

TERRITORIAL BEHAVIOUR OF THE TSESSEBE (*DAMALISCUS LUNATUS LUNATUS* BURCHELL) IN THE KRUGER NATIONAL PARK

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ABSTRACT

This paper forms part of a general bio-ecological study of the tsessebe (*Damaliscus lunatus lunatus* Burchell) presently being undertaken in the Kruger National Park. Territorial demarcation and maintenance is achieved by various ritualized displays and marking techniques. Territory marking includes both visual and olfactory methods. Agonistic behaviour is evidenced by dominance and threat displays while territorial conflicts may result in actual fighting. The various behavioural patterns relating to territoriality are discussed with an evaluation of their possible significance in the social organisation of the species.

Recent evaluations of the numerical status of tsessebe in the Kruger Park have indicated a total population in the order of 600 to 700 animals. (Pienaar and Van Wyk, unpublished report). This beautiful antelope must therefore be regarded as one of the rare species in the Park. It is the present policy of the research section to conduct comprehensive bio-ecological studies on the less numerous and over-abundant species of the Park, in order to gain sufficient information on their social and ecological requirements on which to base a scientifically sound management programme. The present paper must therefore be seen merely as part of the overall project. This paper is, furthermore, limited to the behavioural aspects of territorial organisation in the species. From a game management point of view it will also be necessary to evaluate territoriality in an ecological context.

PRESENT DISTRIBUTION AND STUDY AREA

The present distribution of tsessebe in the Kruger Park is restricted to the central and northern districts. In the central district herds are scattered over a wide area while the majority are concentrated in the northern district. They exhibit a distinct preference for the open plains adjoining the Lebombo mountain range on the east. Scattered herds are also encountered in the mixed Combretum/Mopani woodland savanna along the western half of the district (Pienaar 1963).

Observations were carried out whenever an opportunity presented itself, but the majority were made on a population numbering approximately 100 animals on the far north-eastern reaches of the Lebombo flats. Topographically this included the area between the Nkulumbene River in the south and the Hlamalala drainage zone in the north. This area is represented by flat, slightly undulating plains with rich, black cotton soil of basaltic origin. The major vegetation type has been designated by Pienaar (1963) as "mopani scrub and tree savanna". The general physiognomic feature of the area is fairly large, open grassland areas amongst stands of shrubs and trees in varying densities. Apart from the shrub and tree form of the Mopani, *Colophospermum mopane*,

which is dominant, other trees and shrubs are also present and include: *Combretum imberbe*, *Sclerocarya birrea*, *Lonchocarpus capassa*, *Dalbergia melanoxylon*, *Grewia*, spp., *Dichrostachys cinerea*, etc.

The grass stratum is characterised by dominants such as *Themeda triandra*, *Panicum coloratum*, *Schmidtia bulbosa* and *Cenchrus ciliaris*. Other important species include *Heteropogon contortus*, *Digitaria* spp., *Urochloa mossambicensis*, *Eragrostis* spp., and *Aristida* spp.

An important feature of the area is the wide, open, grass covered drainage lines which dissect it. These depressions are very similar to the typical "dambos" of central southern Africa. Important grasses in these areas are *Sporobolus robustus*, *Ischaemum brachyatherum*, *Sporobolus schlechteri*, *Sorghum versicolor*, and *Setaria woodii*.

THE STUDY POPULATION

The entire Kruger Park tsessebe population consists of small herds scattered around the permanent watering points. In the above-mentioned study area, observations were concentrated on six different herds, representing a total of 58 animals. Each breeding herd typically consisted of the territorial bull, a number of cows and their accompanying young. Over the study period of one year the herds have proved remarkably stable and though more than one herd may share the same watering point, each is confined to its own territory.

Associated species occurring in the same habitat as the tsessebe include elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetus taurinus*), eland (*Taurotragus oryx*), roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*), kudu (*Tragelaphus strepsiceros*), reedbuck (*Redunca arundinum*), steenbuck (*Raphicerus campestris*) and zebra (*Equus burchelli*).

Carnivores capable of preying on the tsessebe range from lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), hyena (*Crocuta crocuta*) to the black-backed jackal (*Canis mesomelas*) and side striped jackal (*Canis adustus*). Occasional deaths among calves may also be inflicted by pythons (*Python sebae*) and possibly even by martial eagles (*Polemaëtus bellicosus*).

