TERRITORIAL BEHAVIOUR OF THE BLACK WILDEBEEST

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ABSTRACT

The territorial behaviour of the black wildebeest was studied from 1968 to 1970 in the Willem Pretorius Game Reserve and other reserves in South Africa.

Territoriality is a prerequisite for reproduction. Non-territorial males are barred from partaking in the rut. Territorial males may occupy a territory from their fourth year on, but the majority of territorial owners were five years old or more.

Territorial males formed a network of territories, although single territorial males could also be observed. The spacing between individuals varied between 180–450 m in the Willem Pretorius Game Reserve; spacing of territorial black wildebeest as well as the number of territorial males depend on the density of the population.

Territorial black wildebeest showed a strong and lasting attachment to their territories. The species was territorial throughout the year although absenteeism became prevalent after the rut.

Territorial black wildebeest advertised their territories and defended them against intruding conspecific males. Advertising behaviour included demonstrative-threat advertising derived from marking as well as acoustic, static-optic and dynamic-optic advertising. The species did not demarcate a territory with either faeces or urine, or pre-orbital or interdigital glands.

The encounters of territorial males were governed by highly ritualised motor patterns (Challenge Ritual). The ritual includes both aggressive and non-aggressive behaviour patterns.

The Challenge Ritual ensures that only the fittest male can maintain his territory and thus partake in the rut. Furthermore, it serves to "satisfy" the social needs of the solitary bulls in the highly gregarious species. Other functions of territorial behaviour include the separation of sexes and the spacing out of the population.

The known agonistic and territorial behaviour of the various species of the tribe Alcelaphini is compared and discussed. The differences and similarities in behaviour do not follow the taxonomic separation of the various species but are indicative of different habitats.

Territorial behaviour in large African mammal species has been the subject of a number of studies in the recent past. Territorial behaviour in the tribe Alcelaphini has been recognised and discussed cursorily or in detail for the following species: blue wildebeest (Talbot *et al.* 1963; Estes 1969; Watson 1969), hartebeest (Backhaus 1959; Dowsett 1966; Gosling 1966; Kok, personal communication), blesbok (Lynch 1971), bontebok (David 1970), tsessebe (Huntley 1970) and topi (Walther 1968a).

Burchell (1823) described the solitary black wildebeest bulls as far back as 1823 and their territorial advertising, although he was not aware of their social significance in a wildebeest population. Territorial behaviour in the black wildebeest was mentioned for the first time by Estes (1969).

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Study area

The observations were carried out mainly in the Willem Pretorius Game Reserve, which comprises approximately 10 300 ha in the central Orange Free State. The reserve harbours the largest black wildebeest herd in the world (443 in August 1970). It is situated in the species' former range (von Richter 1971) and the herd represents a re-introduction.

The Willem Pretorius Game Reserve is divided into two parts by a large irrigation dam. The south side of the reserve, where approximately two-thirds of the black wildebeest population occurs, is open, rolling grassland with a few scattered *Acacia karoo* trees. The north side is more broken with a denser woody vegetation in the hilly areas. Black wildebeest frequent only the open parts around the lake shore.

Further observations were carried out in the S.A. Lombard Nature Reserve in the southwestern Transvaal; in the Giant's Castle Game Reserve, the Golden Gate Highlands National Park and the Mountain Zebra National Park.

PROCEDURE

The study commenced in late 1968 and terminated in April, 1971. Visits were paid to the Willem Pretorius Game Reserve at 3 month intervals and at longer intervals to the other reserves. To facilitate the study, 12 subadult and adult bulls were marked with collars of a nylon weave material covered with polyvinyl plastic (red strips with yellow geometrical designs) in April 1969 in the Willem Pretorius Game Reserve. Nine bulls still retained their collars in April, 1971, one had died and two had lost their collars.

Observations were carried out with a 40 x 60 telescope and binoculars. The shyness of the animals, partly due to annual catching operations, hampered the study insofar as the animals could not be approached very closely.

RESULTS

THE WILDEBEEST POPULATION AND ITS SOCIAL ORGANISATION

All black wildebeest populations in South African game reserves are sedentary, as the size of any reserve prohibits any large scale movements. As water and grazing is easily available throughout the year, movements were limited to daily excursions by the various herds and the territorial bulls to the watering places, i.e. in the Willem Pretorius Game Reserve to the lake shore. This sedentary behaviour in the reserves contrasts strongly with the reported seasonal large-scale migrations of the species in the past, in east-westerly and north-southerly directions (von Richter 1971).

