SOCIAL ORGANISATION AND MOVEMENTS OF TOPI *(DAMALISCUS KORRIGUM)* DURING THE RUT, AT ISHASHA, QUEEN ELIZABETH PARK, UGANDA

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ABSTRACT

Topi, on which there have been few previous studies, were investigated in order to understand the manner in which they use open grassland and to provide data for comparison with other Alcelaphines. The mobile mode of existence of topi at Ishasha provided a special interest. About 4 000 topi were using the 80 km ^{2} of savanna. They comprised a single congregation and individuals grazed in all parts of the range as members of moving and changing aggregations that split and amalgamated freely. All females, accompanied by 6-month-old calves were organized into a mosaic of 'harem' groups, each tended by a herdmaster bull. These groups were temporary and females were constantly escaping from one bull's sphere of influence or 'ward' to join another. The bulls maintained a network of wards and displayed antagonistically towards one another. They also excluded other males which formed loose arrays at the periphery of the aggregations. Where herdmaster bulls had lost all females from their wards they dropped their status for a while and joined peripheral males. Age at puberty, and the activities of the several age-classes of topi are described.

The topi *Damaliscus korrigum* (Ogilby) is a conspicuous and common inhabitant of the savannas of East Africa and the genus has a widespread distribution in Africa south of the Sahara (Sidney 1965). In Uganda topi occur in two separate areas, in the east and in the south west, and the species has a wide but discontinuous distribution in the neighbouring countries of Kenya (Stewart & Stewart 1963) and Tanzania (Stewart & Talbot 1962). No intensive study of the species has been made, although they have been included in several studies of the grazing activities of herbivores (Talbot 1962; Field 1968; Bell 1970; Vezey-Fitzgerald 1960). The Damaliscus or bastard hartebeests (the topi and its allies), the hartebeests, and the wildebeests comprise a distinctive tribe of African bovids, the Alcelaphini, and much recent work has been concentrated on the blue wildebeest *Connochaetes taurinus* (Talbot & Talbot 1963; Watson 1969; Estes 1969) and Coke's hartebeest *Alcelaphus buselaphus* (Gosling 1969). It is of particular value, therefore, to gain new information on the topi to compare with these related species.

My observations were made on the topi herds in the Queen Elizabeth Park in south western Uganda. Topi occur only in the southern part of the Park and the major congregation exploits the open grasslands at Ishasha. They range over a well-defined area of 80 km^2, that is bordered by the Ishasha river in the west and by a small escarpment in the east, parallel to and near the road to the Congo (Fig. 1). To the north east the area is closed off by the Ntungu river, but topi occur again beyond this river system on the grasslands at Kikyere.

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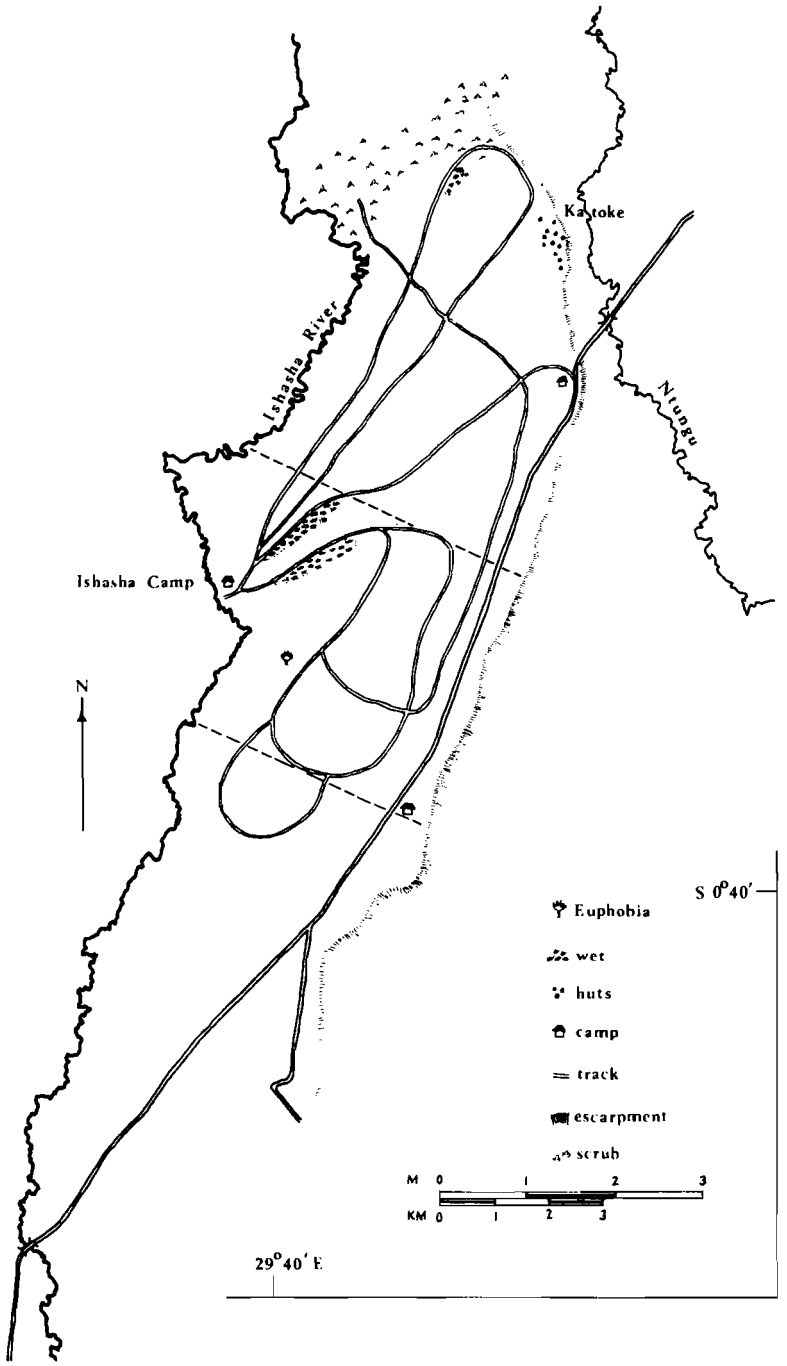


