

On sociology and behaviour in impala (*Aepyceros melampus suara* Matschie)

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Introduction

The horned ungulates or bovidae offer a challenging opportunity to the study of homologous behaviour patterns. Like Cichlids, Anatinae, Laridae, Pelicaniformes, Phasianidae etc. they represent a group with many, closely related, yet different species, i. e. with a rich radiation. Furthermore in bovidae as in the above mentioned groups the innate components of behaviour are well pronounced. But while those groups of fish and birds stimulated a considerable number of studies on homology of behaviour, none of the mammal groups has so far been thoroughly investigated in this sense. Some steps have however been made in this direction (ANTONIUS, 1937; SEITZ, 1941; LEYHAUSEN, 1956; WALTHER, 1958; to mention a few representatives). But obviously these studies are hampered by one or both of the following facts:

1. The observations were carried out with captive animals and lack the sociological background of wildlife conditions;
2. The comparative studies do not include all the species of a family or relation group, but only a casual selection.

This applies also to bovidae. Only for a few species certain sectors of behaviour have been carefully surveyed (WALTHER 1964a). Only during the last few years a small number of species of bovidae has been thoroughly investigated under wildlife conditions. Some of these studies are still in progress: McHUGH (1958) the American bison, BUECHNER & SCHLOETH (1965) the Uganda kob, ESTES (1965) the wildebeeste, KILEY-WORTHINGTON (1965) the waterbuck, WALTHER (1964b) Thomson's and Grant's gazelle. But many more species of bovidae are only superficially known in sociology and behaviour.

This paper deals with the behaviour of impala. The way of life of the species is outlined, the social relations and the behaviour patterns proper to the species are examined.

During most of 1963 and partially in 1964 the author observed impala in Nairobi National Park and the region of Kipleleo, Aitong and Mara Bridge (Mara Masai Game Reserve) in Kenya. Further observations have been made during shorter visits to Tsavo National Park, Amboseli Game Reserve and Manyara Park.

A. Remarks on the ecology of impala

1. Habitat

In the study areas the three basic characteristics of an impala habitat are:

- a. cover, either relatively thick bush or light forest with undergrowth and grass patches;
- b. water available during most of the year;
- c. a slope or slopes, ranging from slight to moderate; the latter condition is normally implied in a. and b.

Sometimes impala move out of their main habitat to adjacent grass plains, but the abandonment of the home ground for any length of time is only likely to occur under exceptional circumstances (see B. 5b).

Zones with specific impala habitat are often restricted, and therefore there may be little contact between such population-units. If undisturbed the herds as well as the individual animals stay in a preferred area of their home range. Some of the individuals or herds can be observed for many days within the same area of 200

to 400 yards radius. Sometimes, however, spontaneous day to day movements of up to half a mile or more may occur. A quick change of locality is most often caused by disturbance. Serious disturbance can result in a sudden move over half a mile or more, temporarily out of the normal home range.

2. Overlapping of habitat

There is a considerable number of other herbivores, mainly ungulates, whose habitats partially overlap with those of impala (see LAMPREY 1963). Grant's and Thomson's gazelle live more often in open plains, but are frequently seen in impala areas. This is also true for Burchell's zebra, kongoni, topi (Mara region) and, to some extent, wildebeeste. Forest and bush species such as bushbuck and dikdik, and also the waterbuck live partially in impala country. In the areas studied giraffe, baboon and warthog are also seen in impala habitat.

3. Association with other herbivores

The above mentioned species not only share their living areas with impala, but often appear in association with them. In the case of giraffe, warthog, waterbuck and dikdik the association appears to be fortuitous or at least unstable. But in the case of gazelle, zebra, kongoni, topi, bushbuck, baboon and, less frequently, wildebeeste, there is a tendency to join actively with impala and vice versa. These mixed groups often feed, rest and move together, a correlation in behaviour which must depend on a "parasocial need" or association-tendency, and which has a survival value, representing a cooperation in the avoidance of predators. It can frequently be observed that an alarm given by members of one species alerts the whole association. Apparently the benefits of this cooperation even outweigh the disadvantages of a large number of animals feeding within the same limited area.

4. Predators

Lion, leopard, cheetah and hunting dog prey on impala of any age. Eagle owl, and possibly a few of the larger eagles, prey on small lambs. Lambs as well as sick and injured impala fall victim to hyaena and jackal. Casualties recorded during the period of observation were:

<i>Predator</i>	<i>Impala killed</i>
Lion	2 juveniles
Leopard	1 female
Cheetah	1 female
Hunting dog	1 female, 1 juvenile
Eagle owl	1 juvenile
Jackal	1 juvenile

But despite the wide variety of natural predators, their pressure on the impala population seems to be low. This is due in part to the nature of the impala habitat and in part to the technique of avoidance developed by the species. As far as our observations have shown, only human interference can really endanger the existence of the species. Permanent timidity and shyness in impala are solely induced by contact with man.

5. Injuries

In the Kipleleo area a few impala with injuries were observed such as cuts of varying severity, one broken leg, other injuries of the locomotory system causing limping. These injuries can be attributed to the rocky and rugged terrain of Kipleleo and Ol Joro Orowa and in the case of males to fighting (see E. 4c). The examination of one male shot at Kipleleo revealed several superficial cuts and grazes on the muzzle, forehead, ears, lower chest and shoulders (WATERIDGE, personal communication). Some of these may have been the result of fighting, others of pushing in haste through dense bush. In the Nairobi National Park several males were seen that had lost one horn or part of a horn, almost certainly while fighting. Over several months one lame female was observed with an enormous, partially necrotic tumour at the carpal joint of one foreleg.

B. On formation and general behaviour of social groups or herds of impala

1. Group composition and solitary animals

Impala normally live in herds of which two main types can be observed:

a. *Female or breeding herds* consist predominantly of females numbering from two to 100 or more together with dependent young animals and with one dominant male (herd male).

b. *Male or bachelor herds* consist of from two to about 60 males, including yearlings, fully grown and perhaps some old individuals.

In the Forest Area of the Nairobi National Park, with its many small valleys and relatively dense vegetation, these two types of herds are normally clearly separated; they are comparatively small and stable in composition. In more open country (e. g. the Kipleleo area, the Somali Ridge and Athi River Basin in Nairobi National Park) the female herds are less stable. Two or more female groups may join together, but later the resulting larger herd will split again in an unpredictable manner. In open country female and bachelor herds are often seen side by side, moving together for hours. It was mainly here that other social groups were found which did not fit in with the herd types already mentioned.

In all the observed impala populations the female herds are denser than the male herds, the individuals staying closer together. Bachelor herds are more spread out. In addition, some adult bachelors show a high degree of independence and may be found more than 200 yards from the nearest male herd. Yet in many cases they maintain a social connection with the herd, which is made evident by frequent listening and looking in its direction and by participation in its general movement during the day. Females were observed in isolation shortly before lambing and during the succeeding period when the lamb did not follow its mother continuously, or in cases of sickness.

2. Factors affecting herd formation

a. Female and immature impala are gregarious; the social bond however is not homogenous throughout the herd. Often, when an apparently old female starts moving with a definite motivation, she is immediately followed by one to three adult females, and perhaps by a few immature individuals and lambs. These animals, which seem to be especially attached to one another, are almost certainly a mother and her daughters of former years with their respective offsprings. In relaxed situations another type of social bond may prevail: the tendency to join among individuals of

the same age group. Within the female herd the smaller lambs often keep together; yearlings can be seen playing in a subgroup. Mothers with very small lambs may also form a subgroup within the female herd. It has to be assumed however that the formation of the larger female herds is not only due to these special social relations, but to a more general social bond between all the members, which in females can be lacking or is blocked during the lambing period.

b. The dominant male contributes to the herd formation by shepherding the female herd more or less intensely, especially during the daytime, thus keeping it a compact community. He urges stragglers to join a slowly moving herd by a kind of "nodding", a symbolised butting (or a butting "intention-movement") (Fig. 1). If, for any reason



Fig. 1. Dominant male urges stragglers to join his female herd

(usually flight induced by danger) the female herd is split up, the male has been observed to go in search of detached females and to shepherd them back. Sometimes single females attempt to leave the herd and, if the dominant male interferes they try to avoid him by flight. The male may then follow in full gallop chasing such a female either until she rejoins his herd or he may finally give up the chase.

c. The special relationship between a dominant male and his females implies male competition over the possession of females. In fact, it is through successful competition that one male becomes "owner" of a female herd, and he maintains his position by an intolerant and aggressive attitude towards the other males. He chases young males out of the female herd when they are 10–12 months old. This is especially pronounced at times when fully adult rival males, trying to establish a female herd of their own, contest his privileges. Then the chasing of young males that are still attached to their mothers represents "displacement activity": instead of attacking the strong rivals he "goes for" the weaker youngsters and thus demonstrates his superiority without taking a risk. If his demonstration fails to stop his real rival, he will threaten or even attack him.

d. The dominant male's herding activities and his intolerant and aggressive behaviour are often combined with various forms of courtship. When he has chased away a rival and has returned to his herd, he will often go from one female to the next addressing special "courtship gestures" to each one (See D. 4).

e. When the male yearlings are driven away from the female herd and thus separated from their mothers, they join the bachelor herd, within which they sometimes form a temporary subgroup, keeping closer together than the adult males. Bachelor herds are not shepherded. Furthermore, the adult male impala has not such a strong tendency to aggregate with individuals of his own sex. In dominant males and their challengers gregariousness must be connected with sexual drives, the striving for a female herd and the intolerance towards any rivals that are in possession of females. In the male impala there seems to be hardly any dominance drive as such. Sometimes a bachelor may cause another one to step aside by a nodding of his head. But only in the presence of females possessive behaviour and vehement competition are induced. On two occasions two adult males were seen that owned the same female herd without showing reciprocal intolerance and competition during a few days of observation.