The sedentary behaviour is reflected in the social and to a certain extent also in the territorial behaviour of the species. Estes (1966; 1969) and Watson (1969) remark also on the difference in certain behavioural aspects of the blue wildebeest in migratory and sedentary populations in East Africa.

During the study period the ratio of adult males: females fluctuated seasonally due to catching operations. In August 1970 (after the removal of animals for distribution) the sex ratio of the adults was 60 males : 100 females; a preponderance of females was also recorded in the S.A.

Lombard Nature Reserve, while in the Mountain Zebra National Park, from which no animals have been removed so far, the sex ratio is nearing parity.

A black wildebeest population can be separated into three distinctive social organisations; for a detailed account refer to von Richter (1971a).

(I) The female herd, which consists of adult and subadult females with calves, yearlings and an occasional sub-adult male. Most of the yearlings are females although a small percentage of male yearlings might survive in a female herd. The "cutting out" of yearlings described by Estes (1969) for the blue wildebeest also occurs in the black wildebeest, but with much less vigour and vehemence. This is not due to a genetic difference in the behaviour of the two species but reflects the sedentary behaviour of the species in the reserve and the annual catching operations, when usually young females are removed from the individual herds. The average herd size is 29,7 adult females, yearlings and calves. The members of a female herd show a remarkable attachment to each other and strange animals are not tolerated in the herd. The female herds occupy a home range, which they leave only reluctantly. Several herds are known to have stayed for 18 months throughout the rainy and dry season, in the same area.

(II) Bachelor groups consist exclusively of non-territorial adult, sub-adult and yearling males. Attachment between the members of a bachelor group is less strict than in a female herd, and bachelor groups constantly roamed throughout suitable habitat in the reserves, staying for shorter or longer periods in specific areas. A bachelor group will occasionally attach itself to a female herd. The most outstanding feature of a bachelor group is the nearly complete absence of any display of territorial and sexual behaviour patterns and the great tolerance shown to each other. The significance of this for the general social and biological organisation of the species will be discussed in more detail below.

(III) This social unit is the territorial or solitary male. The ratio of territorial bulls to non-territorial bulls in the Willem Pretorius Game Reserve varied due to catching operations during the study period. Between 28 and 55% of all adult males occupied a territory; in December 1969 the percentage went up to 76% on the north side of the reserve. If the number of territorial males is related to the total adult population, there are 14 to 15% territorial males or 6 to 9% of the total population. Estes (1969) reports that up to 50% of all adult males occupy a territory at any time in Ngorongoro Crater, *viz.* 8 to 16% of the total population. Watson (in Estes 1969) reports that 40% of all adult males (20% of the total population) in the migratory blue wildebeest population in Serengeti are territorial during the rut assuming a 100 : 100 sex ratio of adults. Ratios of territorial to non-territorial males in other reserves substantiate that in the black wildebeest as in the blue wildebeest (Estes 1969) the number of territorial males is density dependent. The following discussion will be centred on the territoriality of the black wildebeest.

THE TERRITORIAL MALE

All territorial males in the Willem Pretorius Game Reserve were judged according to the shape and size of their horns and general body size to be at least four years old; the majority was probably five years and older. That is in accordance with the findings of Watson (1969) for the Serengeti population. Estes (1969) reports that in Ngorongoro bulls may procure a territory when they are 34 to 40 months old; a few were observed to participate in the rut at 28 to 29 months. Blue wildebeest bulls are physiologically capable of reproducing between their second and third year (Watson 1969). On a few occasions 28-month-old black wildebeest males were observed displaying mating behaviour towards females and mounting without erection. In all the observed instances these young males made use of the opportunity when the territorial male busied himself with other females or was temporarily absent.

Individual males might be, however, capable of reproducing earlier. Van Zyl (personal communication) reports that a 16–18-month-old male was kept in captivity with a female, which he served successfully. Notwithstanding the few quoted exceptions, a wildebeest male can only reproduce if he is in possession of a territory. Younger males who might succeed in entering a cluster of territorial males during peak rutting season still must procure a territory to be able to breed. Adult males who are relegated to a bachelor group, show little or no sexual drive. Reproduction is therefore coupled to possession of a territory; a male without a territory is a "psychological castrate" (Estes 1969).