Topi are noted for the large herds into which they sometimes congregate and those at Ishasha are no exception. I have not been able to find, however, past counts of the numbers present. In 1958 Sidney (1965) saw "herds numbering 300; 400; 700 and 1 000": these were separate aggregations counted on June 6th and 7th (Sidney, in litt.). In 1961 there was a serious outbreak of disease among the topi herds, thought to be 'bluetongue'. The effects of this epidemic on numbers is not known but when I visited the area in September 1962 I noted large herds with abundant calves at foot (Jewell 1963). No recurrence of disease has been reported.

Topi have a well marked calving season in the months of July to September and this is likely to be related to the rains (see discussion in Gosling, 1969). As a consequence the population is comprised of well-defined annual cohorts and some of these can be recognised in the field as distinct age-classes. The gestation period is about 7½ to 8 months (Asdell 1964), and in the conspecific tsessebe has been recorded in two individual females as 235 and 241 days (Huntley 1971). My period of study coincided with the main period of the rut.

THE STUDY AREA

A brief description of the Ishasha grasslands is given in Field and Laws (1970) as it contained their study area 10. Rowell (1966) describes the area more fully (but particularly in relation to its exploitation by baboons) and gives rainfall records at Ishasha camp through two years. Much information on the vegetation of the area was given to me by Dr. J.M. Lock and I was able to study the vegetation map prepared by him at the Nuffield Unit of Tropical Animal Ecology.

The Ishasha grasslands are almost on the equator, lying between 0°33′ and 0°43′S, and are 29°40′E (Fig. 1). A little rain usually falls in every month but there are two wet seasons in April and in September/November respectively. During my period of study it was generally dry and rain was not noticeable until the end of February. Total rainfall at Ishasha Camp for January, February and March 1970 was 60 mm, 47 mm and 87 mm respectively (NUTAE, Seventh Annual Report, duplicated).

The grasslands comprise a mosaic of short grass communities with scattered fig trees and one of these communities in particular is characterised by Lock as *Themeda triandra/Acacia sieberiana/Ficus gnaphalocarpa* savanna. Other important communities in the area are *Themeda triandra* grassland with *Brachiaria platynota; Sporobolus pyramidalis/Maerus edulis* grassland with dwarf shrubs; and small but abundant patches of *Cyanotis lanata* "succulent steppe"; whilst of secondary importance are areas of seasonally waterlogged *Eragrostis heteromera/Eragrostis exasperata* grassland and *Diospyros abyssinica/Eucles* sp. */Tarenna graveolans* dry thicket.

The grasslands are surrounded on all sides by other types of vegetation. Gallery forest lines the Ishasha river and is fringed by dense thickets; thick scrub, in which *Capparis tomentosa* is prominent, characterises the Ishasha River Flats to the north, and similarly dense vegetation colonizes the Ntungu river system to the north east. In the east the Park is flanked by a small escarpment (Fig. 1) and agricultural land lies beyond this.

FIGURE 1

The study area. The map shows the most southerly tip of the Queen Elizabeth Park. The Ishasha River forms the state boundary with Congo and the eastern boundary of the Park follows the road. Tracks shown within the Ishasha plains area are the approach road and the Northern Circuit above it and the Southern Circuit below. The area between the two parallel dashed lines is Area 10 of Field and Laws (1970).

PROCEDURE

The period of study extended from January 13 to April 7 1970. My base was at Ishasha Camp and during this period of 85 days I was absent from the study area for 19 whole days and for a few hours on 25 other days. I made two flights over the study area to see the general lie of the land and confirm the distribution of the topi. All ground observations were made from a Landrover. My routine on a typical study day was to find the whereabouts of the topi within half an hour of first light, by 0730h, and to continue observing them until midday. They were watched again from 1500 until dusk at 1915, but on several days watching was continued through the early afternoon and on a few occasions the topi were observed before dawn and after dusk, using a lamp powered by the Landrover battery.

The equipment used comprised Zeiss 10 x 50 binoculars, a Pentax 35mm camera with standard and 400 mm telephoto lens, a Gründig pocket tape recorder and a prismatic compass. Most observations were recorded at once in writing. Hand tallies were used for counting.

Many animals carried distinctive natural marks including conspicuous scars, torn ears, broken horns and peculiarities of coat colour. These marks were carefully recorded and 31 individuals, mostly adult males, were recognised in this way. A further 10 bulls were captured and marked by paint on the horns and with plastic collars. Immobilisation of these animals was carried out in collaboration with Dr. S.K. Eltringham and Mr. M. Woodford, who will publish details elsewhere. The Capchur gun was used and the immobilising agent was a mixture of the neuroleptic Azaperone and the narcotic Fentanyl.

RESULTS

The total number of topi

Censuses were attempted on three separate dates. Only adults were counted as calves were obscured by them and by long grass. On February 7 a huge congregation was assembled in the south of the area and 2 000 adults were counted from one vantage point. A recount, driving round the topi gave 2 280. The rest of the plains were searched but only 513 adults were seen grouped in one large aggregation and a few small herds: total 2 793. On February 24 the entire population was on the northern plain divided into two congregations, of approximately equal size and with a total of 3 061 adults. On March 23 the topi were in four separate aggregations numbering 527; 76; 2 176 and 253 adults respectively: total 3 032. It is probable that some animals always remained unsighted in depressions in the ground and it seems reasonable to take the highest total of 3 061 as the best estimate of adult numbers. The total number of calves has been estimated as 735 (see later section); adding this number to that for adults gives a total of 3 796 for the entire population.

