in isolated patches of evergreen forest right down the eastern side of the continent to the Drakensberg in the Cape Province. Such patches of forest are often well separated by wide areas of country into which *mitis* fails to spread at the present time, though these are usually occupied by *aethiops*. Separation has obviously been in effect for some time, as subspecific differences are usually apparent between populations in different segments of the discontinuous range. At the same time it is difficult to escape the conclusion that, at some time, the populations were continuous between the various segments. As Tappen (1960) has stated: "The frequently discontinuous distribution of monkey species in Africa indicates that they spread continuously to the maximum limits of their present ranges when ecological conditions were favourable, and subsequently became extinct in the territories unoccupied, as climate changed".

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If it were possible to define, in precise terms, the ecological requirements of *mitis*, it would be equally feasible to reconstruct the conditions which must have prevailed, when the southern range of the species was a continuous one. It is hoped that field studies on *mitis* will provide the information required for such a reconstruction.

Preliminary investigation suggests that ecological requirement may not be the only factor limiting *mitis* to patches of evergreen forest; it is possible that if *aethiops* bands were not so ubiquitous in the adjoining countryside, a gradual spread of *mitis* would occur, particularly along strips of riverine forest. But it is precisely in these strips of river-fringing vegetation that *aethiops* is so well established, and it is here that the spread of *mitis* is inhibited, not by unfavourable habitat, but by an inability to compete with the vervet troops. Field work in areas where both species occur together will elucidate the nature of the contact between the two species, and under captive conditions, controlled experiment is planned where equivalent troops of the two species will compete for the same food supply. It is not impossible that a restricted distribution of *mitis* might be maintained by a dominant-subordinate relationship between troops of the two species. Such a relationship would not be as effective within evergreen forest itself, as *mitis* could feed in the canopy, while *aethiops* fed closer to the ground.

Any shift in primate adaptation, from forest to savannah is of particular interest for the light it might throw on the Pliocene proto-human situation. It could be argued that if early human ancestors had lacked the ability to leave the forested areas in favour of life in the open savannah, they would not have developed characteristic carnivorous tendencies. Without such tendencies, the incentive to tool-making might well have been lacking.

COMPOSITION AND ORIGIN OF THE CAPTIVE GROUP

In building up the captive troop of vervet monkeys, an attempt was made to select individuals of different ages and sexes in such a way that the final group would be similar to a small natural one. Free-ranging troops usually include some old adult individuals of both sexes and, to begin with, several attempts were made to incorporate fully adult and aged monkeys in the captive group; all such attemps proved unsuccessful and resulted in such severe and continuous fighting as to obscure other behaviour, old individuals of both sexes indulging in these conflicts. It was finally accepted that the only way to produce a stable and integrated artificial troop was to start with only one adult male (in this case, Robert), and one adult female (Belinda) who appeared compatible, and to add to these a group of juveniles and infants of both sexes. This meant that several years would elapse before the age-structure of the group could be said to be normal, but at least the final group would be integrated and of very considerable value from the point of view of ethological study. More than two years have passed since the original troop was assembled and, although conflict between individuals is common, it is not in excess of the amount normally seen in a free-ranging troop. It is unusual for serious physical injury to be inflicted on any members of the troop as it exists at the moment, although attempted introduction of other adults to the troop can result in fatal conflict (see below).

Basic information about the monkeys composing the group is listed in Table 1.

TABLE I:

Name of Monkey	Sex	Position in Social Order	Date of Birth	Origin
Belinda	♀	2	8 November 1958	Umtali, S. Rhodesia
Robert	♂	6	Late, 1958	Zambesi Valley, S. Rhodesia
Johnny	♀	4	Late, 1959	Salisbury area, S. Rhodesia
Capunk	♂	1	December 1960	Lusaka, Zambia
Chi-Chi	♀	3	December 1960	Sinoia, S. Rhodesia
Herbert	♀	5	Late, 1960	South-east Lowveld, S. Rhodesia
Matthew	♂	Unplaced	December 1961	Hartley, S. Rhodesia
Theodora	♀	Unplaced	November 1962	Umvuma, S. Rhodesia

Initially, two other juvenile females formed part of the group; these were subsequently released so that males and females would be more even in number. Earlier this year, an attempt was made to introduce another fully adult male, the intention being to establish what position it would occupy in the dominance order. As will be described shortly, the attempt was not successful and the monkey died of the injuries that it received. In fact, once the group had been established, the only monkeys that could be added to it were infants and young juveniles.