THE INDIVIDUAL TERRITORY

The centre of each individual territory is the stamping ground of the territorial bull, a bare patch of ground covered with dung and devoid of any vegetation due to the constant pawing, horning and rolling on this specific spot by the territorial male. The individual territories are not visibly separated; the presumed border lies halfway between two neighbouring males. Apart from the presence of a territorial bull only freshly used stamping grounds indicate visibly that a territory is occupied. In the Willem Pretorius Game Reserve where some remaining fences sometimes formed fixed borderlines, neighbouring bulls challenged each other through the fence.

Territorial males stay in clusters, forming a territorial network; the territories of various sizes and shapes form a mosaic pattern. The individual clusters are separated in some instances by several kilometres, leaving large areas of seemingly suitable habitat without a territorial network.

On the south side of the reserve five to six such territorial clusters could be observed, while on the north side of the reserve, where suitable habitat is limited to an open vlei, only one such cluster could be recognized.

The spacing between territorial bulls varied considerably in the different clusters and on both sections of the reserve. On the south side the spacing varied between 270–450 m, while on the north side the spacing was between 180–270 m. R.C. Bigalke (in Estes 1969) estimated the spacing of territorial males on a private reserve in the Kimberley division as 800 m. The spacing of the black wildebeest is, therefore, considerably wider than in the blue wildebeest, where Estes (1969) gives 108–145 m for territorial males in Ngorongoro Crater.

The variation in the spacing of territorial males indicates density dependence, based on the available habitat and the number of territorial bulls who compete for a territory. In the closely related blesbok and bontebok the spacing of territorial owners differed considerably and Lynch (1971) attributes the relatively short distances between territorial blesbok to the high population density.

In addition to territorial males in clusters a number of individual territorial males were found. There were no indications that the area where these individual males were encountered constituted a territorial network prior to the commencement of this study. The areas were very seldom frequented by female herds. Estes (1969) also reports these lone bulls in the Ngorongoro population and suggests that they are remnants of a territorial network established in a previous season. The solitary black wildebeest males were judged to be either before or past their prime. Interestingly enough, Lynch (1971) reports a definite dichotomy in territorial behaviour in blesbok, *viz.* a territorial network of prime adult bulls and single territorial bulls, in the majority before their prime.

Blesbok territorial behaviour is, therefore, comparable to the Uganda kob (Leuthold 1966). Lent (1969) also remarked on polymorphism in territorial behaviour in the red lechwe. Territoriality was prominent in "habitat apparently of near-minimal size" while non-territorialism was displayed by the males in more favourable habitat.

The solitary territorial males in the black wildebeest population could be the result of a relatively low population density. Males who are not fit enough to compete for a territory in a cluster procure one in an area where competition is less strong. In a high density population where every available habitat is taken up by a territorial network, these males probably would have to join a bachelor group.

Territorial males in the sedentary black wildebeest population show a strong and permanent attachment to their territories. All individually known territorial bulls occupied the same territory for the whole study period (2 years). The attachment is so strong that the bulls return even after prolonged catching operations when the whole territorial network is temporarily but completely disrupted.

Territorialism is displayed by the bulls throughout the year though territorial activities become less pronounced after the rut. Absenteeism of territorial males was prevalent after the rut. Males would abandon their territories for shorter or longer periods, and temporarily join bachelor groups. However, they would inevitably return to their stamping grounds. One bull would regularly leave his territory in the early morning, join a bachelor group and return in the evening. Occasionally several bulls would abandon their territory for a week and only then re-occupy it again. On no occasion was a bachelor bull observed trying to occupy the abandoned territory. Estes (1969), also reports absenteeism in the blue wildebeest, where it was particularly heavy during a prolonged and severe dry season, resulting in poor range conditions. The increased absenteeism in the black wildebeest coincided also with the dry season in the Willem Pretorius Game Reserve but there seems to be no evidence for coupling it with a degraded pasture.