Topi at Kikyere

At this place, 10 km north of the Ishasha area, there is a small population of topi, resident on a narrow grassland plain (area 9 of Field and Laws, 1970). As far as is known they are isolated from the Ishasha population by intervening bush and forest and do not mix with them. I carried out a single census on March 5, 1970 and counted 440 adults and 127 calves.

Movements

The topi at Ishasha appear to belong to a single, integrated, population and at times were assembled as one continuous congregation straggling over the plain. At other times they formed many small and scattered aggregations. These aggregations split up or amalgamated in an apparently random fashion and I saw no evidence to suggest that any particular subdivision of the herds had any permanence, although there was some evidence, to be mentioned later, that certain classes of animals might stay in association.

The topi respected very distinct boundaries to their range, and this appeared to be conditioned by an aversion for thick vegetation. In the earlier phase of my study the topi did not enter even the open bush zone fringing the forest, but later, when conditions had become drier they did infiltrate this zone to reach pools of water. The topi were seen to go to the Ishasha river to drink at only one place, near the camp, where the river bank was devoid of bush. Similarly thick bush provided a barrier to movement in the north. An escarpment forms a boundary to the plains in the north east by Katoke enhutment (which lies in the park). On several occasions the topi grazed along the top of the escarpment and ventured on to the scarp slope but were never seen to go further. Again, in the east on the four occasions when topi crossed the Congo road, they respected this scarp.

The topi moved freely over the entire plains area at Ishasha although at times separate aggregations moved independently. When I first arrived in the area the topi were in two widely separated congregations, in the north and south, and I thought that two sub-populations might exist: this proved not to be so and the month of February provided an example of a complete cycle of movement, illustrated in Fig. 2.

During the first week of February the aggregations of topi were widely dispersed (Fig. 2,a) but by February 9 all had moved south so that only a tiny party of stragglers remained in the north (12 males and 4 females): on the following day these too had gone, presumably to join one of two enlarged aggregations to be seen in the south. These two aggregations remained discrete for the next four days moving alternately eastwards into tall *Themeda triandra* grassland on higher ground and westwards towards the river (Fig. 2,b). All topi then moved further south to graze in the most southerly position in which I saw them (Fig. 2,c). By February 20, however, they were trekking northwards (Fig. 2,c) and by February 23 the southern plains were entirely vacated (Fig. 2,d). For the next few days the most northerly grasslands were exploited and again the aggregations made east-west movements over the area notably gravitating westwards in the evenings (Fig. 2,d) to use waterholes in the margins of the scrub. A pattern of local north-south movements ensued and characterized their behaviour through most of March. At the end of March the topi polarized once more into two major aggregations one of which again concentrated on the grazings north of Katoke, whilst the other moved to the region of the south circular track. The topi did not move to the far south again during my stay, and on my last day of observation (April 7) they were fractionated into ten smaller aggregations, five in the north and five on the central plains.

Observations on marked male topi supported the conclusion that the entire congregation of topi have access to all parts of the range and that there were no restricted home ranges occupied by particular aggregations or herds.