3. The dynamic aspect of impala herds

a. Impala herds are unstable. It is male competition and the resulting dominance of a few males that principally influences the size and composition of the female herds throughout the year and especially during the seasonal mating "peaks" (Mora-Kipleleo: January to March and sometimes early April — L. WATERIDGE, personal communication. In Nairobi National Park 1963: February to April and August to October). During these periods adult bachelors try more assiduously to establish contact with the females and to acquire breeding herds of their own. A so far dominant male may then lose part or all of his herd to a new dominant male.

b. Females also contribute to the disruption and changing status of a herd. Three observations are described here:

1. At Kipleleo a dominant male was herding a large number of females, trying to prevent them from moving in the direction of a nearby bachelor herd. Towards the evening a number of females suddenly broke out of the herd. The efforts of the male to retain the females were not successful, and more and more deserted him in small groups. They moved to an area where they normally passed the night and there another male started courting them.
2. In the Forest Area of Nairobi National Park a breeding herd, guided by an old female, was moving in the direction of another female herd. Despite the intervention of the dominant male some of the females of the first herd left and joined the second one.
3. On several occasions during peak mating activity, female impala, alone or accompanied by immature animals, were observed to leave their herd and join a nearby bachelor herd, where they provoked courting behaviour and competition amongst the males.

c. Females leave the herd before lambing. Highly pregnant females are observed alone or in small groups of two to five. After the birth the mother can still live in isolation from the herd with her lamb hidden in undergrowth most of the time. She may be joined by her yearling of the previous year. Frequently a few mothers with their lambs live as a small group apart from the herd. Such isolated mothers with their offsprings may later return to the original herds, or they are courted and herded by a bachelor who attempts to form his own herd.

4. Leadership and social moods in behaviour

a. With impala, as with many other gregarious vertebrates, activities are "contagious" within the herd. The herd is not only the result of integration in space and time but also in activity. It is however exceptional that all the members of the herd

simultaneously perform the same activity. Usually, one individual starts a new activity and this is taken up by others and gradually spreads through the herd. Some may, however, continue their previous activity, the response to a behaviour impulse not being identical in every animal at every moment. Feeding, resting, standing or lying, ruminating, lifting the head on the alert, cleaning etc. appear as "moods" of the herd.

b. Sometimes the herd is divided into subgroups each characterised by its own activity. For instance, in a female herd, the small lambs are resting together, their mothers are feeding nearby, the rest of the adults stand ruminating, while yearlings are indulging in playful canter. Another type of subgroup behaviour may be mentioned here which impala share with many other antelopes: when a slightly disturbed herd runs off and then stops, most of the lambs join their mothers and start suckling.

c. In some types of herd activity impala have developed a high degree of coordination, as for instance, with mutual licking, which may spread through a herd together with individual cleaning activity (See C. 4.). Again several components of coordination govern the herd movements from one place to another. In female herds an adult female moving decisively in a certain direction induces nearby individuals to follow, then more and more members of the herd join the movement. The lead function is often taken by a mother with a lamb, while the dominant male brings up the rear. The functional differentiation between such a leading female and her followers is most pronounced when an area of high grass or dense shrub has to be crossed. The leader then has the neck upright, the ears erect, directed forwards or turning to the right or left in order to catch a sound. She stops frequently and abruptly, such phases of sudden immobility being most marked in her head. The herd follows in single file, the gait of the followers shows much less tension. In certain circumstances it is not only the decisive manner of an individual's activity, that induces other members of the herd to follow, but the fact that its behaviour includes conspicuous ritualized signs which have a releasing function. This is especially so with alarm and escape signs (See C. 5.).

5. Daily activity — programme

a. It has not yet been possible to observe impala thoroughly during the night, and in this respect our notes are incomplete.

The activity of impala depends largely on the external situation, disturbances being most important. As we shall note later (See C. 5.) impala are readily alarmed. It could not be decided whether there is an innate releasing mechanism reacting automatically to some characteristics of predators, but there is no doubt that the alarm quality of a situation is shaped by experience and "tradition" within the social groups. In particular the reactions to man differ greatly from place to place depending on past experience with human interference. In Nairobi National Park for example, where shooting has not been practised for many years, it is possible to pass within a few yards of an impala herd in a car, or within twenty yards when on foot. The impala walk away slowly while being watched by a stationary observer. On the other hand, in the Kipileleo and Mara Bridge areas where impala were hunted until about three years ago and are consistently subjected to varying human disturbances, they often run away if a car appears within 100 — 150 yards, or as soon as they see a man on foot. It seems that in areas where the impala are often disturbed, they are more active during the night, as they are when less subjected to human interference. Disturbances can induce changes in activity as well as in locality.

b. Another factor influencing the behaviour of impala is the weather. When it is very hot, impala like to lie down, in rain they often stand close together. Climatic

conditions may indirectly modify the behaviour of impala by affecting the soil surface and plant growth.

In the Nairobi National Park the dry grass of a limited area was burnt in September 1963. When the new grass sprouted, the impala herd which normally inhabited the adjacent slope, moved down to the plain and stayed there for several days. L. WATERIDGE has reported, that at Kipleleo, during the excessive rains of November 1963 to March 1964, the plains became waterlogged and later the grass grew very high. During this time the impala extended their movements to the high and steep slopes of Kipleleo and Ol Joro Orowa, avoiding the lower slopes and the adjacent grass plains, which are normally the preferred area within their home range.

c. Because of the highly variable external factors influencing impala behaviour only a generalized account of the daily sequence of activities can be given. In the early morning impala feed. The herds are rather spread out and the herding activity of the dominant male is low. During a period of extensive observation at Kipleleo in August 1963, the major part of the local impala population was found each morning on the same slope, with female and bachelor herds more or less mixed. Several times a disturbance caused this herd complex to move off down the slope. When undisturbed the animals moved slowly down to the lower bushy slopes and grass plains, feeding as they moved. Here changes in the social structure of the herd complex developed; one or two dominant males started to herd females and to drive bachelors away, thus forming compact female herds. Most of the bachelors gathered in loose herds, while others — and also two to four small female groups — remained scattered over the whole slope. During the morning feeding, cleaning and playing moods could be seen in the herds.

As the day gets hotter more and more individuals lie down and ruminate. Towards the evening feeding activity increases again, and as the light fades the herds move towards the area where they pass the night (at Kipleleo areas on the slopes which offer a good sight in all directions). During this move the herd organisation often changes again. In the Nairobi National Park impala often lie down in the dusk. At Kipleleo they seem to be more active at night. Males have been heard to roar at 10 and 11 p. m.

C. Behaviour patterns of normal daily activity

1. Feeding, resting and ruminating

a. Impalas are browsers and grazers. When browsing, the animals may stay at the same place for several minutes. Grazing is normally combined with a continuous slow shifting. As stated above (B. 4.), feeding is a herd activity. Yet this does not exclude that within the herd it is combined with some other activities, e. g. resting and ruminating or play cantering. The feeding activity is always a combination of several behaviour patterns. The animal pulls up a mouthful of grass or plucks some leaves away from a bush. It then chews the food briefly and swallows it, steps forward to reach new food, and so on. During all this time it may flick its tail sideways once or several times, or flick its ears. Very often after pulling up food, the impala raises its head, erects its ears and remains motionless while chewing the food. Sometimes this watchful posture is maintained even longer. In general the individuals feeding at the periphery of the herd lift their heads in an outward direction from the herd, and have shorter feeding and longer watching phases than individuals in the centre of the herd. They sometimes stop feeding for several minutes remaining motionless in "watching posture". These behaviour patterns accompanying feeding must be interpreted functionally as measures to detect predators. (See C. 6.).

b. During feeding, especially grazing, impala normally move slowly in one direction. This is true not only for single animals, but for entire herds. Neither female nor male herds are guided by a permanent lead animal (See B. 4.). The dominant male rarely leads the female herd; one of the females determines the direction. However the male does exert a certain influence in keeping the females together and preventing them from joining bachelors or the herd of another dominant male.

c. At every hour of the day, within a feeding impala herd, some animals can be at rest, yet in the heat of the day often a whole herd is resting, most of the animals lying close together in the shadow of a tree, or more dispersed in the open. Some individuals (especially old females) often remain standing even while all the others are lying. An animal at rest may stretch out its head along the ground, but the normal resting and ruminating position is with lifted neck and head. Feeding, resting and ruminating are herd activities. "Infectivity" of behaviour influenced by each individual's level of motivation and activities that function as means of protection, are never missing entirely throughout the whole herd.

2. Drinking and salt licking

Unlike gazelle, impala go frequently to water. It cannot, however, be stated that when water is available, drinking takes place every day or at a fixed hour. Impala can survive for a limited time in regions where surface water is lacking. When moving towards water herds are in closed formation. Not all individuals drink simultaneously: some drink while others remain watchfully nearby, an informal rotation taking place. An impala drinks for less than half a minute. The animal never steps into the water, but always drinks from the edge of the dam, pond or swamp.

In Nairobi National Park and in the Kipleleo area impala herds were observed visiting a salt lick. These visits do not occur regularly and certainly not every day. Salt licking, too, is a herd activity.