A remarkable fact is that although the black wildebeest is a strictly seasonal breeder, territorialism is exhibited throughout the year. One would assume that territoriality would only be prevalent during the rutting season as the prerequisite for reproduction. Following Estes' (1969) concept that nomadism developed from sedentary and territorial populations, and that the peak calving season has been shaped by predation, the apparent paradox of a well-defined calving season but territorialism throughout the year is explainable. The older behaviour patterns e.g. territorialism have been retained while the species otherwise adapted itself to nomadism in a savanna-type habitat. Territorialism in migratory wildebeest is only displayed during the rut (Watson 1969), while sedentary populations such as in the Ngorongoro Crater and the black wildebeest in South Africa exhibit territoriality throughout the year.

TERRITORIALISM

To classify a species as territorial, certain criteria have to be met. Schenkel (1966a) discusses in detail the concept of territorialism and the implications in using the term. A species should only be termed territorial if intolerance is displayed by the territory owner towards intruders of the same species. So far only male territories are known in mammals, *viz.* the occupant displays intolerance towards other males. The intolerance, however, may also be extended to large scale invasion by females. This intolerance, however, must be coupled to a specific area. A further criteria stipulated by Schenkel (1966a), is that the occupant of a territory must be able to survey his territory constantly to meet immediately any challenge to his rights. That would mean, however, that all species which inhabit areas covered with denser vegetation are *a priori* defined as non-territorial. Impala (Leuthold 1970), hartebeest (Gosling 1966), bushbuck (Verheyen 1955) and waterbuck (Hanks *et al.* 1969; Spinage 1969; Herbert 1970), however, all have been recognised as territorial and all these species inhabit areas which are not open grassveld.

Furthermore, the territorial owner has to make his presence known to other members of the species. The most common means employed by mammalian species to advertise a territory are olfactory, visual and to a lesser extent acoustical signals, either alone or in combination with conspicuous and unambiguous motor patterns. Hediger (1949) for the first time described these functions in mammals as marking. The term advertising, however, is given preference unless an actual mark is left (Schenkel 1966a).

TERRITORIAL ADVERTISING

Four basic categories of advertising a territory can be found in the black wildebeest:

(1) Advertising or demarcation with scent from various body glands, faeces and urine.
(2) demonstration-threat advertising
(3) acoustical advertising
(4) static-optic and dynamic-optic advertising

(1) Scent marking

Black wildebeest have well developed interdigital glands on the forelegs and primitive pre-orbital glands. Pawing with the forelegs is performed by all sexes and age classes and precedes lying down, rolling and defecation, the latter only by territorial bulls. Territorial bulls especially paw vigorously on their stamping grounds, though also away from it. It seems very likely that the sticky secretion from the interdigital glands is transferred to his stamping ground. If a female herd stays in the territory they quite often also proceed to paw and roll on the bull's stamping ground.

The pre-orbital glands are shallow and cannot be opened or closed at will. The secretion impregnates the long tufts of hair which cover the glandular area. Males frequently horn the ground or rub their foreheads on the stamping ground. However, the position and the shape of the horns make it highly unlikely that any secretion can be transferred to the ground. Walther (1966) observing captive black wildebeest, reports that both sexes, but the male more often than the female, marked a branch with their pre-orbital glands. Blue wildebeest also rub their pre-orbital glands against trees (Estes 1969). Field observations on the black wildebeest, however, could not confirm Walther's observation. In any case in a treeless savanna, black wildebeest cannot employ the pre-orbital glands for purposeful demarcation.

Walther (1966), however, saw the same motor patterns as for marking being addressed to fellow members of the herd, but only between animals which were on "friendly" terms. The marking procedure was mostly addressed to the whithers and shoulders, and very seldom to the croup, resulting in the resting animal getting up. I could observe this specific rubbing of the forehead and pre-orbital gland region on two occasions. In both instances a male was standing directly behind a yearling male and an animal of undefined sex, respectively, moving his head up and down, so that his horns passed on both sides of the rubbed animal. Both situations, however, have to be considered as extreme, as the animals were either just caught and brought into a small cage or were confined in the crush.

Pre-orbital gland marking during courtship behaviour is known in gerenuk, dibatag, Lady Grey's waterbuck (Walther 1963; 1966) and some duiker species (Frädrich 1964; Aeschlimann 1963). Wilson (1966) reports a Lichtenstein's hartebeest male repeatedly rubbing his pre-orbital glands on the rump of a female in oestrus. Blue wildebeest occasionally perform head/head and head/rump rubbing between copulations, but this evidently has no sexual significance (Estes 1969). In the black wildebeest, however, the male regularly puts his head on the croup of a female he is about to mount.