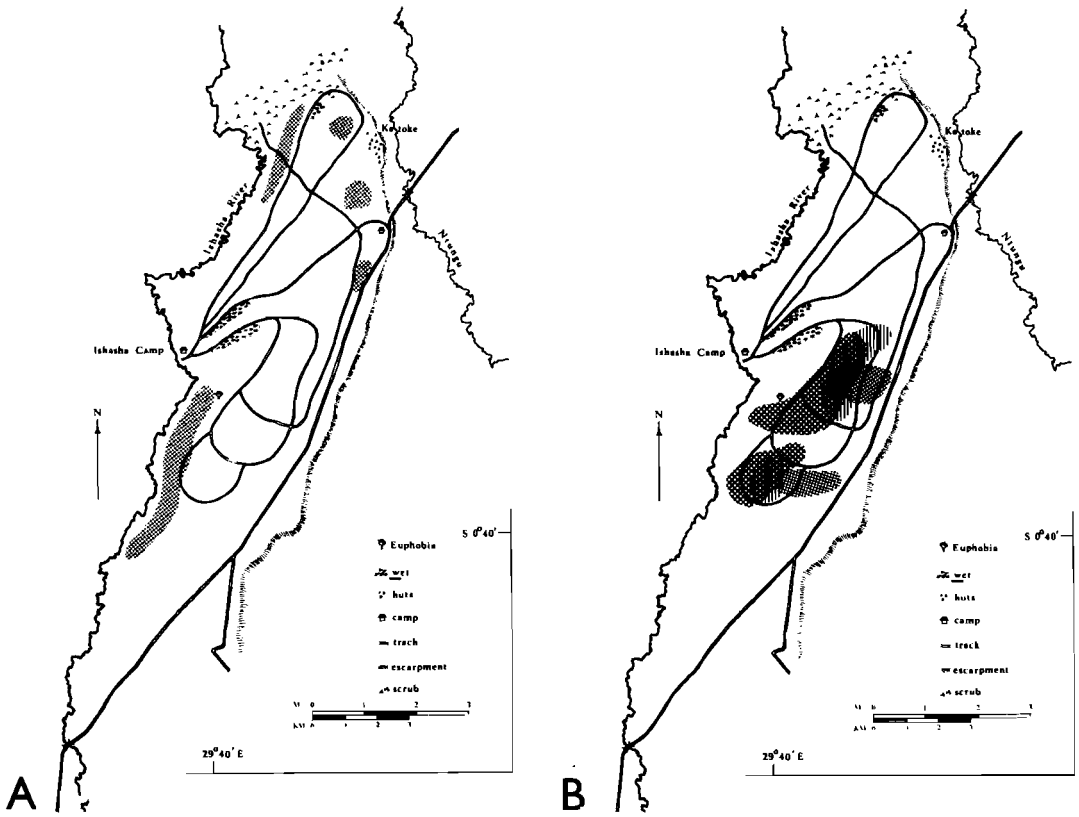
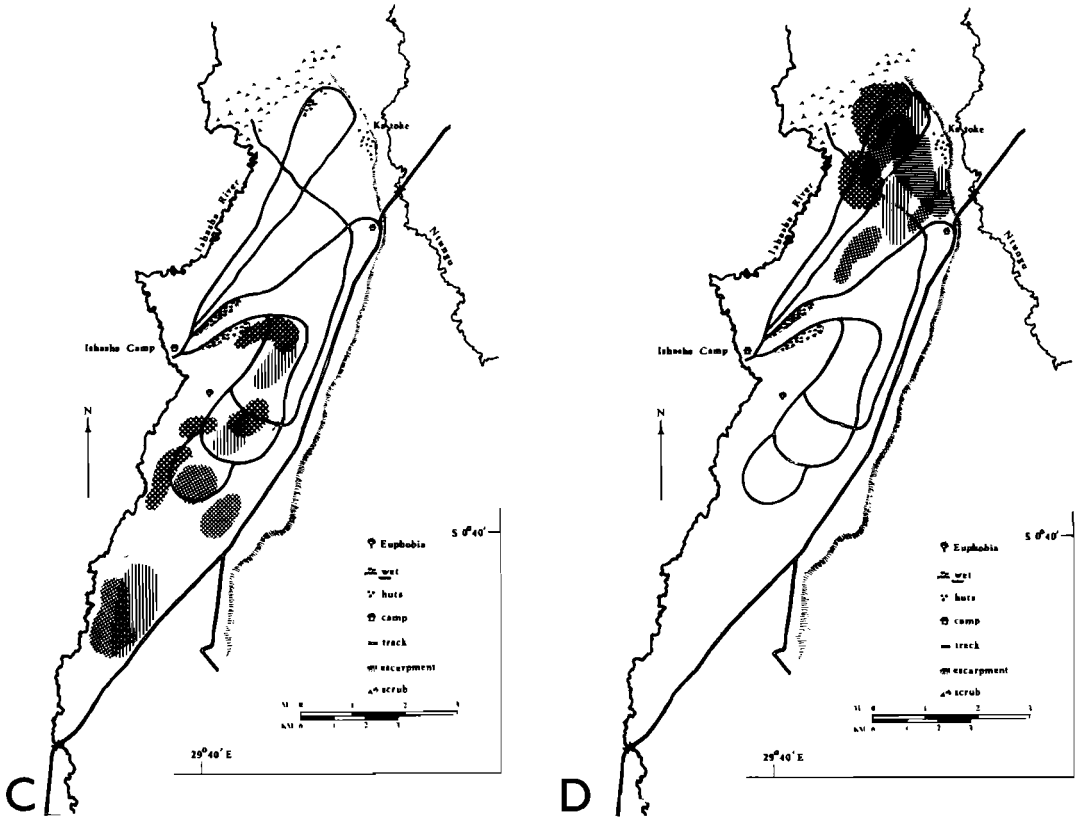


FIGURE 2
The positions of all topi aggregations on given dates in 1971, indicated by stippling. (a) February 3, scattered aggregations. (b) Concentration into two aggregations; dots, February 12; vertical lines, February 13; squares, February 14. (c)* Most southerly positions, dots, February 18; northerly movement, vertical lines, February 19 and squares February 20. (d)* Most northerly positions: dots, February 23; vertical lines, February 24 morning; squares, February 24 evening; horizontal lines, February 25 morning. (Cp. Fig. 1.)
*See opposite page.

Age determination

In topi both sexes carry horns but those of the male are much more robust. Well-developed transverse ridges encircle the horns. Because topi have a restricted annual period of births distinct age categories are evident in the population. If August is taken as the modal month of births then the classes I could distinguish and their characteristics were:

Calves: 6 months old, about half grown in height, juvenile pale fawn coat, horns sprouting (see Figs. 7 and 10).



Yearlings: 18 months old, not yet full adult size, adult colouration, horns with 7 to 9 distinct ridges (Figs. 3 and 6). A shot animal in this class had milk teeth except for the central pair of permanent incisors which were half erupted. (Included with "adults" in overall counts).

30-month-old-adults: Indistinguishable from older animals in size and colouration. Horns with 11 to 13 distinct ridges, not worn, and with wide valleys between the ridges at the base of the horn (Figs. 3 and 7). A shot animal had the central pair of permanent incisors fully in wear and somewhat worn, and the second pair had just achieved full eruption but were unworn.

Older adults: With age the rate of horn growth diminishes and the ridges remain only slightly separated at the base whilst the ridges on the distal segment of the horn become worn away (Fig. 4). In very old animals, males especially, the horns may be quite smooth (Fig. 5). It was possible to recognise a class of males that were probably 42 months old.

The correlations between horn structure and age that were deduced in the field were confirmed in a series of skulls that had been independently assigned to age classes on the basis of tooth eruption and wear. (This work is part of an investigation being carried out by Dr. S.K. Eltringham). Horn growth and wear have been used by other workers as criteria of age in wildebeest (Talbot and Talbot 1963) and hartebeest (Mitchell 1965; Strassen 1969).

FIGURE 4 (Above)
'Middle-aged' male topi, horns showing some wear, probably not older than 4½ years.

FIGURE 3 (Left)
Foreground, 18-month-old male topi; behind, 30-month-old male.

FIGURE 5 (Above)
Old male topi with well-worn horns, photographed while immobilized.

FIGURE 6 (Upper right)
18-month-old female topi.

FIGURE 7 (Lower right)
30-month-old female; the horns and ears of her calf, standing behind her, can be seen.

FIGURE 8
An old female topi.