All the individuals forming the group had been born wild and reared in human company from a very young age; the infants were obtained when their mothers were shot on farms and the infants clinging to them were rescued by the hunters.

ORGANISATION OF THE TROOP

(a) *Establishment of the dominance order*

The day-to-day pattern of life of any individual monkey in the troop is determined by its position in the social order and by the temperament of any monkeys to which it is subordinate. A casual observer of the captive troop, or of a free-ranging one, might conclude that aggression between individuals is random and unpredictable; this is in fact far from the case and, as soon as the observer is sufficiently familiar with the individual monkeys to be able to recognise them, the existing order of social dominance will immediately become apparent to him. Such an order is admittedly more difficult to evaluate in the *Cercopithecus* monkeys than it is in baboons, as has been pointed out by Haddow (1952). Sexual behaviour and gestures of submission, such as presenting, so often seen in wild and captive baboons, are almost entirely absent among vervets, a fact which has led Haddow to suggest that, in the genus *Cercopithecus* generally, the sexes could probably be regarded as equivalent. Dominance is usually only apparent when vervets are competing for food or for the possession of some desirable object, such as the care of an infant, in the case of females. It is fairly clear that a dominant-sub-

ordinate relationship is not as rigid and unequivocal as it is with baboons; this perhaps accounts for the well-known fact that captive vervets are more treacherous towards their keepers than are captive baboons.

A simple method of estimating comparative status of two monkeys in the troop is to offer the two of them a single piece of desirable food; if the dominant-subordinate relationship is clear-cut, the dominant individual will forthwith take the food, while the other monkey assumes an indifferent attitude, giving the impression that it has not even noticed that food is being offered; if, on the other hand, the relationship is in doubt, competition will result usually terminating in an open fight. Mutual fighting is nevertheless uncommon and the accepted relationship is quickly established; this does not mean that a subordinate will never attempt to snatch food from a superior—this often happens and results in pursuit and biting by the superior, with no attempt at retaliation by the subordinate monkey. Instead of retaliating, the bitten monkey immediately seeks out his own subordinate so that the aggression passes in steps right down the social scale until the lowest individual is reached. This unfortunate individual has no one to whom he may refer the aggression that has been passed down to him and will usually try to attack any strange observer outside the cage, or the inmate of the adjoining cage. For some time, the adjoining cage contained a white stork, unable to fly after injury. This unhappy bird had to bear the brunt of all aggression originating at any level of the social hierarchy in the next-door monkey troop.

The existing order of dominance is tabulated in Table I. It will be noticed that the two youngest individuals are unplaced; this is because they are young enough to be protected by the immunity which all infants in a vervet troop enjoy. Up to age of about 18 months, a young monkey can, with impunity, take food from the hand or mouth of any older individual; should this individual object and threaten the infant, an immediate attack is likely from other members of the troop. The distress squeal of the infant elicits an impulsive response from nearby females in the troop (see below).

Two other significant points are apparent in the dominance order now existing: status is not determined by age, nor is it by sex. The most dominant monkey, Capunk, is a male considerably younger than the least dominant animal, Robert, the oldest male. In fact, Robert is currently dominated by all the females in the troop.

It is abundantly clear that initial establishment of dominance of one monkey over another is not a matter of physical strength nor of size, but rather by a recognition of specific attributes. This has likewise been found in Rhesus monkeys by Bernstein and Mason (1963). Among vervets the most important attributes are most probably confidence and imperturbability; these characteristics make possible the steady, level gaze of a dominant primate, a point which has been remarked upon by Andrew (1963). This steadiness of gaze is a well-marked characteristic of the most dominant monkeys in the troop, but is notably lacking in those individuals near the bottom of the social order. Herbert and Robert, the two lowest monkeys, make a habit of constantly looking over their shoulders to see from which quarter the inevitable aggression will come.