A territorial male defecates most frequently on his stamping ground and paws vigorously prior to this; the other members of a wildebeest population, including the bachelor bulls, defecate at random and without pawing. Defecation also occurs frequently during a Challenge Ritual. Urination takes place mostly during the Challenge Ritual. On several occasions territorial males urinated when the observer approached too closely. In this context urination could denote threat.

Demarcation of the black wildebeest territory by scent (interdigital and pre-orbital glands, faeces and urine) is not acceptable. No evidence could be found that another territorial bull took exception to the specific smell of a neighbour. Not infrequently during a Challenge Ritual both contestants defecate and urinate on one and the same stamping ground. Also females, yearlings and calves will use the stamping ground for defecation and rolling.

As the territorial male frequently lies and rolls on his stamping ground, the secretion of his inter-digital glands and faeces will permeate his coat and give him a specific odour of his own. When the bull moves around he is constantly surrounded by it. It is advocated that this gives him self-assurance. Elephants are known to check their temporal glands in situations of uncertainty and insecurity (Kühme 1961). The position of the pre-orbital glands and the formation of the horns make it highly unlikely that secretion can be conferred in any amount to the ground while horning and the absence of trees in typical black wildebeest habitat rules out the use of trees as demarcation poles.

The marking of a tree and fellow members, reported by Walther (1966), is interpreted to be a sign of captive situation, where more archaic behaviour patterns surface again in a stress situation. That would also apply to the two instances reported by me. The greatest significance, however, is attributed to the various motor behaviour patterns which accompany the supposed setting of scent marks.

(2) Demonstration-Threat Advertising

Postures and movements coupled with the depositing of scent marks are very conspicuous and unambiguous in meaning and frequently function as visual displays. Hediger (1949) termed these displays "demonstrative marking", as, however, no actual mark is set the term demonstration-advertising is given preference. Demonstrative threat is addressed to conspecifics in general. The same motor patterns may serve, however, as threat if addressed to a particular individual.

(a) Kneeling and horning

Kneeling and horning the ground is found in all members of the Alcelaphini and denotes threat or challenge. Horning the ground is also recognised as threat in cattle (Schloeth 1961), impala (Schenkel 1966b) and Uganda kob (Leuthold 1966).

Horning in the kneeling position is not confined to territorial bulls but has also frequently been observed in females, yearlings and calves. Horning the ground is quite frequently followed by rolling. Quite often a rolling animal will get up into a kneeling position and move a few metres on the metacarpal joints, vigorously horning the ground. Kneeling – horning – rolling, when performed within a female herd by non-territorial animals, elicits no response from the onlooking animals. In some instances, however, it seems to have an infectious effect, as other animals would follow suit next to the performing female. Estes (1969) following Schenkel (1966b) draws the distinction between horning or weaving high grass in a kneeling position as aggressive, while "bush horning" is performed on the feet as an individual exercise which is non-aggressive, in the absence of trees the blue wildebeest will horn the ground in a standing position.

Actual horning of a bush, in a standing position, could not be observed in the black wildebeest, but territorial males and non-territorial animals have been observed horning the ground in a standing position. On one occasion a bachelor bull virogously whipped the grass in a standing position, then went down on his metacarpalia, horning the ground and proceeded to roll. He repeated the whole procedure shortly afterwards. A second bull performed the identical sequence at the same time. The other onlooking bulls showed no particular interest in the vehemently performed displays. During one Challenge Ritual both contestants performed horning in a standing position. Horning the ground in a kneeling position is frequently performed during Challenge Ritual.

As kneeling is the combat position, horning the ground by a territorial male in this position is definitely a high-intensity threat, especially if performed for the express benefit of an onlooking territorial neighbour.

Horning the ground, as it is performed by females and other non-territorial animals, however, does not fit into the concept of threat. As rolling follows quite often, it could serve to prepare a rolling place, and could as such be called a comfort movement. This is substantiated by the fact that rolling is very uncommon in horned animals and only wildebeest species roll so vigorously (Walther 1966). The possible function of horning the ground as an exercise can also be considered.