Sex and Age Structure of the Population

Sex ratio. The topi herds, as will be related in following sections, are highly organized. The females are herded by dominant males and subordinate males usually clump together in peripheral parts of a large aggregation. It is not possible to count all the males and females in an aggregation because it is necessary to be fairly near to judge their sex correctly and their movements soon disrupt a count. Any one counted sample is not representative because of the clumped nature of the actual distribution of the sexes in the field. The best that can be done, therefore, is to lump all counts together and hope that the gross biases in the samples will cancel one another out. Fourteen counts that provide suitable data were made, the largest sample comprised 673 adults and the smallest 53, the mean being 244. The total numbers of males and of females counted were added and the means calculated to give a ratio of males to females of 98:146 or 1:1,5.

Sex ratio of calves. The calves were not old enough to sex easily from a distance and to do this I had to obtain a clear view of the belly from the side to see the small penis sheath of the male. Only one satisfactory inspection of a sample of 64 calves and their dams was obtained. This comprised

30 male calves, 30 female calves and 4 not sexed.

Total number of calves. The numbers of calves were derived by a procedure similar to that used in indicating sex ratio in adults. Thirteen good sample counts of adults (both sexes) and calves (mean total sample size 439) were obtained and the means calculated giving 354:89 or 24 calves to every 100 adults. If adult males and females are present in the ratio of 1:1,5 this gives a ratio of females to calves of 100:40. Six counts not used in the above calculations recorded only the numbers of females and calves. The mean size of these samples was 282 and they yield a mean ratio of females to calves of 100:63. (As will be seen in what follows this figure may be biased by the samples to give too high a proportion of calves.) If 3 061 adults were present, and the calf ratio of 100:24 is used then the possibly conservative estimate of 735 calves is obtained.

Yearling males. The problem of trying to obtain representative sample counts was greatest for males for two reasons. Firstly, a proportion of the older adult males were dispersed, as herdmaster males, through the ranks of females, and, secondly, associations of peer groups were evident in the bands of peripheral males. It was common to see a group of from 3 to 14 yearling males clumped together in these bands. On one occasion (28 January) a close group of 14 yearling males were seen at dawn, some still lying down, and they had evidently been resting at night together.

A total of 13 sample counts were made in which yearling males were distinguished as a category, the average number of males in these samples being 128; 25,2% of all males counted were yearlings.

Yearling females. The yearling females formed part of the female 'harem' groups and were distributed in twos and threes in these groups. The largest number of yearling females seen together was 9 (January 29) and they happened to be near 11 yearling males.

A total of 11 sample counts were made in which yearling females were distinguished; the average number of females in these counts was 177; 15,8% of all females were yearlings.

Age of attaining sexual maturity. On three separate dates (February 4 and 25 and March 8) I saw yearling females being mounted by herdmaster bulls. From their behaviour it was evident that these females were in oestrus. A female yearling shot on April 1 was already pregnant and carried a foetus judged to be about 10 weeks old. She had evidently conceived early in the rut. Her two central incisors were fully erupted, the remaining incisiform teeth being deciduous. Many 30-month-old females were seen with a calf at foot.

The testes of one yearling male and one 30-month-old male that were shot on March 3 were dissected. Microscopic examination of a smear from the cauda epididymus of the 18-month-old revealed a serous fluid with droplets but no spermatozoa. A similar smear from the 30-month-old revealed a mass of active spermatozoa.

BEHAVIOUR

Structure of aggregations

The behaviour of the topi was striking for the dynamic state of the relationship that it created between individuals. Usually a gradual movement of the whole aggregation took place as they grazed steadily forwards in a particular direction. This movement was maintained by the females who were relentless in moving on to new grazing. The internal structure of all aggregations, on the other hand, was determined by the activity of the breeding bulls, who were constantly engaged in efforts to herd a group of females together and to chase away other males. Active breeding bulls were distributed regularly throughout the congregation and they superimposed on the female ranks a subdivision into a mosaic of temporary harems. (The word 'harem' is employed as a useful term that is in common use, in application to ungulates and pinnipeds, to denote groups of females that are rounded-up by a breeding male. It is not entirely apt because there is much movement of females from one 'harem' to another.) All females of all ages, including yearlings, were brought together in these groups accompanied by their calves. Each harem was clumped within the sphere of influence, or ward, of a bull (Fig. 9). and the bull moved actively round these females chevying them together. A ward was 80 to 100 m in diameter and at its limits it met the wards of neighbouring bulls.

The male topi fell into three categories. The first category was that of the temporary harem-master males that at any given time were acting as breeding bulls and that maintained the harem groups of females. They will be referred to as *harem bulls.* Agonistic encounters between these bulls were frequent but their aggression was also turned against all other males associated with the big herds. As a result these other males, present in considerable numbers, were constantly bullied out of the core of the aggregation and accumulated at its edges as second category or *peripheral males* (Fig. 9). As will be seen, these designations do not necessarily indicate the permanent status of any individual. The third category were lone males which remained for a while, grazing at scattered stations, when no aggregation was near.

The harem bulls, whilst defending their wards fiercely and admonishing their sets of females, could not stem the general forward movement that the females maintained. In any given set of females some would strive to move on to join the next set in advance. Their herdmaster would head them off (Fig. 10) but this brought him close to the ward of the next bull in advance and a confrontation between the bulls ensued. Inevitably some females would break away and join the next set forward. This loss of females from one harem was compensated by a similar gain from the set of females to the rear so that a bull would maintain the numbers of his harem for a considerable time. Although the harem bulls did move forward with the aggregation their progress was held up by the tenaciously maintained network of wards. The result of this differential

FIGURE 9 (Upper right)
Part of an aggregation of topi; foreground, a group of peripheral males; background, harem groups of females.