PROCEDURE

Observations were made from a Land Rover. This proved to be the most satisfactory way of approaching the animals closely without causing any undue disturbance. While the animals are extremely wary of human beings on foot they generally showed little concern for the vehicle. Flight distances varied from about 50 to 150 m. A pair of 10 x 50 binoculars proved to be quite satisfactory for observing detail and notes were taken, as far as possible, at the time of observation.

TERRITORIAL BEHAVIOUR

The term, or concept, "territory" originated from observations on birds and conveyed the basic principle of a defended area and zoologists soon realised that it could also be applied to mammal populations. A number of definitions were subsequently proposed and all centred, in one way or

another, on the main concept of an exclusive or defended area. It has subsequently, however, become evident that different authors attach varying interpretations to the concept of territory. The author has found the definition of a territory, given by Walther (1967), to be the most descriptive and discussions in this paper comply with the requirements, as set out by Walther, of this definition: namely that a territory is "a relatively small area which is established and defended by one male only. Commonly it is defended against other males but is open for sexual partners" (translated from German). In an analysis of the territorial behaviour of tsessebe the following categories can be differentiated.

MAINTENANCE OF THE TERRITORY

In keeping with the general definition of a territory as a defended area, much emphasis is placed on the actual defence, i.e. actual boundary conflicts, by a territory proprietor and neighbouring rivals. However, the information amassed on the territoriality of a variety of species clearly suggests that boundary conflicts in the defence and maintenance of a territory are strongly augmented by a wide range of ritualized marking and advertising procedures. The techniques most commonly employed for marking purposes include olfactory, visual and acoustical methods that have evolved to best suit the particular requirements of each species. In the tsessebe territorial advertising and demarcation plays an important role in the maintenance of the territory and may conveniently be divided into the following categories.

Marking by means of the urine/faeces sequence

Much has been said about the credibility of regarding faeces deposits as a valid means of demarcating a territory. In the two congeneric forms of the tsessebe, *Damaliscus dorcas phillipsi* (the blesbok) and *Damaliscus dorcas dorcas* (the bontebok) it is maintained by Lynch (1971) that the dung patches of blesbok cannot be considered true territory markers. However, the fact that the territorial blesbok male spends most of his time on or near a dung patch and frequently lies down on his own faeces, thereby impregnating his hair with his own characteristic odour, may be considered as visual and olfactory territory demarcation. David (1969) could find no evidence that either bachelor groups or territorial rivals payed any attention to dung patches in the bontebok and therefore concluded that dung heaps could not be considered territory markers.

Unlike the two preceding species the tsessebe has small dung patches, in fact when one considers blesbok dung patches, which measure up to 5 x 2,9 m, the small and numerous patches of the tsessebe are not comparable to those of its congenics, c.f. Huntley (1970). Tsessebe also, however, have a number of favoured resting places, or stamps, distributed about the nucleus of the territory. Through frequent use these areas become denuded of grass and the top soil is eventually loosened by pawing, horning and general usage by the territory proprietor. Although defecation is frequent on these areas the territorial males are less inclined to use one or two stamping grounds to the same extent as their next of kin, with the result that faeces accumulation is of a much lower order. Moreover, defecation is not limited to the territorial nucleus, as in the stamping grounds referred to in blesbok (Lynch 1971) and wildebeest (Estes 1968), but forms a conspicuous part of the territorial male's activity throughout his territory. Whenever on the move, during territorial conflicts with rivals, at waterholes and virtually wherever the male may find himself on his

territory defecation takes place. It appears that any bare patch of ground stimulates the bull to defecate. Other situations in which defecation takes place, in a strong territorial context, include defecation during territorial conflicts, before or after pawing, horning or rubbing the face in the ground.

Though defecation alone occurs considerably more frequently than successive defecation and urination, the latter sequence was frequently observed. In this sequence the male defecates and immediately afterwards urinates from the same stance or after taking a step or two forward. Tsessebe customarily defecate with their hind legs straddled slightly apart and the head held erect with ears outstretched. The carriage of the head could possibly simulate a dominant attitude though this is not as apparent as in certain other territorial species.