Adult male vervets are characterised by the almost luminous blueness of their scrotal sacs; this colour has clear social significance and could probably be described as a status

symbol; the intensity of the blueness is certainly variable and may well be related to the general state of well-being of the animal and its level of dominance. It has been stated that an attempt was made to integrate a fully adult male into the existing troop; this was done gradually and the new male occupied the adjoining cage, in full and constant view of the troop for three weeks before it was released into it. On coming into contact with the new individual, the first reaction of the other male members of the troop was to examine the blue scrotum with the greatest diligence. Eventually, this prolonged scrutiny annoyed the new monkey who became aggressive. Had he been allowed to fight one member of the troop at a time, he would probably soon have achieved a high-ranking position, as he showed clear attributes of a dominant individual. This never occurred however, and the first signs of aggression precipitated a full-scale attack by the whole troop. Within a few days he was completely demoralised and shortly after removal from the cage, died of the injuries he had received. It was particularly noticeable that when this monkey was first placed with the troop, its scrotum was the most brilliant blue colour. As the animal lost confidence as a result of repeated attacks by the troop, the colour faded away to a pale powder-blue hue.

The fact that size alone is not a significant factor in dominance was well demonstrated when a juvenile baboon shared the quarters occupied by the troop. Although the baboon weighed a good deal more than the largest vervet, it was constantly dominated by every member of the troop, all of which took advantage of the baboon's complete lack of confidence.

(b) *Maintenance of the Dominance Order*

The order of authority within the troop is maintained by threat and aggression; as already stated, fighting within the framework of an accepted order is one-sided and non-retaliatory, with a subordinate monkey being threatened or bitten, then redirecting his own anger to the next member down the scale. Looking at the troop as a whole, the pattern of aggression led one to believe that there was much more pettiness and trivial fighting lower down the social scale than there was near the top. In order to test this, every instance of agonistic behaviour witnessed in the troop has been recorded and plotted according to aggressor and victim. Three intensities of aggression are recognised:

Stage 1: Threat involving grimace and chatter only.

Stage 2: Grimage and chatter followed by pursuit without physical contact.

Stage 3: Pursuit with biting.

More results are needed before complete statistical analysis is possible, but all preliminary results indicate that the dominant monkeys are probably as aggressive as those of low status, but that the individuals high in the social scale can retain their positions of authority with Stage 1 aggression only, while low-ranking monkeys have to resort to full physical conflict. This implies that the dominance of high-ranking monkeys is accepted with less persuasion than that of low-ranking ones.

In the course of status fights, subordinate monkeys are most often bitten on their tails, as they crouch down in a submissive attitude after being cornered. Where more than one monkey is involved in an attack, biting occurs all over the body. A useful character for the

recognition of a low-ranking monkey in a wild *aethiops* troop is the presence of fresh scars near the base of the tail.

(c) *Changes in the Dominance Order*

Once established, the dominance order in the captive troop has proved remarkably stable; two clear-cut changes in position have occurred but only in response to unusual circumstances, as will now be described. The first came about in the following way: two monkeys were removed from the troop for three days so that they could be displayed on a local agricultural show. The two monkeys were Capunk, No. 1 in the social order, and Johnny, who at that time was involved in an active dispute with another monkey for a position third from the bottom. (This other monkey, Jenny, is no longer with the troop, having been removed to equalise the sexes.) Upon coming back from the show, and being reintroduced to the troop, Capunk immediately reassumed his role of No. 1 monkey, unchanged and unquestioned. Johnny, however, could no longer compete with Jenny and, within a day, a typical dominant-subordinate relationship had been set up, with Johnny in the inferior position. Clearly, the three-day period in which Jenny's position was unquestioned gave her additional confidence with which Johnny could not compete.

The second instance of status-change involved Robert, the largest and oldest male in the troop who at that time, early this year, was third in position, subordinate only to Belinda (second) and Capunk (first). For the first time, Belinda became highly attractive to Robert from the sexual point of view, and he would follow her about incessantly, trying to smell and handle her genital area. For some time this was tolerated, but gradually Belinda's patience became exhausted and she would turn on Robert, biting him savagely. Whenever this occurred, the other members of the troop came to Belinda's assistance and Robert would be bitten from all quarters. In spite of this his irresistible attraction for Belinda continued, even though the fierce attacks which it precipitated caused him to lose all confidence and reduced him to a demoralised condition. After a week he had lost all social status and did not retaliate when attacked singly by any of the lowest-ranking monkeys. Robert's attraction towards Belinda has now waned, but his position remains the same and he does not dare to approach the feeding table until the hunger of all members of the troop has been satisfied. He also has to bear the brunt of all aggression originating at any level in the social scale and referred down to him.