FIGURE 10 (Lower right)
A herdmaster male (right) chevvying females and their calves back into his ward, ears partly dropped
(cf. Fig. 11 on page 248)

FIGURE 11
A herdmaster bull, inspecting his harem of females and exhibiting the 'head-high' posture, ears pricked up and forward.

progress was that the females, moving forward faster than the harem bulls accumulated at the leading head of the aggregation whilst the trailing tail of the aggregation became devoid of females.

On several occasions counts were made of the numbers of females in harems. The frequency distribution of these counts, shown in Fig. 12 indicates the size of groups that bulls were able, temporarily, to keep together. These counts were made in the main body of gently moving aggregations. Harem bulls stationed at the leading edge of aggregations accumulated large numbers of females: groups of 50; 35; 35 and 31 were recorded at the edge of an aggregation on January 29. On March 22 groups were counted at the northern edge of a congregation that had lately been the leading edge: the largest numbers of females under the surveillance of single bulls numbered 82; 50; 48; 37 and 36.

The second category of males, the peripheral males, was the more numerous and it included all the yearling males. It was a common experience, in approaching an aggregation, to encounter groups of peripheral males at its margin. Numbers in these groups were extremely variable: on January 28, for example, when 44 groups were counted by driving along the outside of an aggregation, the range of group size was from 2 to 23 with a mean of 7. Some groups were compact but elsewhere the peripheral males were well dispersed, some so widely as to be recorded as single individuals. Their disposition was constantly changing, however, and the majority of these

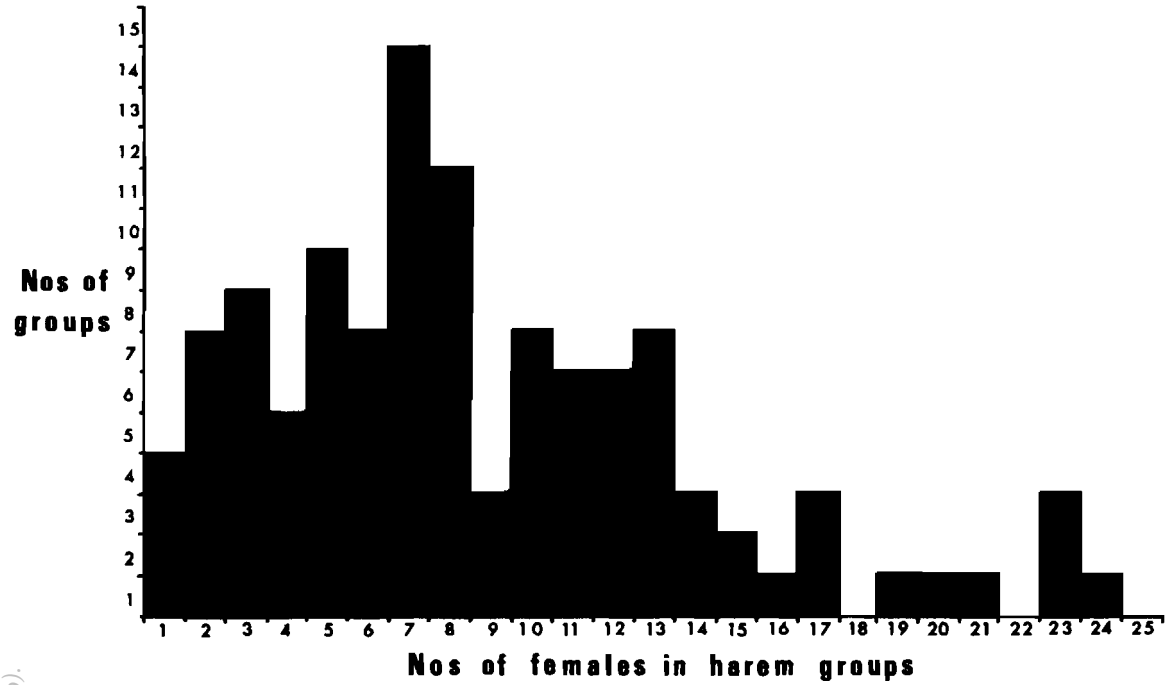


FIGURE 12
Frequency of occurrence of different sized groups of females herded by harem bulls. Total sample size 110 female groups compounded from several sample counts in the centre of aggregations of topi.

scattered individuals conformed to the general movement of the aggregation. Those that did not became lone males.

Peer groups were evident amongst the peripheral males; yearling associations have been mentioned but it was also common to see as many as six 30-month-old males keeping close together. Peripheral males, because of their outlying position, would get temporarily separated from the main aggregation and groups of this kind of over a hundred individuals were occasionally encountered. On February 18 a group of 55 males were counted in a group straggling in the rear of an aggregation. Similarly a small aggregation of topi, 2,5km distant from a main congregation, encountered on March 8, comprised 129 males, 101 females and 53 calves: they were presumably the recent leading or trailing edge of the congregation that had become isolated: only 3 of the males were acting as harem bulls. The greatest number of peripheral males counted in an array at the edge of a congregation was 158.

Movement of aggregations and status change of males

When an aggregation was gently on the move, spreading in a particular direction, the majority of its members were engaged in grazing. The harem bulls, however, were conspicuous amongst them because of their distinctive behaviour. They moved about their wards in an alert manner with the

head held high (Fig. 11), grunting. They ran in a rocking canter and appeared to exaggerate the lifting of the legs so that the yellow coloured shanks were very noticeable. A grunt was often issued with each rock of the run and the head was shaken up and down. The harem bulls made themselves conspicuous, therefore, by carriage, gait and sound.

Sometimes the drift of an aggregation would gather momentum and its leading edge would form into a column heading towards new grazings or to drinking places. When this happended the harem bulls lost control. They often stood facing against the movement, still conspicuous in their stance, but making no effort to interfere with the movement. Finally they joined the column and their identity was lost.