3. Urination and defaecation

As in many other ungulates and in other mammals, urination and defaecation have certain social aspects.

a. Urination and defaecation, like other activities, are infective within the herd. When — without external stimulus — one animal starts to urinate and/or defaecate, several others will do so immediately.

b. Sometimes an external stimulus induces urination and/or defaecation: when a herd is not completely at ease, for instance, with an observer nearby, urination and defaecation can propagate through the whole herd like a wave.

c. Urination plays a functional role in the male-female contact, but this role is much less pronounced and developed than in many other ungulates. In impala no fixed behaviour pattern can be observed by which the male stimulates urination by the female. When he is tending a female near or in oestrus, the dominant male regularly shows sniffing and/or licking of her urine followed by "Flehmen"¹. Otherwise the behaviour pattern may or may not follow urination by a female. After "Flehmen" the male occasionally urinates and/or defaecates himself.

d. In male to male contact there is no urination ceremony at all. Compared with

¹ "Flehmen" (SCHNEIDER 1930-1934) — the animal lifts its head, the nose pointing upwards, contracts the skin muscles of the nasal region and draws the upper lips upwards, baring the gums of the upper jaw, thus causing wrinkles of the nose and changing the shape of the nostrils. "Flehmen" is widespread among ungulates but occurs also in lion and tiger. Its function is chemoreceptory testing.

other ungulates impala show a very low degree of ritualisation in urination and defaecation, and correspondingly these activities do not play an important role in social contact.

4. Comfort behaviour

a. The behaviour patterns of scratching and cleaning show little variation in impala. Those observed are:

1. Scratching of muzzle, cheek and ear regions with the hoof of a hindleg;
2. Licking of back and sides of the body, of the belly and sometimes of the front and hind feet.
3. Social licking of the head, throat, neck and forebreast.

Cleaning behaviour often spreads through the herd as a mood. In the case of social licking a higher degree of coordination can be observed. Two animals join facing one another. Then one animal licks the other with a few strokes of the tongue, stops and is then licked by the other. Alternate licking may continue for several minutes. It occurs in male and female herds.

b. A special type of front rubbing in the male impala will be mentioned later (D. 4.). All impala often show ear and tail-flicking, especially in the heat of the day. This is presumably, a reaction to the irritation by flies. In the rain impala often lift a hindleg and shake it.

5. Avoidance of predators

a. The general vigilance of impala is assisted by certain immanent patterns of behaviour and of posture which all increase the probability of detecting a potential enemy. Those already mentioned are:

- the gregarious tendency
- association with other herbivores
- a complex vigilance behaviour within the herd while feeding, resting, drinking and moving; especially the lifting of head and neck in a motionless posture with the ears playing in upright position (Fig. 2)
- a sudden phase of immobility of the head when walking through shrub or undergrowth.

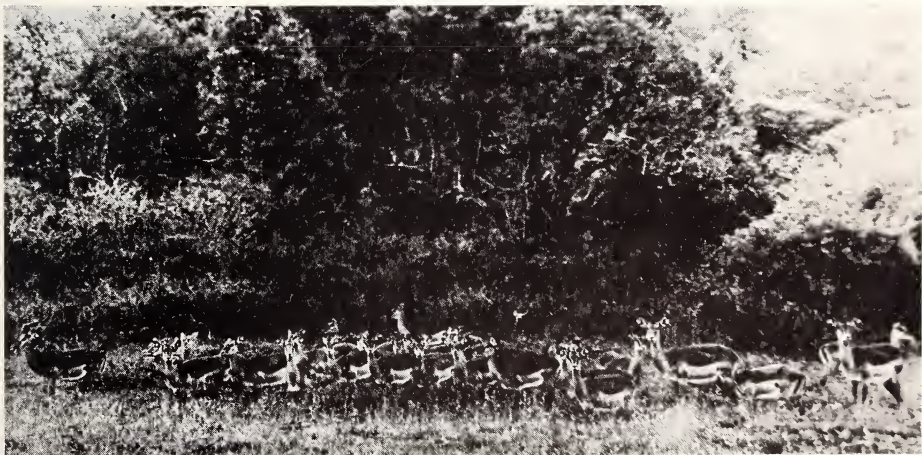


Fig. 2. Vigilance in an impala herd. Every direction is under sensory control by some individuals

A watchful posture is shared by most ungulates. A phase of immobility of the head while walking can be observed in a large variety of mammals and birds living in well covered habitats with mainly vertical growth patterns, e. g. bushbuck, dikdik, duiker, or herons, bitterns, game birds.

In ungulates, these behaviour patterns must be considered in connection with position and structure of the eyes:

The eyes are more or less protruding at the division of the head's frontal and lateral surface;

The pupil is horizontally elongated and in the retina there is a corresponding elongated zone of higher sensitivity;

When the head changes position, the eyes automatically rotate in their orbits to keep the zones of higher sensitivity and the pupils horizontal.

When the head remains motionless, the eyes can overlook the surrounding plain and record anything jutting out of or moving in the plain. In a habitat with vertical structures they record movement and position in relation to the structures.

b. When impala are alarmed without apparently seeing the disturbing subject, their behaviour takes on the character of a detecting technique. The ears rotate in the direction under suspicion. The animal scrutinizes the spot, the head being held obliquely. If cover partially hides the cause of disturbance, the impala may (as does the European roe deer) move its head sideways and up and down in an effort to locate it exactly.

c. Sometimes the impala will lower its head as if about to start feeding and then suddenly look up and remain motionless. It is very likely that this behaviour sequence is another detecting technique, adapted to the normal reaction of stalking predators, which is to approach their prey as soon as it starts feeding.

d. When impala have identified a disturber, but are not greatly frightened by him, they face or turn away from him, rotating the ears in his direction. If he now makes a sudden noise, they will face him again.

In cases of alarm of greater degree, they face him, remain motionless and suddenly give the alarm cry — a very sharp snort. Then a few tense steps are taken followed by immobility and the nervous snort again.

e. The final reaction to persistent disturbance is invariably flight, but there are many variations of "style" to these escapes. Following disturbance of low degree, an impala herd may walk away slowly. Individuals at the rear of the herd often catch up in a short canter. Again the first escape action may be a sudden start with a conspicuous head-

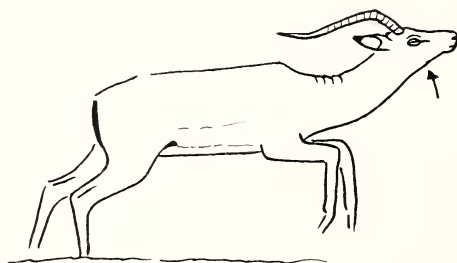


Fig. 3. Starting the flight with head jerking upwards

jerking upwards (Fig. 3) followed by a fast gallop, which soon slows down. The impala then stop and turn to look at the disturber before quieting down.

f. After a serious alarm impala flee at full speed, some performing the well known high jump in every direction. This may be observed more often in shrub and bush cover than in open grassland. Functionally, these jumps enable the impala to observe its enemy while escaping; they also have the effect of confusing predators whose hunting technique involves concentration on a single animal. Sometimes the escape reaction is released by situations that can not involve much or any danger; e. g. two zebra pass nearby chasing each other in play, a male Thomson's gazelle is chasing a female, a zebra scratches its skin on a small dead tree which suddenly breaks with a crack. In some of these cases the presence of the observer may have induced a higher

degree of "escape readiness", and in the sense of stimulus-summation (SEITZ, 1941) only a little extra stimulus was necessary to release the escape reaction.

g. It was noted earlier that the reactions of impala to man depend on their previous experience of human beings and are entirely different in different regions. In this connection the adaptability of avoiding and escape reactions is very striking.

6. Playing

a. It is not intended to discuss thoroughly which behaviour patterns of impala should be considered as play and which not. But some major characteristics of play may be mentioned. Most animal activity reveals an urge, tendency or drive, which "aim" at either a "consummatory situation" or a "consummatory activity" (CRAIG 1918). To have the stomach full of food, to own a territory, nest, burrow or a sex partner, to keep a certain social status, to get warm in sunshine or cool in water are consummatory or aim-situations in animal life. Mating is perhaps the most pronounced example of a consummatory activity. Hunting, eating, ruminating or fighting, on the other hand, not only appear as means of attaining an aim-situation, but are to some extent aims in themselves.

When an animal has attained a consummatory situation or performed a consummatory activity, it will be satisfied until the urge or drive rises again.

In contrast *Play* does not aim at a consummatory situation or activity, and even if the play involves certain aims, it may be repeated again and again, perhaps with variations, irrespective of whether the aim has been reached or not. In ungulates it is not very easy to recognize the different kinds of play. We have a much better understanding of play activity in primates and carnivores, chiefly because they play with objects and partners, as we do ourselves. But two types of activity in impala can be recognized as plays: "canter plays" and "play fighting".

b. Canter plays were observed only in breeding herds. Normally a yearling starts the play, galloping around, erecting the white tail, and performing a few high jumps, followed by a sequence of "style jumps" in which all four legs jerk the body off the ground at once, "pronking". A "style trot" is also very often performed by pushing with one front leg and alternate hindleg simultaneously, to give an "affected" gait, bouncing at every step, "stotting". "Pronking" and "stotting" can be observed in many ruminants, especially in deer, and in bovines from Thomson's gazelle to the American buffalo (bison).

It may be mentioned here that "pronking" and "stotting" are performed by certain ruminants after detecting a predator (Thomson's gazelle, Grant's gazelle, kongoni).

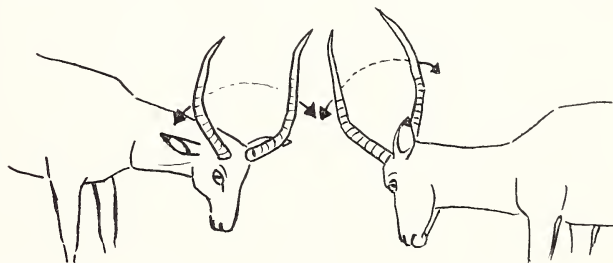


Fig. 4. Front to front position in playfight. The arrows indicate the head-and-horn rotation

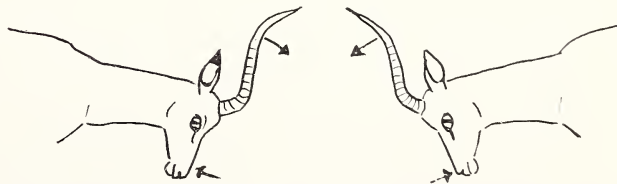


Fig. 5. Butting intention movement in playfight

Both seem to have similar functions to the high jumps in impala together with an alarm function for all members of the species (B. 4.).