(b) Pawing

In black wildebeest pawing is not performed independently but is always the prelude to lying down, rolling and defecation. All sexes and age classes paw lightly with the foreleg, seldom alternately with both legs before lying down. Alternate pawing in high intensity is performed prior to rolling. Pawing alternately as a prelude to defecation, however, is only performed by territorial bulls. After pawing the bull will move a body length and defecate. Pawing in cattle is coupled with ground-horning and in high intensity with defecation and is interpreted as threat or a sign of self-assurance (Schloeth 1961).

Pawing prior to rolling and defecation probably serves to remove a certain ambiguity from kneeling and defecation (Estes 1969). To lie down, any wildebeest first has to go down on its metacarpalia. If a male paws vigorously before kneeling, he announces that he is going to horn the ground and/or roll, *viz.* he is in an aggressive mood. The defecation position for both sexes is not different; by pawing prior to defecation a male changes the inconspicuous act into a threat. Territorial males would regularly paw and defecate when the observer approached them on their territory. On a few occasions a territorial bull, returning to a female herd after having chased away an intruder, would paw and defecate in view of the herd. Estes (1969) reports that captive black wildebeest males would paw intensely and defecate in response to visitors.

Pawing followed by defecation is performed virtually in any Challenge Ritual by both contestants, sometimes repeatedly during the same encounter.

(c) Rolling

All members of a wildebeest population roll more or less vigorously. Its primary function is to rid the coat of parasites, hairs etc. Infrequently after getting back on their feet the animals shake the whole body. If an animal commences to roll, this sometimes acts as a releaser as the remainder of the herd will "queue" to get their turn on the rolling place. Individual animals will also move close up to a rolling one and proceed to paw and roll. As already mentioned under horning, animals will horn the ground prior to or intermittently between rolling. A female herd has favourite rolling places in its home range which can become quite large, shallow pits. From the resting position the animal will proceed to roll on one side, kicking all four legs into the air, return to the resting position, and roll on the other side. While lying on the back, the horns penetrate the ground, the head being moved with a jerking motion.

Prior to rolling or in between an animal will stretch its neck on the ground and move from side to side, scratching throat, chin and, by turning the head slightly, also the side of the neck. Occasionally neck scratching will be performed on its own. Neck scratching is purely a maintenance activity, and is considered to be an evolutionary "fore-runner" of rolling (Walther 1966).

Walther (1965a) reports rolling in bison, *Bison bison,* and yak, *Bos grunniens,* and interprets it as a demonstration of strength. Schloeth (1961), describing a relict of rolling in the semi-wild Camargue cattle, interprets it to be threat as well.

Rolling performed during a Challenge Ritual in the full sequence, with fore-going pawing and horning, could certainly be interpreted as threat as (Estes 1969) has already indicated for the blue wildebeest. In all the other reported instances rolling serves as a comfort movement.

(3) Acoustical advertising

The song of male birds has long been recognised as a means of advertising a territory. Vocal displays as an acoustical advertisement in mammals has recently been reported for the Uganda kob (Leuthold 1966), reedbuck (Jungius 1971) and probably the mountain reedbuck (Irby, personal communication) and the Vaal rhebuck (Esser, personal communication). Estes (1969) describes the advertising calls of both wildebeest species. The advertising call of the black wildebeest is a very loud, two-syllable sound uttered through the open mouth, the head being moved downwards and then upwards. It could be described as "ge - nu" which incidentally is the Hottentot name for the species.

The territorial bulls call most frequently during the rutting season, when the individual animals of a territorial network take up the call from each other. Approaching conspecifics and also human beings will regularly be met with the call by territorial bulls. When a male is herding or chasing, the call is frequently heard and also when he returns to a female herd which is in his territory. During the mating season males will call very vigorously while inspecting or mating females. Estes (1969) reports that he never heard the call during a Challenge Ritual. On a few occasions black wildebeest males engaged in an encounter were heard to call at each other just before they withdrew. The situation in the Willem Pretorius Game Reserve did not permit clarification as to whether female herds are attracted by the call, a function Estes (1969) did not rule out.