The specific functions served by defecation in a territorial context are believed to closely interact with the marking methods. Before elaborating on the possible functions of this and subsequent marking devices, it is appropriate to consider the nature of territorial demarcation in general. Taking into consideration all the available evidence at hand it becomes quite apparent that the various marking methods applied by territorial species have definite significance for both the territory proprietor as well as would-be transgressors. Marking methods of an olfactory nature such as the use of excreta and the secretions of various skin glands for marking purposes, places the stamp of a particular animal on its territory. The consequent sense of ownership, or possession, immediately places the proprietor animal at a psychological advantage over its rivals. Conversely, rivals entering a territory are inhibited by the sense of alien ownership and therefore also suffer a distinct disadvantage in any conflicts which may ensue. Marking devices are further augmented by the mere presence or ritualized threat behaviour of the owner-animal and lead to further inhibition of the intruder. It may therefore appear that intruding animals pay little attention to markers e.g. dung heaps, secretion deposits, etc., though their importance in differentially conditioning the two rival animals, i.e. the territory owner and the rival, in conflict situations cannot be overlooked.

It is in the above context that the rôle of faeces/urine marking must be seen. Little individual heaps of droppings are deposited throughout the tsessebe territory and – in combination with the other marking methods – leave a trace of the owner distributed over his territory. The preference of tsessebe to defecate on bare patches of ground has obviously evolved to gain maximum benefit from this marking device and Huntley (1970) has noted that numerous dung patches are to be seen on the roads in the tsessebe range, and because the dung decays very slowly, they serve as efficient visual and olfactory markers. The habit of tsessebe to defecate on their “stamping grounds” and then to lie down on the deposits further assures that the odour is conveyed by the owner himself. Compare also blesbok (Lynch 1971), bontebok (David 1970) and wildebeest (Estes 1968).

Pre-orbital gland deposits and face rubbing

Tsessebe have well developed pre-orbital glands. The secretion of these glands is a transparent, sticky gel and it may often be seen as a moist smudge below the orifice of the gland (Fig. 1). Pre-orbital glands are present in both sexes though from general appearance seem to be most active in the territorial males. Lynch (1971) was able to confirm that blesbok males have larger pre-orbital glands than females and that the tear-like smudges below the gland were only obvious in territorial males.

The secretion in the tsessebe is most commonly deposited on short upright grass stalks



FIGURE 1

The head of a territorial tsessebe bull, illustrating the orifice of the pre-orbital gland and its secretion.

(Huntley 1970). In the process of transferring the secretion to the grass stalks the animal tilts its head to allow the object free entry into the orifice of the gland. After agitating the stalk in the gland opening for several seconds, the animal's horns and forehead and, less frequently, its face, are rubbed on the stalk (Huntley 1970). Lynch (1970) has also described this form of "glandular weaving" for blesbok. In blesbok it is particularly well developed and the regular weaving of the horns over objects onto which the secretion has been deposited leads to the accumulation of thick layers of the substance in the cavities between horn annuli. This procedure is simulated by tsessebe though it is not as prominent as in the blesbok. It is therefore apparent that, apart from the immediate area around the gland, most of the face and also the horns become contaminated by the gland secretion.

Glandular weaving has also been recorded for the bontebok (David 1970). As in the tsessebe, weaving is not well developed in the bontebok and David suggests that it may represent a relic pattern which has lost its functional significance. He further suggests that the pre-orbital gland has no functional value in demarcating the territory in bontebok.

The habit of Thomson's gazelle, *Gazella thomsoni*, to repeatedly deposit the secretion of the

pre-orbital glands on specific objects, such as twigs, leads to the accumulation of the substance on these objects and they eventually take on the form of spherical balls (Walther 1964). This behaviour has also been noted for dikdik (*Madoqua kirki*) and klipspringer (*Oreotragus oreotragus*) (Tinley 1969). This type of glandular marking does not hold true for tsessebe who do not mark the same object successively but mostly deposit the secretion at random on suitable objects.

Face rubbing is also performed by both males and females and consists of the animal going down onto its knees or lying down, and stretching the head and neck forward while rubbing the lateral surfaces of the face on the ground. Rubbing frequently occurs on old termite mounds or in the loose sand at resting sites.

A cow was once observed bending her head back and rubbing her face against her shoulders. This form of rubbing is however infrequent. In a study of the Lichtenstein's hartebeest (*Alcelaphus lichtensteini*), Dowsett (1966) found that animals customarily rubbed their faces on their flanks, resulting in persistent, black marks from the sticky exudate of the pre-orbital glands. Face-rubbing the flanks in tsessebe is extremely infrequent and no marks resulting from it could be found.