Impala have yet another performance that seems to be peculiar to this species. It is a special type of gallop in which the hindlegs are thrown up together, then both forelegs alternately; the result is an exaggerated "rocking". Sometimes the hindlegs are flung up so energetically that the forelegs can push twice before the hindlegs again touch the ground. Only in Grant's gazelle a similar but much less elaborate performance was observed.

The young impala starting the canter play with galloping, normal and style jumping, stotting and rocking, moves away from the herd, then turns back, passes near the

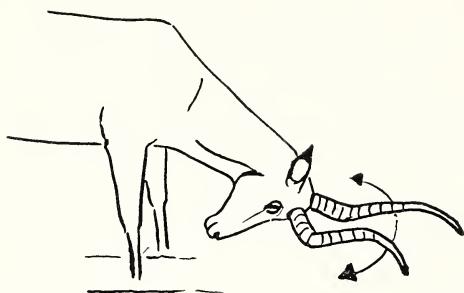


Fig. 6. Horn shaking. It occurs in playfight and as a dynamic form of showing off between rivals

herd and moves off again. As it does so, very often the younger animals (and sometimes even adult females) join this performance thus forming a play group. They move together in a close but changing formation, sometimes in single file, and always moving in a more or less circular tour. From time to time the playing impala stop, draw breath, then start all over again. Suddenly or gradually the playgroup dissolves, its members rejoining the rest of the herd in its activity.

c. Play fighting occurs among males only, from juveniles still tolerated in the

female herd up to adult bachelors. Youngsters in bachelor herds play most frequently. Play fight or fight proper can be clearly distinguished, but transitional stages exist.

In play fights the situation does not indicate competition over social dominance or ownership of females. The style of the movements does not reveal great tension and most of the corresponding displacement movements do not occur. The animals do not push or beat or twist vigorously with their horns. Movements are performed that in a real fight would be useless or even risky. The main patterns of play fights are:

1. remaining motionless in the front to front position (Fig. 4)
 2. facing each other without touching, and rotating heads and horns around the neck as axis (Fig. 4)
 3. performing simultaneously "butting-intention movements" (Fig. 5)
 4. butting with horns sometimes hardly touching each other
 5. butting more energetically, but still without social tension
 6. standing with interlocked horns, pushing only slightly
 7. jumping away from the partner, followed by frolic jumps and horn shaking in various ways (Fig. 6), turning round once or twice and returning to the partner.
- It should be mentioned that play, though lacking the aim of a consummatory situation or activity, is not without function; in fact play often exercises behaviour techniques and has an important part in social integration.

D. Herding and general courting

1. Herding and chasing

The dominant male's herding activity, and aggressive attitude towards other males have already been mentioned (See B. 2. and B. 3.). Both are intensified in the case of

aroused male competition and especially when a disturbed herd complex is disorganised after escape. Males and females may then be considerably scattered and mixed, the females forming casual subgroups around some leading individuals. In this disorganised situation special types of social activity are observed: one female of such an accidental subgroup may go in search of another female, perhaps her mother; she will listen, look and eventually walk towards another female group. Often movements of this kind are joined by entire subgroups, and this results in a general tendency of most females to get together. This tendency is, however, often interfered with by males: some of the bachelors try to herd and court isolated female groups. This activity is soon opposed by the dominant male. Roaring, with his tail lifted (See D. 3.), he starts chasing single females through the whole scattered herd and young males out of it. Sometimes he walks to an open place near the scattered herd and stands motionless in "proud" attitude. Then he again chases a young male or a female. These dynamic and static types of display slowly induce the females to join up and the bachelors to keep more and more distant from them. The dominant male then begins to circle the collected female herd and to walk or canter between it and the bachelors. From time to time he suddenly pursues a yearling or passes slowly with a proud gait in front of an adult bachelor, causing him to keep his distance. Having established dominance and order by this predominantly aggressive activity, he will then begin to direct courting behaviour towards the females (See D. 2.).

2. General courting of dominant males

Herding and chasing could be summarised as activities with clearly aggressive components of different strength. The dominant male also addresses to his females an "erotic" or courting display, especially in alternation with aggressive activity against rivals.

a. *Nose forward posture with empty ("vacuum") licking* (Fig. 7): The male walks some steps in the direction of a female with lifted nose, so that neck and head are pointing forward in one horizontal line, the horns consequently being lowered backwards. The male then performs an empty "licking movement". After a few steps the male changes direction, addressing the same gesture towards another female. Sometimes the female walks away with the male following for some steps, his licking then being directed towards the hindquarters. As we shall see later, the male impala also makes this licking gesture (in a slightly different form) as part of his premating behaviour (See F. 2.). In various forms, the same licking gesture can be observed in the courtship of many bovidae and cervidae, and it is very likely that there is a close relationship to the most important infantile activity – suckling. It is a common fact in birds and mammals that patterns of infantile behaviour are often related with those of sexual and caressing contact, i. e. based on the same dispositions.

b. *Pawing and licking gesture and lateral display*: The dominant male often performs a special display when females of his herd are lying on the ground. Two forms were observed:

1. Pawing and licking gesture: he approaches the female from behind, performs a pawing movement with one foreleg, during which he often touches the rump of the female. The female then rises and

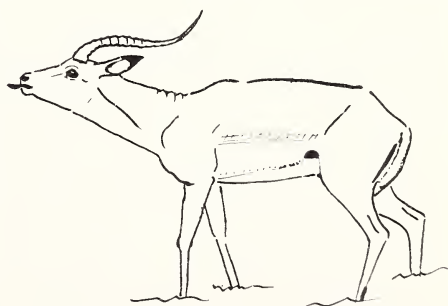


Fig. 7. „Nose forward posture“ with empty licking

walks away, the male following for a few steps, making licking movements in her direction.

2. Lateral display, observed in quite similar circumstances: At Kipleleo a male circled a female who was lying down, then stopped at her side, showed a quivering movement of the lowered tail with the white hair of the sides and underneath erected, then lifted his tail, stretched his nose forward and turned his head partly towards her. The female normally rose to her feet, whereupon the male went off to the next recumbent female and repeated his display. As the impala in the Kipleleo region were shy, these observations were made by binoculars from a hill at a distance of about half a mile. It is thus uncertain whether this description of the male display is complete or not. On Somali Ridge, Nairobi National Park, the male circled the female as described above but then bent his head sideways down to sniff the female's perineal region (Fig. 8).

- c. *Rising on hindlegs* (Fig. 9): This display was observed only in situations of strong competition, several times between a herd owner and a rival who was about to herd one of the other's females, and three times between members of a bachelor herd, after a female had deliberately joined them. In the following conflict one bachelor proved to be dominant chasing all the others away from the female.



Fig. 8. Lateral display. The male bends his head sideways down to sniff the female's genital region

In all these cases the male after threatening his opponent(s) came back to the female with tail lifted; rising on his hindlegs a few yards away from her, he walked a few steps on two legs in her direction while she moved slightly away. He then dropped to his forelegs and remained motionless and the female also stopped moving. During this display the male shows a partial erection of the penis.

Apparently this courtship sequence is derived from the act of copulation. Similar patterns of male courtship occur in other antelopes (e. g. wildebeeste, hartebeeste, Grant's gazelle). From a more comprehensive point of view it may be stated that symbolic sexual activities such as symbolic spawning (fish) and copulation (birds, mammals) are widespread courting activities amongst vertebrates.

- d. *Grunting display*. When a female herd is moving near bachelors the dominant male in the middle of his females often turns left face and right face and produces a grunting sound through the nose in a quick sequence of about two per second, "a-a-a-". This soft sound is combined with an audible expiration. The male's posture shows a certain tension, neck upright and nose lowered, reminiscent of a fallow stag in rut. This display seems to have a functional value in attracting the females to the dominant male and thus preventing them from desertion.

- e. *Bleating display*. The dominant male shows the grunting display while moving within the female herd. On several occasions the greater part of a female herd was seen moving from an open grass zone into dense bush, while the dominant male was chasing a rival. Returning to his herd he moved along the edge of the bush zone uttering from time to time a short series of bleating sounds through the open mouth while lifting head and nose in the direction of the nearest females. Each bleating series was composed of three to four single sounds "aaa-a-a(a)", the first one longer, louder and coarser, resembling somewhat the bleating sound of the "roaring" sequence (See D. 3.), but being softer, the others similar to the grunting sequence mentioned above.

As to the motivation the bleating display seems to be intermediate between the

grunting display and chasing with roaring. The male calls for his females which are away from him, but he does not drive them together. It can be assumed, that from the point of view of function it is an attracting display.

3. The roaring display (Fig. 10)

a. The vocal sequence called "roaring" consists of one or two very sharp snorting sounds produced, like the alarm snort, by expiration through the nose, and of a series of 4–6 coarsebleating sounds repeated at very short intervals (2–3 sounds per second). When roaring the male has his tail lifted with the white hair erected and his head and nose stretched forward as in the nose-forward-posture. While snorting his mouth is closed, while bleating it is open. The display occurs in standing, walking, short canter or full gallop and in a wide range of situations, mainly in different forms of courtship and in chasing. Apparently it is the expression of *activated male dominance*. As in many similar cases in mammals and birds the actual communicative meaning or function depends on the whole situation, especially on the behaviour patterns which accompany the display and on the "recipient" of the display.

For instance, by means of the "roar" a female can be induced to stay with a male or a rival is stimulated to show a reaction ranging from flight to challenge.