It is possible to imagine what the circumstances might be for the loss of social status of a monkey in a wild troop. Any debilitating illness could well have this effect; likewise, any temporary absence from the troop would provide an opportunity for another monkey to take over a position. Some positions are clearly maintained on a tenuous footing, while others, like that of Capunk, are probably well-nigh unshakable.

FACTORS IN GROUP COHESION

(a) *Grooming and its Relation to Social Order*

With regard to baboons it has been established (Bolwig 1959 and Hall 1962) that grooming

is an occupation practised particularly by females; Hall has also pointed out that it is not only the incidence of grooming that is important, but also the thoroughness with which it is performed. Observations on the captive vervet troop have shown that grooming is practised far more often by females than by males; in fact the male Robert has never yet been recorded to groom at all. The other two males have been seen to groom very occasionally, but as in Hall's observations, with much less thoroughness than in the case of females.

Grooming is most often seen in the mid-morning, when the first feeding session is over and the satisfied monkeys are resting in the sun. If a monkey wishes to be groomed, it normally lies down passively in front of a prospective groomer; frequently, however, a female will start grooming another monkey while it is still feeding, or engaged in some other activity.

All evidence so far obtained suggests that, in the captive troop, grooming is random and quite independent of position in the social order. Thus, a low-ranking monkey can with impunity lie down in front of a strongly dominant one with good prospects of being groomed. Over a period of three months, all instances of grooming seen in the troop have been recorded; results are tabulated below and plotted in Figure 1. It will be seen how much more frequently females indulge in grooming than males and the frequency with which dominant and subordinate partners are groomed will also become apparent.

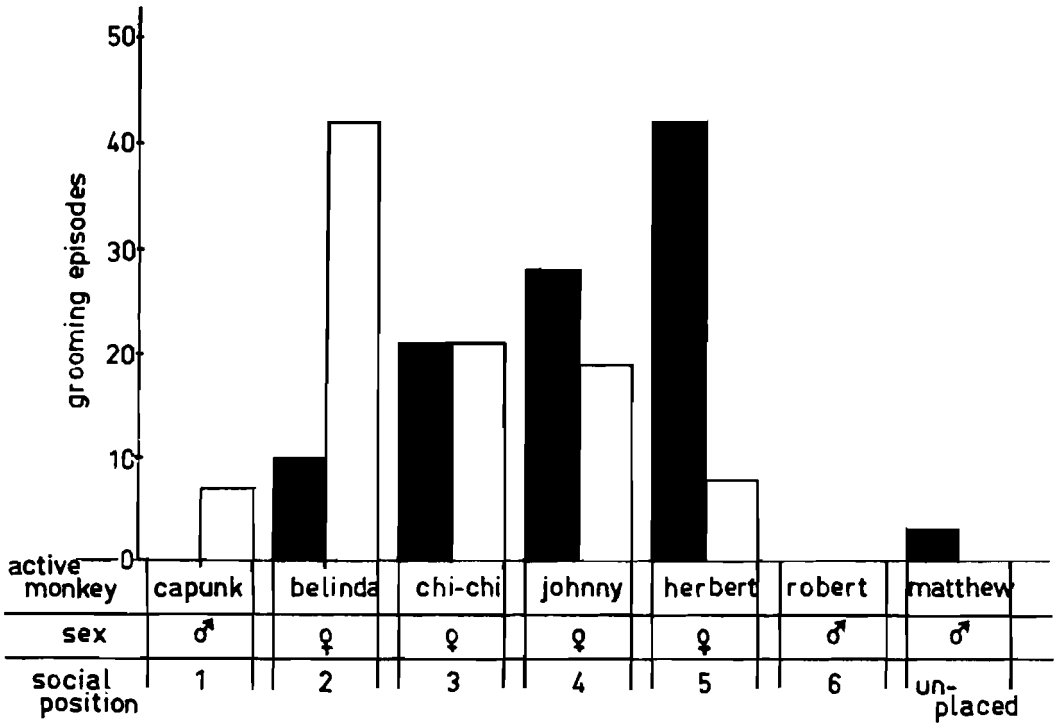


FIGURE 1. Histogram of grooming seen in seven vervet monkeys over a three month period, showing the grooming by dominant (black areas) and inferior (white areas) partners.