From the functional point of view it is clear that the impregnation of a large part of the face with the pre-orbital gland secretion and the habit of tsessebe of rubbing their faces on the ground and termitaria ensures that the glandular scent is distributed over a wide range in the territory, thereby endorsing the ownership of the territorial male.

Soil horning

While horning the soil, tsessebe fall onto their knees and vigorously plough up the soil with their horns. Both the bulls and cows perform this activity and, especially after rain, clods of damp soil may be seen adhering to their horns. The significance of this behavioural pattern in territorial activity is believed to be of a diverse nature. It may further advance the scent marking of the territory by giving off pre-orbital gland secretions which may have accumulated on the horns due to glandular weaving; the ploughed up earth could also serve as a visual marker to intruders and finally soil horning also simulates threat behaviour and as such serves as a further inhibition to intruders.

In the bontebok David (1970) distinguished between two different forms of horning, "forward" and "sideways" horning. Forward horning involving forward movements with both horns simultaneously touching the ground, were regarded as mere comfort movements. In sideways horning each horn is alternatively drawn through the ground and is performed by territorial males on their dung heaps. This form of horning is considered by David to represent threat behaviour.

Pawing

Pawing the soil with the front feet takes place occasionally but is not of frequent occurrence. Both front feet are usually used in turn and consists of short, repeated scraping movements in the soil.

Referring to interdigital glands Pocock (1910) states that "the interdigital cleft is large and highly glandular on the front feet, (while) it is reduced to a shallow depression on the hind feet". It is therefore reasonable to assume that, similar to the pre-orbital glands, the interdigital glands of the tsessebe may also play an important rôle in the demarcation of the territory. In view of the large cleft in the gland it is also reasonable to expect that the glandular secretion is constantly



FIGURE 2

Static-optic marking by a territorial bull from a disused termite mound.

rubbed off onto objects during the daily routine of the animals. This facilitates the scent marking of the entire area of activity of the animals and as such may represent one of the most important marking devices of the species. Pawing has not been observed in the bontebok (David 1970).

Static-optic marking

Certainly the most direct, and possibly the most effective, way for a territorial male to advertise his territory is to expose himself to would-be rivals. The habit of territorial males, in many of the species exhibiting this form of social organisation, to make themselves conspicuous and their presence known to rivals by merely standing idle in their territories, has been referred to as static-optic marking (Hediger 1949). This form of territory advertising has been described for a wide range of species, including among others Grant's gazelle (Walther 1965), blue wildebeest (Estes 1968), bontebok (David 1970) and blesbok (Lynch 1971).

In tsessebe, too, this form of territory advertising is most conspicuous with males exposing themselves on their territories to neighbouring males (Fig. 2). Territorial bulls also utilize elevated situations such as old termite mounds on which to stand to gain maximum benefit from this form of advertising. Walther (1968) has also observed this phenomenon in the East African topi *Damaliscus lunatus topi* and David (1970) in the bontebok. Tsessebe males standing in this fashion often appear alert with ears held away from the head while gazing intently in various directions. This has led the author to believe that tsessebe not only advertise their own presence but that they also actively seek out trespassing or approaching rivals from these vantage points.

Static-optic advertising is most obvious during periods of inactivity and it is notable that during such periods the bull customarily isolates himself from the cows and young. The bull withdraws to anything from 50 to 300 m from the herd and, although casting a watchful eye over his harem, remains on his own for most of the resting period. This has the advantage of immediately making the presence of the male all the more conspicuous.

To illustrate the demarcation of the territory in tsessebe the following example may be quoted from field observations. During the afternoon of 28-12-'70 a herd of five ($\delta+3$ ♀+♂ yrling) was

observed in the vicinity of a waterhole. All the animals in the herd were resting close to one another during the afternoon and arose at 1645 h to resume grazing and other activities. The cows moved away to an old termite mound 15 m from their resting place. After grazing around the mound for some time the cows started rubbing their faces on the mound.

When the bull arose he moved 3–4 m to where one of the cows had defecated. The bull stooped to smell the spot, nibbled at a few grass tussocks and urinated on the same spot. After this the bull moved 250 m away from the herd and started pawing the ground alternatively with both front feet. He then dropped onto his knees and rubbed his face in the same spot and then lay down (1700 h).