- b. Roaring was observed in the following situations in the context of courtship:
1. A dominant male in trying to prevent a few females from joining the herd of another male rose on his hindlegs and alternately, stood roaring at irregular intervals. While roaring, he had his neck and nose stretched forward, the tail lifted and the penis half erected and oscillating sideways.
 2. For reasons unknown a female herd was split into two parts which were about to join up again. At this moment, the male who had been with one part of the herd, started roaring in the manner described above.
 3. In a similar case of a partly split female herd, the male left the main herd in order to shepherd the smaller group back. When he had brought it to about 30 yards from the main herd, he cantered into the centre of the latter and roared as described before.



Fig. 9. Rising on hindlegs. By a short canter the female often keeps her distance

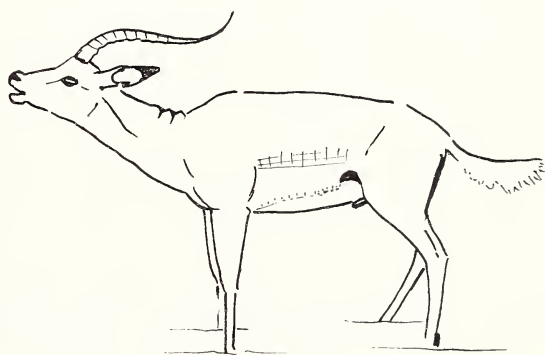


Fig. 10. The roaring display in the context of general courting

4. While a dominant male was chasing away a rival his female herd entered dense undergrowth and scattered. When returning near his herd, the male gave the bleating display (D 2. e.) moving along the edge of the higher vegetation. A few females joined the male, but the major part of the herd remained hidden. Suddenly the male entered the undergrowth and ran through it and the scattered herd in full gallop, repeating several times the roaring display, and then from all sides females came jumping out of the thicket and joined in normal herd formation.
5. On a few occasions an adult single male was observed roaring repeatedly. In one case several females of a nearby large breeding herd left their herd and its dominant male and joined the roaring lone male. He immediately started herding and general courtship behaviour, repeating his roaring display again and again.
6. Sometimes when a bachelor herd is near a female herd, the dominant male does not (as described earlier) chase away some of the weaker bachelors, but gets involved in a conflict with a strong rival, who only gradually retreats under the incessant threats of the dominant male. During this time one or more other bachelors may invade the female herd, roaring and following one female after another in a half courting half chasing manner.
- c. The roaring display combined with aggression is often exhibited by the dominant male while he is chasing females, male yearlings, weaker bachelors and even strong rivals (See E. 1).

4. Face-rubbing and horning

The behaviour patterns, which shall be described here, are not proper courtship activities, yet they are characteristic for male behaviour and are quite often produced by the dominant male. Therefore it is not unlikely that they influence, in a general indeterminate way, the response of the females to the male.

a. Male antelopes of many species with preorbital glands deposit their glandular secretions in their surroundings in a behaviour sequence typical for their species.

The dominant male impala rubs his face on a bush or shrub whilst moving his head up and down with a range of 10 to 20 cm. This however has no scent-marking function, since impala have no preorbital gland. In a quiet situation face-rubbing is not often performed, but when the dominant male returns from chasing a rival, he usually displays face-rubbing near his herd. The behaviour pattern has however no clearly defined place in the social contact of impala, nor is it part of a ritualised contact sequence. On rare occasions bachelors too were observed rubbing face in a perfectly peaceful situation and also without eliciting any response from a nearby impala.

b. Horning, i. e. pushing or beating of a tree, bush or shrub with horns or antlers, has a wide distribution in the families of Cervidae and Bovidae. In impala bush-horning and soil-horning occur in different social situations. The latter is an aggressive display and will be described later (E. 1).

When the male impala is pushing or beating branches of a bush or of a small tree with his horns repeatedly, the butting movements are often synchronised with the rebounding of the branches or the tree, so that the performance reminds one of that of a boxer exercising on a punching ball.

This behaviour pattern is identical in dominant males and in bachelors. A response to it from another impala was never observed and its social significance seems to be even smaller than that of face-rubbing.

Subadult bachelors were seen face-rubbing and then changing to tree-horning; especially in this combination it made the impression of a playful individual exercise. Yet it is sometimes performed by the dominant male near his females in the same context as face-rubbing.

E. Competition and fighting

1. Occurrence of social conflict in impala

a. By far the most of the social conflicts in impala arise *between males* striving for the possession of a female herd. In other words they occur between a dominant male and a bachelor or between two dominant males. All observations of conflicts with a different motivation will be summarised here briefly.

b. Aggressiveness *between females* was observed only in the following situations:

1. In a few occasions a fully grown female while moving or grazing in close association with others was seen to walk against a smaller female performing a symbolic biting attack with head stretched forward and lowered ears. The attacked animal always moved out of the way before being actually touched. In a few instances the attacking females was leading a lamb, a fact that could perhaps explain her unusual intolerance. In other cases competition over a special food plant may have been involved.

2. In an open grass plain (Forest Area, Nairobi National Park) a small female herd of twelve animals without dominant male was seen moving in single file through the grass. When the leading female stopped to feed all the other animals closed up to feed at the same spot. Soon competition arose: some of the fully grown females attacked weaker animals. The attack consisted of a sudden rush and a push with the front in the direction of the flanks of the weaker individual; this one gave way for a moment, but tried to come back to the feeding place from another side.

c. Conflicts *between bachelors* are not frequent and either of very short duration representing a casual type rather similar to female conflicts, or they belong to the context of the striving for dominance but lack some of the elements seen in dominant males.

1. When walking or feeding near each other one bachelor can be seen to threaten another by walking in his direction with a nodding of the head similar to that of a herding male. In all observed cases the threatened animal gave way.



Fig. 11. Fighting excitement amongst bachelors. The superior male is facing away



Fig. 12. The superior male horns the soil, while the inferior withdraws ready for defense

2. Showing off, with competition in different degrees, was observed amongst bachelors on only few occasions, and then in one of the following four situations:
 - A female joined up with a bachelor herd (See B. 3.) provoking competition among the bachelors followed by courtship of the one who managed to chase the others away (observed three times).
 - A bachelor "A" was chased by a dominant male; when the latter returned to his herd, another bachelor "B" took up the chase of "A" on his account. This one escaped by a more or less circular route passing near the dominant male and then ran off, whilst "B" slowed down near the dominant male and was now threatened and eventually chased away by him (two observations).
 - Sometimes a sudden common excitement characterized by showing off can be observed in a bachelor herd. All the fully grown bachelors have the tails lifted, several rush at others who at once face them with lowered head, whereupon the "attackers" normally change direction. In most cases the showing off is apparently not addressed towards a peculiar individual. Yet sometimes two bachelors suddenly face each other (Fig. 11 and Fig. 12) and one of them starts to horn into the soil, an aggressive display which will be described later (E. 1). As suddenly as it has started the "showing off excitement" disappears again, the tails are lowered and the animals no longer face one another. A bachelor who has started to horn the soil may continue this for a moment longer with lowered tail and without an opponent to face. In one instance only was a fight observed between two bachelors who were probably on the way to competition for male dominance. The style of the fight did not differ from a fight in which a dominant male is involved (See E. 1.).
 - Near Ormanyi Dam (Nairobi National Park) a competition between two bachelors was observed on two consecutive days, in which one of the two bachelors would not tolerate the other one near the male herd. He compelled

him to retreat whenever he approached the herd, in the same manner as a dominant male would repel a bachelor from a female herd (See E. 3. b.). The final result of the competition was not observed.

All the above mentioned minor conflicts in the female herd and between bachelors give evidence of a social hierarchy within the herds, which however does not manifest itself very often.

2. The variations of conflict between male impala

a. The following discussion is confined to conflicts for dominance between a dominant male and a bachelor or between two dominant males. These conflicts show many variations. Some of the most obvious conditions determining the course and character of the conflict are:

- the proportional power of the two rivals,
- the level of aggressive motivation,
- the degree of inhibition, that is fear, competing with the aggressive tendency.

With these terms three important dimensions of the competitive situation are outlined; they are to some extent dependent on one another and they may change during the course of the conflict. In all the observed cases a male who had not yet acquired a female or females was inferior to a herd male. But in spite of their inferiority, and though they were chased by the herd owner, some bachelors tried again and again, sometimes for days, to approach a female herd. As soon as a so-far bachelor succeeded in herding a female he appeared much more self confident and sometimes became an equal rival to the dominant male.

b. The following diagrammatic presentation is an attempt to show the main types of conflict in male impala as determined by the varying factors mentioned above. Though this presentation does not consider nuances, it makes possible a certain order in the description of the most frequent observations.

1. In the case of *conflicts between unequal rivals*, the situation is theoretically very complicated, the various factors participating in different proportions in the two animals. In practice the level of aggressiveness of the superior and the degree of inhibition of the inferior have to be considered.
2. *Conflict between equal rivals* are characterized by their "symmetric" aspect. In the course of sequences of reciprocal threatening and fighting sooner or later one

Table I

Diagram presenting the main variations of conflicts between unequal rivals

		Level of Aggressiveness of the superior male (= sm)	
		low	high
Degree of inhibition of the inferior male (= im)	low	sm compels im to retreat by repeating attack intention movements from a close distance. In stepping backwards im presents his horns in defence to sm's threats.	sm shows a long and aggressive display of proud posture, lateral showing off, volte jumps, horn shaking, soil horning and finally attacks im. im reacts with flight and is chased by sm.
	high	sm walks to im and chases him over a short distance, stopping after a final rush with an "empty" push of his horns.	sm chases im in full speed as soon as the latter approaches the female herd; the chase continues over a comparatively long distance.