At the other pole of an aggregation harem bulls were left behind without females to restrain. These males often resorted to grazing for a while and then moved to join peripheral males. Having done so they became indistinguishable from their companions and fell into this other category. This change of status was witnessed on many occasions, and having dropped the role of harem bull the male behaved like any other peripheral male. It submitted to being chased by active harem bulls and moved at the periphery of the herd. Alternatively the male might stay in the area for one or two days as a lone male.

Observations of the marked males confirmed that status could change and alternate. Five naturally-marked males were recorded as harem bulls and later as peripheral males, and three were recorded in the reverse sequence of roles. Two harem bulls were immobilized and marked but subsequently were recorded only as peripheral males. The immobilization may have upset them but a third harem bull, when seen on the morning after immobilization, retained his role. That same afternoon he had changed status and joined a group of peripheral males but next morning he was again a harem bull and in the afternoon yet again peripheral. This sequence had occurred in one area with little general movement of the aggregation. This male was seen on six subsequent occasions, over 22 days, on different parts of the plain but always in a peripheral role. A peripheral male that was immobilized was seen two days later as a harem bull. Two days after that, when the aggregation had moved 5 km he was again a harem bull. Subsequently he was seen only as a peripheral male. Another peripheral male that was immobilized was seen only in this role on the 15 occasions on which it was subsequently sighted. This animal was 30 months old.

Age and status in males

In the earlier part of the study period all harem bulls were recorded to be old or "middle-aged" – this latter term being applied to bulls that were older than 30 months, but whose horns were not excessively worn (Fig. 4). It was noticeable that bulls with horns completely smoothed and shortened by wear (Fig. 5), and presumably belonging to the oldest age class, were frequently harem bulls. They were often thin and past their prime but it was to such animals particularly that the behaviour associated with herding females imparted a marked enhancement in apparent stature. Although harem bulls were always losing females to challengers (or gaining them) and their spheres of influence were restricted by adversaries, I never saw an established harem bull displaced from his ward through the act of a challenger. A field-record of February 10 records an incident in which an old harem bull was challenged by a young male (30 or 42 months old). The young male was the larger, had longer horns, and its coat was a darker, more glistening colour but these attributes did not give him victory.

Later in the study, however, and at a time when I presume the peak of the rut had passed, younger males were successful in acquiring status. On February 28 and in early March a number of harem bulls were observed that were not older than 42 months and later in March, 30-month-old males occasionally acquired this status: 18-month-old males never contended for harem master status.

Amongst peripheral males active aggression was low although elements of agonistic behaviour were frequently enacted. Clashes occurred, but in what appeared to be a playful context; peripheral males of all ages were involved. The 18-month-old males most often engaged in bouts of playful fighting together, but later in the rut they too seemed more ambitious and on March 22, for example, I noted for the first time 18-month-old males vigorously facing both 30-month and older males in peripheral groups. A common activity amongst males was horning at the ground and this became a communal pursuit at dust scrapes and at termite mounds. This activity was, presumably, the main cause of wear on the horns.

Lone males were always to be observed somewhere on the plains throughout the study period. They were to be seen, widely scattered in distribution, grazing, lying or standing, but usually in areas that lay in the wake of a moving aggregation. They remained for a few days and then disappeared. These lone males were mature bulls, they were never 18-month-old males and I did not certainly record 30-month-old males behaving in this way.

Herding and mounting by harem bulls

A major activity of harem bulls was herding and inspecting the females in their wards. At times, when general movement was slight, the females would be grazing or lying in an area 40 to 80 m in diameter and the bulls' wards would extend 150 m across. For part of the time a bull grazed but ever so often he set off running or pacing round his set of females (Fig. 11). He ran to head off any females that had grazed too near the limits of his ward (Fig. 10). In doing this the male adopted a nodding head carriage with ears emphatically dropped and the nodding could change to a threat of horning: in this gesture the head was tucked in and then swept upwards in a feint jab. The straying females and their calves usually turned and, encouraged by the male, hurried back to other females in the group. Occasionally a female rounded on a male and clashed horns with him and at this the male usually stopped his pursuit and turned his attention to other females.

Limiting the straying of females was not the only purpose of the male's patrol, he also investigated the females to discover those in oestrus. His approach to a female for this purpose employed a distinctive soliciting behaviour. In this the nose was thrust forward and the head and neck held horizontal with the back in a "low-stretch" posture. The ears were erect and pricked forward and the bull advanced cautiously, with stealthy steps, directing his nose at the female's anal region and uttering a rapid "bleating-grunt". The bull's tail might be limp or slightly raised, but if he was highly motivated as when investigating a newly-arrived female or in the presence of an oestrous female, the tail was raised stiffly and held horizontal. The male paused with his nose very near the base of the female's tail and appeared to be testing her condition by smell. Male topi never exhibited flehmen. If the bull detected no potential receptivity in one female he moved on to investigate another.

The bull roused lying females. He approached their rump and many jumped up before the bull had reached them, but others rose as soon as he touched them with his snout. Frequently he

tarried to smell the place where a female had been lying.

When a female was detected in oestrus the bull paid her persistent attention, and the female, in turn, tolerated his advance and stood with tail slightly raised. The male nosed and nibbled the female's tail base and vulval region and sometimes raised a foreleg, particularly if he was at an angle to the female and not in line behind her. The bull then leapt to mount, bending the neck down and pressing his snout against her withers. Intromission was usually achieved immediately and the bull ejaculated with a single thrust. After sliding off the female the bull stood still in an alert posture. On paying renewed attention to the female the bull would repeat the soliciting bleat and then nibbled and licked the vulval region, and thrust the tongue into his nostrils. Mounting might not be attempted immediately and this attention had some of the characteristics of a post-coital display.

A female in oestrus was mounted repeatedly by her immediate harem master bull, and inseminated frequently; eventually, however, she would break away from his ward and perhaps run through several advance wards before settling, temporarily, with another bull where again she was repeatedly inseminated.