At 1720 h the bull again arose and started off in the direction of the cows in the dominance posture. Approximately halfway to the cows the bull started scraping the ground with his front feet, homed the soil, rubbed his face on the ground and then defecated – all on the same spot. The bull then again resumed the dominance posture and moved on towards the cows. When the bull reached the termite mound he smelled the site where the cows had rubbed their faces and again defecated. After this the bull led the herd further afield and they resumed grazing.

DEFENCE OF THE TERRITORY

As in all territorial species, boundary conflicts and the active defence of the territory are some of the prominent activities of territorial tsessebe males. Defence of the territory may conveniently be divided into the following categories.

Patrolling

A great deal of time is spent by the territorial bull in patrolling his territory. During these patrols bulls quite frequently withdraw from the herd and leave their harems for as long as eight or more hours. Bulls may either leave their harems during periods of grazing or during the resting intervals. Territorial patrolling has also been observed in the topi (Walther 1968).

Initial surveys have indicated that tsessebe defend relatively large territories. These are to the order of two to four km² and therefore explain the extensive patrolling by the males. When patrolling the males maintain a steady gait with the ears extended in an alert attitude. During these patrols the males defecate at regular intervals. Territory patrolling not only serves the function of marking the territory and of making the male conspicuous in his own domain but also brings the male into direct confrontation with neighbouring rivals.

The Challenge Ritual

When a territorial male detects the presence of a rival on or near his own territorial boundary, he immediately hurries towards his rival in the same determined manner as when he patrols his territory. As the territory proprietor meets his rival, he repeatedly throws his head up into the air in up and down movements, known as head casting (Fig. 3). If the rival accepts the challenge he will reciprocate in a similar fashion and the two animals assume a reverse/parallel stance to one another and continue to bob their heads up and down. While maintaining the reverse/parallel stance they also tend to wheel around in a tight circle. If the two animals are well matched the



FIGURE 3

The nose-up posture of the head casting display of a territorial bull. Note the lateral presentation stance of the displaying animal.

head casting becomes more intense and one or both at times even rear up on their hind legs while casting. Casting also takes place from the lateral presentation stance in which the displaying animal assumes a broadside position in front of the other.

If one of the animals retreats and runs away the dominant male will usually give chase and attempt to gain a position ahead of the inferior male. Even while giving chase at speed the challenger keeps throwing up his head and once he has succeeded in passing the retreating male he will jump up into the air and simultaneously turn his flank to the other male (lateral presentation) and throw his head up. If this stops the fleeing animal, head casting between the two is again resumed as described above.

Head casting in tsessebe may be interpreted as threat behaviour and therefore a manner in which a rival may be intimidated into submission even before two contending animals have made bodily contact. The more intensive the casting becomes the higher the animal attempts to lift his head until the demonstrator eventually rears up on his hindlegs. This obviously confers a higher degree of 'threat-value' to the display and precedes actual fighting.

Though head nodding is fairly conspicuous and of frequent occurrence in the bontebok it is associated rather with the movements of the animals than with any part of the challenge ritual (David 1970). Of all *Damaliscus* spp., head casting appears to be peculiar to the tsessebe.

Fighting

If a conflict between two males is taken beyond the display sequence the two will break from the reverse/parallel or lateral presentation stance and revert to a face-to-face position, standing 2 – 3 m apart. From this position they suddenly drop onto their knees with the lower jaw pulled in, thus tilting the curved horns forwards. At a low intensity level the males will jump up again and continue with head casting. However, the usual procedure, when the males drop onto their knees, is to lunge forward and clash their horns together, and then immediately to retreat a metre or two and again lunge forward. This is repeated a number of times although one or both of the males may jump back onto its feet and return to its knees with a resumption of the clashes. These

frequent, though brief, clashes may, nevertheless, still be considered as low intensity fighting during which either of the two males may withdraw at any stage.

Displaying and low intensity fighting occur frequently during boundary disputes and are the main forms of direct aggression between two rivals (cf Walther 1968). Severe or high intensity fighting occurs infrequently and is represented by a continuation of horn butting which eventually develops into a vicious pushing duel between the two rivals. During the pushing duel the two males, still on their knees, interlock their horns and, with tails either drawn in between the legs or switching from side to side, try to push one another off the mark. The severity of this pushing duel may be judged from the clouds of dust kicked up in the "heat of the battle".