Table II

Diagram of conflicts between equal rivals

		Level of Aggressiveness	
		low	high
Degree of inhibition	low	Static phases with showing off at distance. Dynamic threatening and displacement movements hardly occur. Animals soon turn away.	Momentarily prevailing aggressiveness results in sudden vehement clashes, long lasting overwhelming aggressiveness in long intense fighting.
	high	No conflict occurs.	Static phases predominant, rivals threaten incessantly without attacking the opponent. They are on their guard. Frequent displacement movements (yawning, licking etc.) as outlets of tension.

of the rivals may collapse. The conflict thus loses its symmetry while a dominance of one of the males is established. In Table II. only those types of conflict are included which show "symmetry".

A more detailed description of conflicts in male impala will follow under E. 3. and E. 4.

3. Scenes of conflict between unequal rivals

Subsequently four conflict scenes representing the four main types of Table I. will be described.

a. Low aggressiveness of the dominant male // rival (bachelor) considerably inferior: "short rusk with empty horn-push".

A more detailed description of conflicts in male impala will follow under E. 3. bachelor herd away. Sometimes he stood motionless in the "proud posture" between his females and the bachelor herd (See D. 1.): every now and then he walked towards a bachelor, stopped in a distance of 7 to 10 yards from him and again adopted the "proud posture" (Fig. 13). Suddenly he attacked and chased the bachelor over a short distance. The climax of the chase was a spurt with horns pointing forward followed by a push upwards (empty horn-push). He then slowed down and stopped.

b. Low aggressiveness of superior male // rival only slightly inferior: "compelling move" (this situation may occur between a dominant male and a bachelor or — less frequently — between two dominant males). In one case the animals faced each other at close distance. After some circling one of the males suddenly lowered his horns forward causing the rival to adopt a similar posture in defence. The latter, slightly inferior, soon tended to withdraw by stepping backwards, while the superior constantly follo-

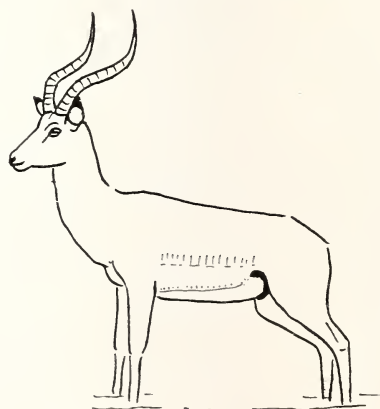


Fig. 13. „Proud posture“

wed, thus keeping the initiative, and adopted the above mentioned attack posture again and again. The two males moved over 100 yards away from the female herd owned by the superior male. The "compelling move" normally ends in one of the following ways:

- The superior male stops menacing and turns back to his herd, or
- In a moment of lower pressure by the superior male the inferior turns and runs away over a short distance, while the superior stops and looks at him and then turns back to his herd.

c. High aggressiveness of superior male // rival considerably inferior: "long chase with roaring".

In the Forest Area of Nairobi National Park a dominant male stood in "proud posture" near his female herd, obviously at full attention in a definite direction. There, between bushes, a bachelor appeared, stopped and looked intently in the direction of the herd and the herd male. Suddenly the latter started a chase at full speed with his tail lifted, uttering repeatedly the sharp short snort and less frequently the full roaring sequence. The weakening of the sounds indicated that the chase was leading over more than 100 yards away from the herd. Later the herd male appeared again and turned his head in the direction from which he had just come. He then approached the herd and rubbed his face against a bush. After watching and listening again in the direction from which the bachelor had appeared, he entered the herd and displayed the nose forward posture with empty licking in the direction of one female after another. Observations of similar chasing scenes which occurred in open country, revealed that a long chase often ended with a terminal rush and an empty horn push. After the chase the dominant male usually returns to his herd in a slow canter or even at a fairly speedy gallop. He may stop near his herd showing face rubbing or bush horning, or he may immediately enter the herd complex performing the nose forward posture or – less frequently – the roaring display with courting character. Though the dominant male demonstrates his superiority during these encounters, it is the bachelor who is initiative. Indeed, he often tries to approach the female herd again as soon as the dominant male has returned; therefore the chasing scene may be repeated many times and over several days. It should be mentioned here, that the chasing with roaring is much the same if the herd male is pursuing a female, a male yearling or a rival, with the exception that in the first case the hornpush is not performed.

d. High aggressiveness of the superior male // rival only slightly inferior: "volte-jump display", horn-shaking, soil-horning and chasing.

In the open plain at the foot of the Forest Area of the Nairobi National Park a male impala was herding some 30 females. Two other males approached the herd from the side opposite to the herd male. When he walked around his herd in their direction they at first did not move, then one of them turned and slowly walked away. The herd male approached the remaining one who still stood motionless. When about five yards from him he stopped and both males stood in front of each other in "proud posture" turning their heads somewhat to the side. Now – nearly simultaneously – both males turned in the same direction and walking slowly presented their sides to each other. After these more static phases of showing off the herd male produced a more dynamic display performing volte-jumps with his tail lifted and with lowered horns. Then he shook his horns in the horizontal position from side to side (*Fig. 6*) horned the soil (*Fig. 12*), pulling off heaps of grass and all at once he rushed towards the other male, who immediately turned and ran off and was chased by the herd male over approximately 60 yards. During the pursuit the dominant male had his tail lifted. As stated earlier horn-shaking and soil-horning are not performed by dominant males only. They were also observed amongst bachelors (See E. 1. c. 2.) but then did not lead to a chase, that is to assert a superiority-inferiority relationship.

4. Scenes of conflict between equal rivals

In open country as for instance in the Kipleleo area or in the Somali Ridge and Athi River Basin of the Nairobi National Park, where the local females sometimes join in a larger herd complex and sometimes split up in smaller social groups there is a chance for a small number of powerful males to acquire temporarily the position of a herd male. But as soon as the smaller groups of females tend to gather these males get into competition, unless they give up their herd male position for the time being. In fact they usually avoid conflict and therefore the larger herd complexes are quite often not herded, especially not during the night. So in the morning such larger herds contain males and females more or less mixed. In the Forest Area of the Nairobi National Park on the other hand, the female herds are smaller and more neatly separated from each other. It was however in this region where conflicts between equal rivals were observed. As was stated earlier (See E. 3. b.) under these circumstances a bachelor sometimes persistently tries to acquire females and may succeed in herding a mother with a small calf and perhaps a yearling, or a small group of mothers who had separated temporarily from their herd. As soon as he is "owner" of a few females he behaves self-confidently as any other dominant male. Since the social bond between his small female group and the main female herd, which was interrupted during parturition, will regain efficacy, some females of the main herd will tend to join with the individuals of the split-off group and vice versa. This situation invariably invokes conflict between the males.

In Table II only three different situations are mentioned. The level of aggressive motivation mainly depends on the distance between the two males, being low only when they are not near each other. But in this case it seems impossible to state different degrees of inhibition. The following three cases will illustrate the three situations considered in Table II.

a. Low level of aggressive motivation: static phases with showing off at distance.

Between Ormanyi Dam and Somali Ridge a male was herding and courting some 30 females. The leading females moved towards a slight elevation where the view opened into the valley. When they reached this spot they watched intensely with ears erected towards another female herd some 400 yards away. The dominant male who had followed the herd movement at the rear joined the leading females and eventually adopted "proud posture" (Fig. 13) in front of his herd facing the distant herd. There the dominant male behaved in a similar way and both males kept their position in front of their respective herds.

b. High level of aggressive motivation // high degree of inhibition: threat behaviour, displacement movements.

In the Forest Area of Nairobi National Park two males exerted themselves over several months to herd on their own account females who had previously formed one herd. Again and again the two parts of the herd tended to join and in fact individual females often moved from one part to the other despite the intervention of the respective herd male. The male who was just losing females in trying to chase them back ventured near the females of the rival and was immediately challenged by him.

In one case male "A" was chasing two females who tried to join the herd of the neighbour when male "B" galloped against him. "A" changed direction and in slowing down the two males met approximately halfway between the two herds. During the following encounter they sometimes stood in "proud posture" with heads turned sideways (Fig. 11), then they walked in a restless, "nervous" manner circling each other, often changing direction in circling. Sometimes one male suddenly faced the opponent with a minute downwards-movement of his horns, the very beginning of an attack, which was immediately parried by a corresponding preparation from the other male.

The scene revealed high tension, a permanent readiness to attack and to parry an attack as well as an inhibition to carry out an attack when the opponent was ready to counter it. The conflicting tendencies of attack and inhibition resulted also in displacement movements: both rivals showed empty licking and, frequently interrupting these movements, a hasty yawning with horns lowered backwards. It may be mentioned here that empty chewing or biting and especially yawning occur in many mammals as displacement movements in social conflict, whereas empty licking seems to be quite peculiar to impala.

In one case the observer happened suddenly to come upon the two males mentioned above. Though he was within ten yards of both rivals they did not leave the spot. Suddenly "A" whilst facing away from "B" in "proud posture" uttered the alarm snort, whereupon "B" stopped his circling. He just started to move in the direction of his females when "A" suddenly rushed vigorously towards him. "B" turned and both males clashed at once with their horns producing a loud cracking noise. This observation proves the high level of tension: a little disturbance of the equilibrium by an external influence can cause vehement aggression. Encounters of the equilibrated type normally last less than a minute and are finished while both rivals separate to join their females.

c. The preceding chapter has set forth that in a situation of tense competition a little disturbance of the equilibrium can release a sudden unrestrained attack. This means that a momentary inferiority of one rival can cause the aggressiveness of the opponent to prevail over his own inhibition. Yet on rare occasions the aggressiveness excels the inhibition in both partners simultaneously without any inferiority on one side and a real fight will arise. This was observed four times during this study. Two main phases of fight were noted:

1. violent clashes when both rivals rushed against each other,
2. continuous twisting and pushing with interlocked horns.

Both phases alternate in a lasting fight. A clash may be followed by twisting and pushing. After this phase the fighter sometimes separate for a moment to rush again at each other with fresh violence.