Active Monkey		Social position	Total number of grooming incidents	Grooming of superiors	Grooming of inferiors
Capunk	♂	1st	7	0	7
Belinda	♀	2nd	52	10	42
Chi-Chi	♀	3rd	42	21	21
Johnny	♀	4th	48	29	19
Herbert	♀	5th	50	42	8
Robert	♂	6th	0	0	0
Matthew	♂	Unplaced	3	0	3

There is no doubt that the desire to groom, and to be groomed, is an important feature in group cohesion. In some circumstances, active grooming seems also to serve the function of a tension-releasing activity (see below).

(b) *Care and Protection of the Young*

The presence of an infant in a troop of baboons or monkeys appears to strengthen group cohesion in that the females tend to group round it, waiting for an opportunity to handle or care for it. This has been remarked upon in the case of wild baboons by Washburn and De Vore (1961) and with reference to wild vervets by Maberley (1963).

At the time of writing, no infant had been born in the captive vervet troop under consideration, but the juvenile male, Matthew, was placed with the troop when about one month old, just having started to eat solid food. On being introduced to the troop, all the females immediately clustered round him, making high-intensity wanting noises (described below) and vied with one another for an opportunity to carry him. On several occasions, females were seen to offer him pieces of food which he accepted. At that time, two of the monkeys, Herbert and Johnny were thought to be juvenile males but the maternal behaviour which they showed towards the infant was so apparent that they were examined in more detail; both proved to be juvenile females. The males showed no particular interest in the infant and ignored it completely.

The observations so far made show that there is only one context in which concerted group action of the troop can be elicited and that is in protection of an infant when it is threatened. This was painfully demonstrated to me on one occasion shortly after the infant had been placed with the troop.

I had gone into the cage to catch the young monkey for a routine check on weight and size. While being caught, the infant emitted a high-pitched distress squeal and, without warning, I was attacked simultaneously by all the females in the troop. Once the females had started the attack, the two males joined in as well. After this incident, the infant was monopolised by the oldest female, Belinda, who carried it constantly, until it was independent five months later. She protected it with vigorous threat at all times and until now, no further measurements have been possible on it.

This particular infant monkey, Matthew, received a head injury when its mother was

killed in the wild state; from time to time the injury has resulted in an epileptic fit during which the monkey collapses and loses consciousness for a short time. On several such occasions I have attempted to remove the limp body from the cage; on all of these I have been threatened and bitten by the females who are normally extremely docile towards me. They would characteristically group round the prostrate monkey a d one would attempt to carry it off, holding it in her arms while walking awkwardly on her h nd legs.

Female protective behaviour is shown very early in life and an infant female, less than three months old and weighing one and a quarter pounds showed strong maternal tendencies to an infant male which was reared with her. In any frightening situation, she would pick him up and attempt to walk away with him. Such behaviour was never shown by the male.

(c) *Sleeping Associations*

Another factor contributing to the cohesion of an *aethiops* troop is the strong desire shown by its individuals for mutual physical contact at night. During the day one monkey might be separated from the rest of the group without particular signs of distress but, as darkness begins to fall, it will make vigorous efforts to reunite itself with the group. The present troop of seven normally sleeps in two groups, one of three and the other of four. Whereas grooming appears to be conducted independently of social order, sleeping association is almost certainly determined by this order. Thus the upper three in order of dominance sleep together while the lower four form the other group. More observations are needed before the complete inflexibility of these associations can be confirmed; these observations are currently being made.

COMMUNICATION WITHIN THE GROUP

Communication between individuals in a vervet troop is carried out by voice, facial expression and stance, much in the same way as has been described for Rhesus monkeys by Hinde and Rowell (1962 a and b). It appears that among vervets, all vocalisation, together with its appropriate expression or stance, can be classified in one of the three following categories: (a) Wanting, (b) Alarm and (c) Aggression.

Calls indicative of these three states are produced in different intensities, as set out in Table 2. No attempt is made to describe the individual sound produced in any detail as such descriptions are invariably subjective; it is hoped to analyse the calls sonographically at a later date. It is likely that all the sound discussed here correspond to the "arr" calls described for the *Cercopithecus* genus by Andrew (1963).