No evidence could be found of severe injuries which could be directly attributed to these fights. A number of animals, both male and female, were found with broken horns and it is probably reasonable to assume that at least some of these were due to fighting. In one particularly severe bout of fighting between two bulls the horns of the inferior animal got caught around the neck of his adversary. The dominant bull then proceeded to push the other down into the ground until he almost lost his balance before he could free himself. However, the lesser animal sustained no injuries during this fight.

It could, therefore, be concluded that fights serve the primary function of enhancing the 'psychological' superiority of the victor and, conversely, of bringing the rival into 'voluntary' submission. This further accentuates the rôle of the elaborate threatening displays which precede fighting and during which the dominant/submissive relationship between two males may be determined, thereby averting actual fighting.

During the entire challenge and fighting sequences the participants frequently break and indulge in activities such as defecation, scratching of the chin or neck with a hind foot or short spells of grazing. These diversions from the actual conflict situation fall within the limits of so-called displacement activities and are closely linked with these displays of antagonism.

The following field observation will suffice to illustrate the typical challenge ritual and fighting in tsessebe: At approximately 1200 h on 10-7-'70 a herd of six tsessebe (A) were found resting 500 m West of their watering point. Half an hour later a herd of seven (B), which occupied a territory to the north of the waterhole, was seen approaching the waterhole with the herd bull 150-200 m ahead of his harem. When male B had approached to within 250 m of the waterhole male A, which was approximately 400 m from male B, arose and immediately started off in the direction of male B. Male B then stopped and awaited the approaching male A. Male A's herd did not follow him but remained at their resting site while male B's herd remained 150 m behind their bull. Only one cow came closer (to 20 m from male B).

As the two bulls met both lifted their heads and started casting. Head casting was interrupted when one or both started grazing or scratching the neck with a hind foot. After these interruptions head casting was again resumed. If either of the two bulls tried to move away the other would take up a lateral presentation position and continue with head casting. Occasionally the displaying animal would also rear up onto its hind legs.

Suddenly male B broke away and charged at the cow from his herd, which had been standing 20 m away. The cow immediately retreated to where the rest of the herd was standing (150 m away). While the charge was in progress, male A desperately tried to get ahead of male B and, on succeeding, jumped into the the air, with head held high and turned his flank to the other male.

Male B then stopped the chase and threat behaviour again ensued. Male B then went onto his knees and male A took up a position in front of male B. Both bulls then started grazing and scratching their necks until they approached one another, face-to-face, dropped onto their knees and viciously clashed horns. These sequences were repeated several times during a period of 25 minutes. Head pushing became so severe that at times the two animals were actually blurred in a cloud of dust. During the process male A pushed male B back over a distance of 30-40 m and during one of the clashes the horns of male B hooked over male A's horns. Male A then determinedly tried to push male B's head down to the ground. As soon as male B forced himself loose he jumped up and raced off into a thicket with male A in hot pursuit. Both then disappeared from sight. Ten to fifteen minutes later male A rejoined his herd.

Termination of territorial conflicts

In the foregoing discussion mention has been made of the apparent reluctance of rivals to engage in actual fighting bouts and the infrequency of high intensity fights. In other words it may be concluded that preliminary threat behaviour and low intensity fighting may give opponents ample opportunity of 'sizing one another up' with the alternative of either withdrawing or continuing the conflict. In unevenly matched individuals the conflict may never get beyond the exchange of threats when the inferior animal retreats, or it may reach the stage of low intensity bouts of horn clashing.

A retreating animal is invariably chased furiously by the more dominant one after withdrawing from a confrontation. It has also been observed that if a territorial male is confronted in the territory of another male the intruder is markedly submissive towards his adversary. After withdrawing from such a conflict and being chased back into his own territory the initial intruder regains his confidence and a much more evenly matched confrontation takes place between the two on their communal boundary. These confrontations are usually terminated when either one of the two bulls returns to his herd in his own territory. Conflicts of this nature clearly illustrate the psychological influence that territorial ownership exerts on tsessebe in the determination of the dominance/submissive relationships amongst the territorial males.

Territorial male: female relationships

In the Kruger park tsessebe herds generally consist of seven to eight individuals. The males defend permanent territories and each harem herd is confined to the territory of a particular male.