(4) Dynamic-optic and static-optic advertising

A territorial bull is easily recognised by his stance; he holds his head high (head-up posture, Talbot *et al.* 1963) while all non-territorial animals carry their heads at or below shoulder level. A territorial male usually canters with a very pronounced gait, head high and setting down his legs rather stiffly when approaching an intruder. It is the head-up posture set into motion (Estes 1969). Herding and chasing is also a manifestation of territoriality. The bull gallops at high speed, head at or below shoulder level, moving his head up and down, lashing his tail from side to side and making intentional jab movements when passing the flank of a female or bachelor group.

The mere presence of a male either standing in head-up posture or resting on his stamping ground is sufficient advertisement to other conspecifics that the territory is occupied. It fits the concept of "static-optic marking" (Hediger 1949) or advertising.

White-tailed gnu, the alternate name for the black wildebeest, denotes the long and very conspicuous white tail of the species. Primarily a fly whisk and used as such very frequently, the white tail has assumed social significance, especially in territorial males. Black wildebeest moving or grazing keep their tails down, occasionally switching it from side to side. Territorial males will lash it from side to side when approaching an intruder, when cavorting, kicking and bucking either during an encounter or when made to flee; bulls and non-territorial animals swish them vigorously, sometimes giving the impression of a rotating fan. When charging another bull, chasing a bachelor group or an individual male, or herding back escaping females, the tail is raised high like a flag. Bachelor males chasing each other in large circles also carry the tail straight up. The tail is employed most conspicuously in a submissive posture adopted by non-territorial black wildebeest. A molested animal will raise its tail and hold it horizontally, at the same time displaying a stretched-out neck; if molested further the tail may be raised higher and held horizontally over the back. Walther (1966) described this appeasement behaviour for the first time in captive black wildebeest.

Females hold their tails horizontally when urinating and raise them slightly less when in oestrus and when they are inspected by a male.

THREAT BEHAVIOUR

The motor behaviour patterns described under the heading, demonstration – threat advertising, are displayed almost exclusively by territorial males. As we will see later, they can all form part of a

Challenge Ritual between territorial neighbours.

A number of motor patterns are, clearly intimidating and are performed by territorial and non-territorial animals alike. A territorial male will display these motor patterns in the majority of cases during a Challenge Ritual or when he is approached on his territorial ground.

(1) Cavorting

The most impressive threat behaviour, second only to actual combat, is cavorting. Territorial males will cavort around each other, lashing and swishing their tails, tossing and shaking their heads, standing on their forelegs and kicking with the hindlegs. They might jump into the air with all four legs off the ground, kicking with their hindlegs or standing on their hindlegs, lower jaw pulled in and thrust their heads from above towards an opponent. Two territorial males may display cavorting at the same time, racing parallel to each other along the presumed boundary, heads much closer to each other than the hindquarters.

The same performance can be evoked by grossly disturbing a bachelor or female herd, and putting them to flight. A territorial male, which has been approached and forced off his stamping ground, will perform this impressive-looking display. *Cavorting* on a low intensity level can also be observed in the games of calves and yearlings and within bachelor groups.

Cavorting is the common response of a wildebeest made to run away. It is an example of a behaviour pattern where aggressiveness and flight is being released simultaneously (Tinbergen 1964). Running away is a clear indication of fear, while all other components are equally obviously aggressive. Estes (1969) describes and interprets *cavorting* in blue wildebeest in the same way.

(2) Head-shaking

In the majority of cases this forms part of *cavorting* but it can, however, also be displayed on its own, especially during the Challenge Ritual of territorial males. *Head-shaking* is also displayed by non-territorial animals. Apart from its display in the Challenge Ritual and in *cavorting, head-shaking* is addressed to inferior or submissive animals *viz.* a cow towards her calf or a yearling.

(3) Head-throwing

Head-throwing or *head-nodding* is perfomed by territorial and non-territorial animals alike. As already pointed out by Walther (1966), *head-throwing* is an intention movement to jab and is most frequently addressed towards the rump and the flank and seldom toward the head. Territorial bulls display it during the Challenge Ritual, though it occurs quite irregularly, and also when chasing or herding bachelor and female herds. Territorial males will carry their heads at or below shoulder level when displaying *head-throwing. Head-throwing* is, however, most frequently observed within female herds. Females will intimidate each other in this way, and especially when threatening calves and yearlings. A resting animal will quite frequently respond with *head-throwing* when another animal stands directly behind it.