Females came into oestrus (as indicated by observed mountings) throughout the whole period of my study. The first observed mounting was on January 21 and the last on April 1: a total of 31 females were seen to be mounted. The week in which most mountings were seen was the last one in February but my observations were too irregular to indicate whether this represented a peak during the rut.

Females and calves

During the rut the calves, then mostly about 6 months old, stayed close to their dams, and each dam and calf suffered the vicissitudes of transit from one herdmaster bull to another. Although the calves grazed as assiduously as other topi they were still being suckled by their dams.

I occasionally recorded in my field notebook that I appeared to be in a "high calf area". On January 19, for example, when counting harem groups in the centre of a large aggregation I counted 183 females and 135 calves in 19 groups; a ratio of 100:73. In contrast on February 4 I counted all the topi in a small aggregation and there were 6 harem bulls, 34 peripheral males, 143 females and 37 calves: a comparable ratio of 100:26 (the difference between these ratios is highly significant, on χ^2 test $P=<,001$). Towards the end of the study period I saw several small groups of topi (moving separately but hardly warranting the designation of 'aggregation') comprised of males and females with no calves.

The calves themselves evidently held attraction for one another: they frequently engaged in play, in chasing games, in horn-engaging clashes, and in horning termite mounds together. The largest group of calves seen together was 10 and they had gathered on the edge of a mud wallow. These associations of calves might have provided the basis for the formation of the yearling peer-groups that persisted amongst the topi aggregations.

DISCUSSION

The topi at Ishasha attain a high density when compared with herbivores in other grassland areas. Within the Queen Elizabeth Park they are locally more dense than any other large mammal, being recorded at an average density of 83,17 per km² by Field and Laws (1970). At the time of my study their average density was 47,4 per km² (3 796 topi using 80 km²) but Field and Laws traversed a part of the area most favoured by the topi for their regular counts and so the total numbers of topi actually may not have differed greatly at the time of their study (1963–67). In contrast, topi in the Rukwa valley, in Tanzania, were recorded at a much lower density, about 2 000 being present in the 760 km² of plain (Vesey-Fitzgerald 1955). Possibly the topi did not use all this area but moved over only part of it in phase with seasonal flooding.

It is evident that movement is of great importance in the ecology of topi. The topi at Ishasha are referred to locally as "migratory" but this is not an appropriate description as they do not exhibit any regular directional movement. Rather they comprise mobile, freely-ranging herds that appear to exploit a discrete habitat, providing an example of a herbivore with an extensive group home range (Jewell 1966). Elsewhere, as in parts of the Serengeti, topi are sedentary and territorial, and the tsessebe (*Damaliscus lunatus*, but probably conspecific) is reported to be territorial (Child, Robbel & Hepburn 1971). This dichotomy of habit in the species has led to important behavioural adaptations. In this the topi parallel closely the related Alcelaphine genus the blue wildebeest *Connochaetes taurinus* in which the same well-known dichotomy has been fully described by Estes (1966; 1969). The behaviour of topi herdmaster bulls has all the elements of territorial behaviour except that they do not defend a territory fixed in space, and so cannot create scrapes or dunging points to mark it. Because of this connotation of territory I have avoided this term in describing the bull's sphere of influence and have found 'ward' a useful term with less rigid associations. Similarly I have avoided the term 'herd' to describe either the large aggregations of topi or the groups dominated by harem bulls. In many bovids the herd is a semi-permanent social unit and the word is usefully kept for such associations. I have called the female groups 'harems' although this is hardly appropriate in view of the rapid turnover between them (Watson (1969) adopted the term 'pseudo-herd' for wildebeest). These female groups, in topi, comprise only females and their calves but the yearling females are included amongst them. It is possible that yearling females stay near their dams and try to keep in groups with them, a kind of association exhibited by many bovids (Grubb & Jewell 1966). In some alcelaphines, as in Coke's hartebeest *Alcelaphus buselaphus cokei*, the young males stay with their dams until about 2 years old (Gosling 1969), but in topi, whilst they remain with their mothers at 6 months old, they are evidently expelled before reaching 18 months.

At least a proportion of female topi conceive as yearlings but this is not exceptionally precocious for alcelaphines: blue wildebeest (Watson 1969) and Lichtenstein's hartebeest (Mitchell 1965) also first conceive at 16 months old. On the other hand blesbok *Damaliscus dorcas phillipsi* (R.C. Bigalke, in litt.), tsessebe (Child *et al.* 1971) and bontebok *D. d. dorcas* (David 1970) have been observed to remain non-fecund until over two years old.

In this study I was not able to keep track of associations between females: they appeared to be mercurial and harem groups split and recombined constantly. Other workers have observed, however, in sedentary populations of alcelaphines, that female groups can have marked cohesion.

David (1970) reported that bontebok females formed small groups which were enduring in nature and semi-exclusive in character, and Huntley (1971) observed similar behaviour in a small population of tsessebe; W. von Richter (personal communication) observed black wildebeest females *C. gnu* to stay in cohesive groups that were antagonistic to newcomers. In my study the non-random distribution of females with a calf at foot, and the observed clumping of yearlings, gave a hint that some enduring kinds of association between individuals might be present. This suspicion gains support from the reports that females in the same state of pregnancy appeared to consort together in blue wildebeest (Watson 1969) and in topi (Vesey-Fitzgerald 1955). It is evidently important to an understanding of social organization to know more of the nature of female associations.

ACKNOWLEDGEMENTS

I would like to acknowledge the help and encouragement that I was given in this work by the late Mr. F.X. Katete, former Director of the Uganda National Parks. The Parks staff gave me much helpful assistance in the field. Dr. S.K. Eltringham, Director of NUTAE, provided many valuable facilities and both he and Mr. M. Woodford helped in the immobilization of animals and in piloting survey flights.

The work described is part of an investigation supported by research grants from the Royal Society, the Percy Sladen Memorial Fund and the Research Fund of the University of London.

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