Only in one case could the natural end of such a fight be observed: after about 6 minutes of twisting and pushing alternately with violent rushes, one of the males reacted more and more in defence only to the attacks of the opponent. Eventually he ran off and was chased by the victorious rival. In another case park visitors disturbed the fighting males and both ran off and joined their respective herds. In two more cases the end of the fight, which had lasted more than 20 minutes, could not be observed for external reasons.

Fighting can cause serious injuries (See A. 5.) especially if a male succeeds in surprising his opponent with a rushing attack thus eliminating his defense.

DAVID SHELDRIK (Game Warden, Tsavo National Park East) reported an incident, in which a sudden rush resulted in breaking the foreleg of the surprised rival. It was mentioned earlier (A. 5) that some males with broken horns have been observed in the Nairobi National Park. Four of these were seen alone, apparently not taking part in further competition. On one occasion a male with a bleeding horn stump was observed in the Forest Area (Nairobi National Park). He walked alternately roaring and listening and gave the impression of being in search of a female herd. Another male often seen at the escarpment of the forest area near the first Somali Boma, could maintain dominance over a female herd after having lost one horn. He was observed herding some 40 females and chasing rivals successfully for more than two months.

F. Mating behaviour

Mating was seen only five times, and in all these cases it was impossible to observe the development of the mating bond continuously. Some sequences of the premating behaviour were observed many more times, but either they were discontinued or the observation could not be carried out until copulation occurred. Therefore the following statements have preliminary character. The data so far collected allow a general outline of mating behaviour in impala, but they do not permit statements as to the possibilities of variation in the precopulatory behaviour sequences.

1. The first premating phase: courting approach followed by chasing

Quite frequently a dominant male who is very active in herding and general courting, suddenly concentrates his activities on one female of his herd. He stands about 10 to 15 yards behind the feeding female, constantly watching her. Sometimes, when the female walks slowly he follows maintaining the distance. Out of this watching phase the male can suddenly start to chase the female. But this chasing differs from chasing in the context of herding in the following points:

- The male does not roar while chasing the female.
- At the very beginning of the chase the male often shows nose forward posture with empty licking (compare with *Fig. 7*), but these behaviour patterns disappear after the first steps, i. e. as soon as the female moves off.
- After the male has chased the female over 50 to 150 yards, both slow down and stop simultaneously.
- Then the female slowly walks back to the herd, sometimes feeding on the way, while the male follows again maintaining the distance.

Watching phase, chasing and walking back to the herd can be repeated many times. Quite often the premating contact is discontinued as the male too begins to feed.

2. The second premating phase: courting approach followed by genital licking

The change in the status of the female is characterised by her increasing tolerance of the male's courting approach. When the male, after watching her from a distance of five to ten yards, suddenly steps towards her with nose forward posture and empty licking, the female no longer runs away. The male correspondingly does not chase her, but maintains his posture and when he has reached her from behind he licks in a quick sequence of tongue strokes her genital region. The female first remains motionless, then walks some steps away, while he remains in the same place now in a normal posture. After the elapse of a minute he suddenly adopts nose forward posture again and the scene is repeated. At this stage of premating behaviour the distance between male and female during the phase of inactivity is reduced more and more, as the female's reaction of walking away from the male gets weaker. But it was often observed that after some time of premating activity, the intensity decreased and the premating contact was interrupted. It may be mentioned here that during the premating the male reacts with smelling and "Flehmen" whenever the female urinates, but this type of contact has no fixed place in the premating behaviour.

3. The third premating phase: mounting without copulation

At this stage of premating behaviour the distance between male and female has virtually disappeared. On sudden impulse the male now shows genital licking followed immediately by rising on his hindlegs. The female then walks forward and the male

follows for some steps on his hindlegs before dropping to his forelegs. In two cases the male hardly touched the female in precopulatory mounting. In others the male showed a regularly repeated vertical movement of the tail, and then mounted the female. While she walked away, he leaned on her rump and tried to keep pace. In most cases the male showed erection while mounting, but it was not possible to clarify this point generally.

4. Copulation and postcopulatory behaviour

Copulation was observed four times after precopulatory mounting had taken place repeatedly. In one other case a herd was observed while watering. When leaving the water the male showed precopulatory mounting once only, and when the normal time interval between two mountings had elapsed copulation followed. Presumably in this case watering had interrupted the premating behaviour.

In copulation the male does not lean on the female's croup, nor does he hold her loins with his forelegs. He rises onto his hindlegs and while the female steps forward he rushes forward bipedally to execute intromission, which does not last longer than one second. While the female still steps forward, the male first drops with his breast on the female's rump, then to his forelegs. After copulation the male shows an outburst of aggressiveness. Snorting and roaring and with his tail lifted, he suddenly chases another female or a young male for a short distance. Then he rejoins the herd and begins to feed.

5. Some remarks on functional aspects of the mating behaviour in impala

The characteristics of mating behaviour in impala have to be considered in connection with the social way of life proper to the species:

- There is no rutting season.
- Dominant males permanently herd a group of females and defend its possession.
- They live in a restricted home range, but do not defend a territory.

This implies that aggressiveness and competition between males is a permanent element in the social life of impala and not, as in many other antelopes connected with mating behaviour. The same is true of courting, herding and chasing, as activities of the male by which he exerts "erotic attraction" for and dominance over a female herd. Therefore the premating behaviour is comparatively poor in behaviour elements as well as in function. It leads to tolerance of the male's approach by the female near oestrus, of his genital licking and eventually of copulation itself, and to accurate sexual coordination.

G. Notes on the mother-child bond

A short outline is only intended here. In previous chapters some characteristics of the mother-child relationship have been mentioned repeatedly. Unfortunately no birth was observed and it was so far not possible to obtain enough accurate data to present a complete description of the development of the mother-child bond.

The mother gives birth in isolation, presumably in the cover of a bush thicket. Very small lambs were observed only in dense undergrowth. Unlike the newborn of plain-dwelling antelopes, but similar to members of the deer family who live in bush or forest, the young impala does not follow its mother within a few hours (as in wildebeeste) or days (as in hartebeeste and gazelles) after parturition. For quite a number of days and during many hours each day the child is hidden in undergrowth, while the mother remains vigilant in the vicinity.

Later the lamb moves more and more frequently around its mother, but during this period the synchronization of movement which appears between mother and child in many ungulates of the open grassland was not observed in impala. Presumably during this phase the child "disappears" in case of danger and does not follow its mother. This is the time when the mothers with lambs tend to join together in isolated nursing groups. The next phase is the integration into the breeding herd. The timing of these different phases shows many variations. Once two mothers have been observed to leave their lambs unconcealed in undergrowth while they joined a rather incoherent female herd without herd male. Several times mothers with small lambs have been seen moving in a breeding herd. Towards the evening they left the herd and formed a nursery group of their own, while the greater part of the herd was grazing approximately 150 yards away. In one case a group of five mothers with lambs did not join a herd at all, but kept on living as an independant group in the neighbourhood of a breeding and of a bachelor herd. Groups of 8 to 12 females, adult and subadult, which were observed in Nairobi National Park and in Kipleleo may be the result of such mother-child groups which maintained their independance.

It is however normal, that mothers rejoin the breeding herds with their lambs. Here the mothers as well as the lambs are inclined to form temporary subgroups especially in relaxed situation.

The behaviour patterns characterising the communication between mother and child do not differ greatly from those in other bovidae. The mother does not seem to call the lamb for suckling, but often the lamb was observed to join its mother and then to push her udder with its nose. As in many other bovidae the lamb during drinking wags its tail vigorously while the mother bends her head down to smell the lamb's perineal region. TSCHANZ (1962) has shown that in the moufflon the mother recognises her lamb's individual scent during this contact scene. Generally it may be stated, that in impala the mother-child communication is very silent.

Discussion

In a comparative discussion of the sociology and behaviour of bovidae the following characteristics of impala should be emphasised:

1. Those features of behaviour which aim at avoidance of predators are adapted to a habitat offering cover possibilities for predators as well as for the prey animals: shrub, bush, undergrowth in light forest. This applies to techniques used for the detection of predators and to alarm and flight patterns as well as to special features of the mother-child-bond in the first weeks after birth.
2. The relationship of the sexes is characterised by the constant effort of the strongest males to possess and tend a female herd. One has therefore to distinguish between herding and general courting of the male on one side and premating behaviour on the other. In defending the possession of a female herd and in shepherding and courting his females, the dominant male creates a monopolized relationship to his herd. The premating behaviour has in addition only to induce the individual female in estrus to tolerate the sexual initiative and approach of the male and to synchronise the readiness to copulate.

This sociological background is reflected in the features of general courting and premating behaviour.

The nose forward posture with licking appears in two variations:

- in the general courting behaviour the licking is only an "empty" gesture,
- in premating empty licking changes into genital licking.

In ungulates generally licking, nose pushing and nuzzling seem to be vicarious. These activities are in a few cases directed towards the nose, more frequently towards the inguinal region and very often towards the genital opening. The nose pushing and the orientation towards the inguinal region indicate an original relationship to suckling. In many ungulates in which licking or nuzzling by the male is directed towards the vulva of the female, these activities adopt the function of "Harnfordern" i. e. they stimulate the female to urinate. They are then followed by a chemoreceptory testing of the urine known as "Flehmen" (SCHNEIDER 1930—1934). This sequence functions as testing the status of the female and it occurs regularly when a bull meets a female or a group of females.

In impala where the dominant male and the females live in close contact, this testing behaviour is apparently superfluous. Correspondingly in general courting the male does not touch the vulva of the female, neither in the nose forward posture nor when addressing a lying female. Genital licking or sniffing are symbolised, and the sequence of urination by the female and Flehmen by the male plays neither an important nor a clearly defined role. It is only in the premating contact that empty licking develops into genital licking and that urination by the female regularly releases Flehmen by the male.