In many territorial species males establish fixed territories though the nursery herds are not confined to particular territories. Rather, the nursery herds traverse the various territories at will, and are vigorously herded by the territorial males in an effort to retain them on their territories. Though the male may sometimes achieve this goal his success is usually only of a temporary nature; after remaining in a particular territory for a varying length of time the females move off and into the territories of adjoining males (Walther 1964; Estes 1968; Lynch 1970). In these cases herding of the females takes the form of ritualized displays and constitutes an integral part of territorial behaviour.

Although the nursery herds in tsessebe are each confined to a particular male's territory, herding is nevertheless one of the prominent activities of the territorial bull. Herding is achieved by means of the ritualized dominance display and the bull assumes total leadership of the herd.



FIGURE 4

The "ears down, tail up" posture of the tsessebe bull during the dominance display.

In the closely related topi of East Africa, bulls defend territories which are 200 to 400 m in diameter. A nursery herd is not confined to the territory of a particular male, though they may remain in the territory of a male for a few days at a time (Walther 1968). This differs significantly from the position found among tsessebe in the Kruger Park. As yet, no thorough study of the social behaviour of this species has been undertaken. However, the densities of the populations vary considerably from one area to another e.g. on the Liuwa Plain of Barotseland herds of over 150 animals have been reported (Benson 1969). It is not known to what extent the densities of the various populations influence the social behaviour of the tsessebe, though it is believed that the position pertaining to the Kruger Park is an adaptation to the local environmental conditions.

The dominance display of the tsessebe bull is probably the most attractive of the various displays performed by this species. When displaying to the females the bull raises his head aloft with the nose pointing forward. The ears are held rigidly down the neck and point towards the ground (Fig. 4). In the low intensity form of this display, the bull retains his normal walking gait while the tail hangs loosely down or is withdrawn between the hind legs. In the high intensity form the legs and tail also enter into the display. The bull's movements are slow and delicate while the front legs are lifted high at the knee with each stride forwards and placed down carefully and gently, the movements slow but deliberate. The tail is lifted in accordance with the intensity of the display and in extreme cases is lifted above the horizontal plane. By means of this display the bull asserts his dominance over the cows.

The dominance display is one of the most frequently repeated displays of the territorial male. It has already been mentioned that the bull often isolates himself from the females and young in territorial advertising or while patrolling his territory. Should any disturbance arise while the male is separated from his herd he immediately hastens to the herd and on approaching and rejoining them he assumes the dominance display. The reaction of the females to the display is to group together in a tight unit. If one of the cows is still reluctant to join the herd the bull herds her to the others while retaining the display posture. This performance is repeated every time the bull rejoins his cows after being absent for some time. The high intensity form of the display is almost



FIGURE 5
The submissive display of tsessebe calves.

invariably assumed when the bull returns to his cows after a dispute with a rival male. The display is also conspicuous at waterholes where there is occasionally contact between adjoining herds.

By assuming leadership of the herd the bull determines the movements and general activity of the females within the territory. When deliberately moving away from one area to another the bull exhibits the same posture as when patrolling his territory or approaching a rival; once the bull has started moving away, the females and young follow suit in single file. On reaching its destination the herd becomes more relaxed and resumes grazing or other activities. Because the "leadership posture" of the bull is the same as when he is patrolling his territory, it may be assumed that it not only serves to subordinate his herd but also inhibits rival males and may therefore be regarded as visual territory advertising.

Territorial male: immature relationships

A close mother-calf relationship exists in tsessebe and due to the particular position of the territorial bull in the herd he is automatically and totally dominant over the youngsters. Bulls in fact, do not assume any obvious display posture to exert their dominance over the immatures. If a male approaches a youngster it displays the submissive posture which is equally as attractive as the dominance display of the bull. Submissiveness is signified when an immature lifts his head up high, pulls its lower jaw in tightly towards its throat with the ears held straight up above the head. Simultaneously the tail is held rigidly and horizontally away from the body (Fig. 5). If chased by the bull the immature retains this posture while giving long, stiff-legged bounds (stotting action). If the chase is severe this pace is too slow and the calf reverts to the normal manner in which the animals run at high speed. This applies to both male and female calves.