(a) *Wanting*

Only two well-defined calls are produced by a very young vervet infant, both serving the function of attracting the attention of the mother to the infant's needs. The medium intensity "gargling" call, made with lips protruded and formed into an O, frequently passes into the high intensity version, characterised by a wide open mouth and pronounced lip-retraction. Both calls persist into adult life, the gargle being often shown by a hungry animal at the sight

of much-desired food, or by a female at the sight of an infant; the squeal persists when the monkey is in pain or when it is severely frustrated and when this call is made by an adult male, its pitch is much lower than that of the female or infant version, although the mouth position is the same.

TABLE 2: THE BASIS OF COMMUNICATION IN A CERCOPITHECUS AETHIOPS TROOP

Eliciting context	Call	Mouth position, expression and stance	Group Significance
WANTING:			
Low intensity Sight of a desired object, approval, constant contact call promoting group unity.	War-Hor-Hor	Mouth partly open with slight pursing of lips, i.e., brief orbicularis oris contraction.	Little.
Medium intensity Sight of highly desirable object, normal infant call when requiring attention.	Prolonged war-hor-hor or gargle.	Lips protruded and pursed into O i.e., marked and prolonged orbicularis oris contraction.	Some.
High intensity Infant distress; distress through hunger pain or exasperation.	Squeal.	Mouth open, lips retracted in a low grin.	Great.
ALARM:			
Low intensity Anxiety about unusual animal, object or sound; distant predator.	Whispered stutter.	Mouth open, lips retracted in low or high grin. Head bobbing and standing on hind legs.	Great.
High intensity Close approach of potential predator.	Harsh stutter, (inhaling and exhaling).	Mouth opened, lips retracted in high grin, eyes opened wide, hair on body bristling.	Very great.
AGGRESSION:			
Low intensity Threat as a result of irritation.	Closed chatter.	Mouth closed, eyebrows raised, head thrust forward. Head down stance. (Some individuals show silent threat with raised eyebrows and pursed mouth.)	Little.
High intensity Anger.	Open chatter, (inhaling and exhaling).	Mouth open, lips partly retracted in preparation to bite.	Little.

The typically adult "wor-hor-hor" call is made by young monkeys from the age of about one month onwards. This is the most commonly used vocalisation in an undisturbed monkey troop, made when feeding, moving through the trees or practising any of the normal routine activities. It signifies approval; the sight of food or of a companion and, by virtue of its frequent repetition, serves to keep the troop together. When prolonged for several seconds, a "war-hor-hor" is converted into its higher intensity version or "gargle".

(b) *Alarm*

Both calls signifying alarm are innate in their performance, though the appropriate contexts in which they are given are largely learnt from older members of a troop. Thus an unsophisticated infant will produce the low intensity alarm call at the sight of any unusual moving object, but it is the reaction of other troop members which gradually conditions it to accept some objects as harmless and others as potentially dangerous.