These considerations apply also to rising on hindlegs: it appears in the form of precopulatory mounting and copulation itself in mating behaviour on one hand, and in a symbolised form, with the female in front of the male in several yards distance, in general courting.

It may be mentioned here, that copulation intention movements and precopulatory mounting are common in the premating behaviour of bovidae. Symbolised mounting, on the contrary, is rare, e. g. it is part of the courting display of the bull wildebeest in rut and occurs occasionally in contact scenes between bachelors of the kongoni.

3. The rivalry between the males aims at the possession of a female herd. Only the strongest males actively participate in the competition, only they are intolerant towards the other males.

Male herds are not only formed seasonally, they persist throughout the year as aggregations of inferior males. The intolerance in dominant males and their rivals also is not restricted to a certain phase of the year, nor is it bound to a territory.

These facts are reflected in the features of encounter between rival males. In many ungulates which defend a home range or a mating territory a number of activities result in setting or maintaining "marks". Pawing, front rubbing, horning, wallowing, urination and defecation are often components of the marking behaviour by the male. In some species front or head rubbing has developed into a highly efficient marking by means of scent glands. In the above mentioned activities the function of marking is predominant when the animal is on its own. When a rival male is near, they often adopt the character of showing off or threatening.

In impala there is no territorial intolerance. In correspondence there is no pawing and wallowing. Bush horning, front rubbing, urination and defecation have no marking function and are very poorly ritualised. Apparently they also do not occur as showing off or threatening behaviour in encounters between males. These functions are fulfilled by other behaviour patterns as e. g. proud posture, lateral showing off, volte jumping, horn shaking, soil horning, butting intention movement, chasing with empty horn push.

Summary

- A. The ecological position of impala, their habitat, association with other herbivores and the relation to predators are outlined.
 - B. The most important types of group formation — female herd with dominant male and bachelor herd — and the factors determining the dynamic aspect of these formations are discussed and the coordination of the activity of the herd and the daily activity rhythm described.
 - C. Daily activities are characterized as such and in relation to the social situation.
 - D. The relationship between the dominant male and the female herd are analysed more closely. The herding activity of the male and the six main forms of his general courtship are described. Another behaviour pattern of the dominant male occurs in the context of courting and as showing off and threat display in male rivalry.
 - E. Social conflict amongst females and amongst bachelors is of short duration and suggests the existence of a hierarchy system within the herds. Severe encounters and fighting only occur between top males and exclusively over the possession of a female herd. The different forms of fights and encounters are explained on the basis of the proportion of aggressiveness and inhibition of the rivals.
 - F. Herding and general courting of the dominant male have to be distinguished from mating behaviour. Premating behaviour and copulation are described.
 - G. The development of the mother-child-bond is outlined in a preliminary form.
- The special features of impala sociology are discussed in view of comparative studies of behaviour in bovidae.

Zusammenfassung

Die Arbeit vermittelt einen Überblick über die Lebensweise der Impala.

- A. Die ökologische Stellung der Art wird skizziert, sowie ihr Biotop, ihre Vergesellschaftung mit andern Pflanzenfressern und ihre Feinde.

- B. Die wichtigsten Möglichkeiten der Gruppenbildung — Weibchenherde mit dominantem Bock, „Junggesellenherde“ — werden beschrieben. Die Faktoren, die in der Gruppenbildung und ihrer Dynamik wirksam sind, werden analysiert. Ferner werden Stimmungsübertragung und Führungsfunktion sowie der tägliche Aktivitätsrhythmus im Herdenverband diskutiert.
 - C. Die Verhaltensweisen des täglichen Lebens, — Fressen, Ruhen, Wiederkäuen, Wasser- und Salzaufnahme, Harn- und Kotabgabe, Komfortverhalten, Feindvermeidung, Spielen — werden in ihrem Einzelablauf und in ihrem Auftreten im Sozialverband charakterisiert.
 - D. Die Beziehung zwischen dem dominanten Bock und seiner Weibchenherde wird näher untersucht, insbesondere wird beschrieben, wie der Bock die Weibchen hütet und wie er sie — auch außerhalb der vagen Brunftperioden — umwirbt. Sechs Formelemente dieses allgemeinen Werbeverhaltens werden beschrieben. Der dominante Impalabock verfügt außerdem über eine besondere Form des imponierenden Auftretens, das sowohl an die Weibchenherde als auch an die Rivalen adressiert wird.
 - E. Sozialer Konflikt unter Weibchen sowie unter „Junggesellen“ ist kaum je heftig oder von Dauer. Meist handelt es sich um eine Art „Zurechtweisung“, von der auf das Bestehen einer weitgehend geklärten sozialen Rangordnung geschlossen werden kann. Zu heftigen Auftritten und Kämpfen kommt es nur unter starken Böcken, und dabei geht es immer um die soziale Spitzenstellung, d. h. um den „Besitz“ einer Weibchenherde. Die wichtigsten Formen der Auseinandersetzung entsprechen dem Verhältnis der sozialen Potenzen der Rivalen und vor allem ihrer Aggressivität bzw. Gehemtheit.
 - F. Vom Hüten und allgemeinen Werben des dominanten Bockes ist das Paarungsverhalten zu unterscheiden. Drei Stufen der Paarungseinleitung lassen sich auseinanderhalten; diese führen kaum je im geschlossenen Zuge zur Paarung, vielmehr bilden Unterbrüche die Regel. Nach der Kopulation, die wie bei den meisten Horntieren nur sehr kurz dauert, zeigt der Bock einen Ausbruch von Aggressivität gegenüber irgendeinem nicht beteiligten Herdenmitglied.
 - G. Die Entwicklung der Mutter-Kind-Beziehung wird nur in kurzer und vorläufiger Weise dargestellt. Von den Huftieren der offenen Steppe, deren Junge schon nach wenigen Stunden oder doch Tagen der Mutter folgen, unterscheiden sich die Impala in der für Bewohner von Wald und Busch charakteristischen Weise: Die kleinen Jungen werden tagsüber von der Mutter oft alleingelassen und legen sich in einem Dickicht gedeckt nieder. Einige Mütter mit kleinen Jungen schließen sich gerne zu Müttergruppen zusammen, und auch nach dem Wiederanschluß an die Weibchenherde können Mütter und auch gleichaltrige Lämmer oft als temporäre Untergruppen beobachtet werden.
- In der Diskussion werden die soziologischen Besonderheiten der Impala im Hinblick auf vergleichende Verhaltensstudien an Boviden zusammenfassend beleuchtet.

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Beobachtungen zur Soziologie des Löwen in der Serengeti-Steppe Ostafrikas

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Obwohl die Ethologie oder Verhaltensforschung an Tieren in den letzten Jahrzehnten besonders in Deutschland große Fortschritte erzielt hat, sind tiersoziologische Fragen von ihr kaum berührt worden. Der Grund zu dieser Vernachlässigung ist in technischen Schwierigkeiten zu suchen. Bei einem in Gefangenschaft gehaltenen Tier muß man sich auf die Analyse seiner Bewegungen beschränken und kann dann höchstens Vermutungen über das natürliche Zusammenleben mehrerer Individuen anstellen; das gilt besonders für das Studium an Säugern. Genaues über deren Sozialstrukturen erfährt man nur in Freilandstudien; diese aber erfordern einen bislang noch unverhältnismäßig großen Aufwand.

Durch den wirtschaftlichen Kontakt mit Entwicklungsländern sind wir heute in der Lage, unsere wissenschaftlichen Fühler in Gebiete auszustrecken, die dem Biologen für seine Forschung geradezu als ein Eldorado erscheinen. Für den Zoologen und speziell Großsäugersoziologen kommen besonders die Nationalparks Ostafrikas in Frage. Hier kann man wirklich intensivste Forschung noch ökonomisch betreiben. Es ist viel kostspieliger, den Biotop für eine vom soziologischen Gesichtspunkt aus interessante Tiergruppe, wie z. B. der Carnivoren, in Gefangenschaft auch nur annähernd nachzuahmen, als dorthin zu fahren und zu beobachten, wo diese Tiere frei herumlaufen. In einzigartiger Weise haben uns amerikanische Anthropologen und Biologen (WASHBURN and DE VORE 1961, SCHALLER 1963) einen Weg der Freilandforschung an Primaten gewiesen. Anliegen dieser Arbeit ist es, zu zeigen, unter welchen technischen Voraussetzungen man Raub- und Huftiersozietäten in ihrer normalen Umwelt, der Steppe, beobachten kann.

Ein besonders günstiges Arbeitsgebiet ist die Serengetisteppe des gleichnamigen Nationalparks in Ostafrika. Ihr mit höchstens knietiefem Gras bewachsener Boden ist auf viele Kilometer so eben, daß man mit einem Geländewagen in kurzer Zeit weite Strecken durchfahren kann, wobei man einen Überblick über mehrere hundert Quadratkilometer gewinnt. In dieser Ebene stehen von November bis März riesige Herden Gnuantilopen, Zebras, Thomson- und Grantgazellen. Kein Tag vergeht, an dem man nicht wenigstens einmal Löwen am Riß antrifft. Besonders gut sind hier Tagjäger wie der Gepard oder der Hyänenhund zu beobachten.

Die Untersuchungstechnik bestand darin, von einem stehenden Geländefahrzeug (Land-rover) aus viele Stunden zu beobachten. Man sitzt hinten auf der Pritsche unter der aufgerollten Plane trocken und schattig, ringsum von einem Gitteraufbau geschützt (Abb. 1) und hat alle technischen Hilfsmittel, wie Photoapparate, Filmkamera und Tonband bereit. Matratze, Schlafsack, Benzinkocher, Wasserkännister und Lebensmittel machen einen für viele Tage unabhängigen vom Lager; notfalls schafft ein Sprechfunkgerät eine schnelle Nachrichtenverbindung.

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