From the preceding discussion on territoriality it has become apparent that at some stage the young males must be evicted from the nursery herds. Male eviction becomes evident soon after the commencement of the calving season and steadily gains momentum as the rut approaches. As tsessebe have a well-defined calving season, that is from mid-September to the end of December, and the rutting season commences early in January, the bulk of the yearling males are evicted from

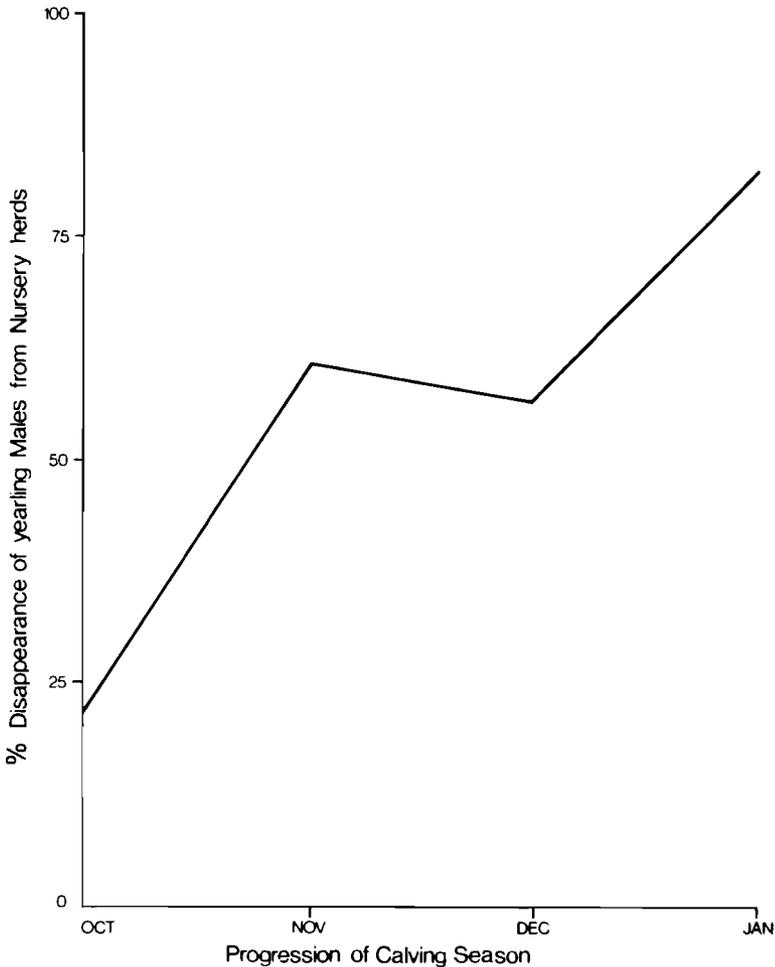


FIGURE 6
Eviction of yearling males from nursery herds.

the nursery herds in the period September to January. This process is clearly illustrated in Fig. 6.

The first sign of the eviction process is when the herd bull persistently chases and harasses the young males. The young males repeatedly attempt to return to the nursery herd until they are eventually driven away. In the eviction process chasing is vigorous and at high speed with the youngsters repeatedly emitting short distress calls.

Yearling males that have been ousted from their nursery herds group together to form bachelor groups. The largest bachelor herd recorded in the Kruger Park consisted of six yearlings. The members of bachelor herds do not necessarily consist exclusively of yearlings but may also include

some older males and at times even a young female. From an estimation of the age of the males in bachelor groups it appears that males older than three years are seldom found in such groups. Among bontebok David (1970) found that animals of all age classes were represented in the bachelor herds.

Bachelor groups do not have any fixed area of activity but move about on the peripheries of established territories. If confronted by territorial males they do not reciprocate the challenge but flee to "vacant" areas where they are free from persecution. These males undoubtedly serve as an important reservoir of potential territorial bulls in the case of death or severe injury to established territorial bulls.

Skirmishing is frequent among the members of a bachelor group and it is believed that males attain full territorial status at the age of three to four years and then become intolerant toward the younger males. Mature lone bulls are frequently seen and probably represent those that have left the bachelor groups and have not yet been able to acquire their own harems. Some of these lone bulls may also have been ousted from their territories by more competent males.

CONCLUSIONS

From the foregoing discussions on the demarcation and defence of a fixed area and the relationships of mature bulls to other individuals of the species, it is quite evident that tsessebe conform to the prerequisites of a true territorial species. Similar forms of territoriality have been noted for a variety of other species (Walther 1964; 1965; Estes 1968; Lynch 1971; David 1970) and serve to validate the definition for this particular type of social organisation.

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