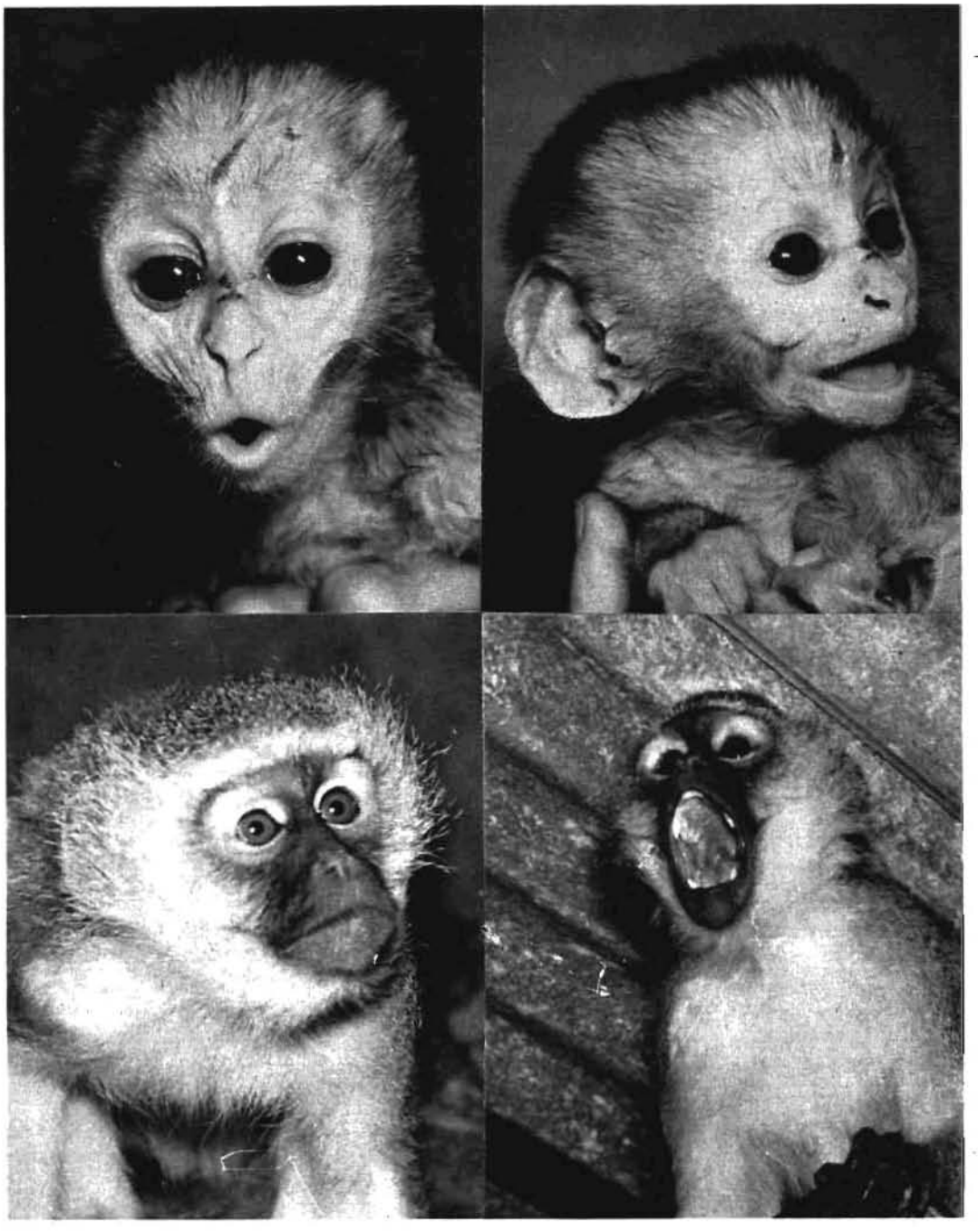
Among adults, the low intensity call seems to signify anxiety more than true alarm, and is made at the sight of a distant predator, such as an eagle or dog, or an unusual object. This call, though made very quietly, has very great group significance, serving to alert every member who hears it. In fact, the quietness probably has survival value, since it is clearly desirable to advise other members of the troop about a predator, but not to draw the attention of that predator to oneself.

If on the other hand, the predator advances on the monkeys and comes so close as to be a serious source of danger, the whispered call changes rapidly into the loud and harsh high intensity version. The mouth position is the same, with pronounced lip-retraction, but the eyes are opened wider and the body hair bristles. The harsh cough, or stutter, is made when drawing air in as well as out. Group significance of this sound is enormous and one call suffices to create agitation generally.

(c) *Aggression*

The two noises signifying threat are similar, but the low intensity one is made with the mouth closed, while at higher intensities the mouth is opened in preparation to bite. The rapid chattering noise invariably goes with an aggressive grimace, in which the eyebrows are raised and the head is thrust forward. An adult vervet monkey has a very darkly pigmented face, but the folded skin round the eyes is unpigmented and almost white. When the face is relaxed, this pale skin hardly shows, so that an impression of overall blackness is conveyed; in threat, however, the pale skin round the eyes becomes startlingly apparent and greatly enhances the effect of eyebrow-raising. Such a display probably has selective value in that effective threat is less dangerous than physical conflict.

A characteristic "head-down" stance is sometimes shown by aggressive vervets; here the hindquarters and tail are held high, while the monkey crouches on its arms with head thrust forward. In this position it will advance and retreat rapidly, continually facing and grimacing at the offender.



Occasional adult vervets may be seen to use silent threat, in which the eyebrows are raised and the lips pursed as is typical for medium intensity wanting. No sound is made and the association of the eyebrow-raising grimace and the lip-protrusion seems incongruous.

The Significance of Lip-Retraction

Reference to Table 2 will show that the only calls having marked significance to the group as a whole are those associated with retraction of the lips into a low or a high grin (see Andrew 1963). Such calls serve to alert other members of the troop to a potential source of danger, either to themselves or to an infant. This observation is of interest in view of Andrew's theory (1963) that "many of the components of the facial expressions of primates (and of other mammals) have evolved from protective responses given to strong stimulus contrast . . . ". He argues that lip retraction is one of these basic protective responses and would originally have been shown when the animal tasted something unpleasant. From this origin, the grin is used in a variety of other contexts, as when in pain or afraid. In baboons, a grin is shown by a subordinate when it approaches a superior; a similar fear-grin is shown by Rhesus monkeys (Hinde and Rowell 1962), usually without vocalisation. In fact, among baboons, the grin has been facilitated almost to the extent of being used in greeting, as in man. No such facilitation can be observed among vervets, where lip retraction still retains its more primitive function of conveying information about a potentially unpleasant situation.

RANDOM OBSERVATIONS

(a) *Feeding*

The use that vervet monkeys make of cheek-pouches is worthy of comment. Even when hungry, it is unusual for food to be swallowed directly after being chewed; generally the pouches are well filled before swallowing starts. On two occasions it has been possible to show that this pouch-filling behaviour is innate and unlearnt. Two infants were reared in complete isolation from other monkeys and both showed the pattern from the first time they fed on solid food. When feeding alone, a monkey derives no benefit from the filling of its pouches, but the usefulness is very apparent when a group is competing for a limited food source. Clearly, the individual capable of packing the most into its pouches in the shortest time will have the most to eat in the long run.

COMMUNICATION IN THE VERVET MONKEY *Cercopithecus aethiops.*

TOP LEFT: An infant making its medium intensity wanting call, with lips protruded and pursed into an O.

TOP RIGHT: High intensity wanting call of an infant: the squeal with lip-retraction.

LOWER LEFT: Aggressive grimace. The head is thrust forward and the eyebrows are raised displaying the unpigmented skin round the eyes.

LOWER RIGHT: High-intensity alarm at the approach of a dangerous predator (a cheetah in this case). The harsh call is produced with the mouth wide open. Lip-retraction is usual.

It is a fairly obvious statement that if a monkey troop has a ready source of food, it will lack the incentive to travel far in the course of a day. The captive troop normally becomes restless only when deprived of food, and a wild troop kept under observation for 10 days on the lower Lundi River in Southern Rhodesia could always be located within a three-miles stretch of river-fringing vegetation. An isolated observation nevertheless shows how far vervets will travel when food is scarce: a small troop was encountered in the Wankie National Park during October 1962, and watched at a particular spot till 5.45 p.m. that day. At 10.30 a.m. the following morning the same troop was watched again at a spot 11 miles from where it had been encountered the previous evening. Positive identification was made by means of a prominent male which showed an extraordinary scar round half its lower abdomen. The same monkey was examined at close range on both occasions. This unusual distance of travel was most likely caused by an acute shortage of food. The mopane woodland was leafless and dry and the monkeys were feeding on the dry seeds of the mopane trees themselves.

(b) *Tension-Releasing Activities*

The sudden removal of a tension-provoking stimulus usually elicits one of three possible displacement activities: exaggerated grooming, tail-scratching or yawning. If, for instance, two monkeys are fighting one another through the wire mesh separating adjoining cages and one of them suddenly breaks off the conflict and disappears, the other is likely to perform one of the three activities listed. It might immediately groom a fellow, but with very exaggerated lip movements and feverish activity of its hands; it might simply sit and yawn; or it might start scratching its tail, working down towards the tip and hardly noticing when the extremity has been reached.

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SUMMARY

The observations were based mainly on a captive group of vervet monkeys, built up to simulate a small natural troop. Organisation within the group, based on social dominance, is examined; special mention is made of the way in which an order of dominance was established, how it is maintained and what the causes are of periodic change. Some of the factors which tend to hold the group together are considered in the light of the social order.

The basis of communication within an *aethiops* troop is discussed and is shown to be dependent on voice, facial expression and stance; calls associated with lip-retraction are found to be of particular social significance, though these have not been facilitated to the same extent as is the case with baboons.

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