Head-nodding, a low intensity head-throwing, is known in the whole Alcelaphini tribe, and is interpreted as a threat motor pattern, which in some species has lost its direct intimidatory effect and has been transformed into behaviour pattern indicating restlessness prior to moving on (Walther 1968a).

Head-shaking and *head-throwing* both have in common the fact that they are usually addressed to inferior animals, which are then expected to give way. In Grant's gazelle a similar situation prevails where *head-tossing* is directed only to inferiors (Walther 1965b; Estes 1967).

CHALLENGE RITUAL

Territorial advertising has an intimidating or challenging effect on other territorial males according to their own status. A territorial male, away from his territory, will in most cases move away quickly when accosted by a territorial owner. A neighbouring territorial male, however, will respond to the territorial advertising as if his own territorial integrity had been challenged. As will be discussed later, territorial neighbours actually seek contact with each other. The encounters between territorial males are ritualized and Estes (1969), who described these encounters for the first time in the blue wildebeest, termed them Challenge Ritual.

The various motor patterns performed during a Challenge Ritual are highly stereotyped and have been found, with a few exceptions, in all members of the tribe Alcelaphini which have been the subject of a detailed study. The sequence and the intensity of the various steps performed during a Challenge Ritual, however, vary considerably and are subjected to external stimuli and internal motivations, a fact Estes (1969) stressed in his discussion of the Challenge Ritual in the blue wildebeest. Accordingly no two Challenge Rituals are identical to each other, as steps may be left out altogether, shown only in low intensity or repeated frequently, resulting in the omission of other steps. No attempt, therefore, will be made to give a detailed account of one Challenge Ritual but to describe and discuss the various steps which occur during a Challenge Ritual. I shall follow Estes' (1969) terminology closely as the Challenge Ritual in both species is almost identical.

(1) Approach and Withdrawal

A territorial male approaching another male's territory will usually do so with his head at or below shoulder level, and will in most instances adopt the *grazing attitude* when he comes very close to the territory owner; he also moves very slowly. This is especially noticeable if the invader has come galloping up straight at his neighbour; he will slow down and start to move in *grazing attitude* towards the other male. The defending male commonly meets the invader also in the *grazing attitude*, or shows disinterest by keeping his head low and waiting for the invader. To meet an invader with *head-high posture* is the most aggressive expression of the defending male. The head posture of a defending male is a fair indication of his present mood.

The *head-low posture* and even more so the *grazing attitude* counteracts the approach, which in itself can be termed aggressive. During withdrawal the invader again, as a rule, keeps his head in the *grazing attitude*, thereby counteracting the retreat, which otherwise could invite the defender to attack. During the peak rutting season, approach and withdrawal can escalate into wild chasing, the defender hotly pursuing the invader. Infrequently it could also be observed that the defending male stood in the *head-up posture* and called loudly after the invader had left.

(2) Lateral Presentation

A territorial owner will quite often display *lateral presentation* towards a trespassing male. The defending male will stand at right angles to the invader, head held high. Again, the manner of holding his head depends on the self assurance of the defending male. *Lateral presentation* is not the prerogative of the defending male, however, as intruding males will also display it, although not as frequently.

If a male crosses the periphery of a territory without any sign of approaching the territorial owner, the latter will quite often simply run past him repeatedly, displaying *lateral presentation.* The accosted male then usually passes behind the territorial male and no further action occurs. It seems, therefore, that *lateral presentation* is a challenge to the right of free passage and/or a summons to a Challenge Ritual (Estes 1969). This is also substantiated by the fact that a similar display has been described for the Tragelaphini (Walther 1964a), and cattle (Schloeth 1961) and interpreted as threat.

(3) The Reverse-Parallel Position

In all the more elaborate Challenge Rituals the contestants will move into the *reverse-parallel position,* standing very close to each other. If the heads are raised the impression is given that both animals display *lateral presentation.* Less frequently the two contestants will move into a *parallel position, viz.* the heads next to each other. *Parallel* and *reverse-parallel position* during agonistic encounters has been described in the Alcelaphini for the blue wildebeest (Estes 1969), blesbok (Lynch 1971), bontebok (David 1970) and topi (Walther 1968a). Originally it was interpreted as threat, but Walther (1965b) pointed out that the *reverse-parallel position* adopted by Grant's gazelle functions as a "golden bridge" which allows the contestants to move away without inviting attack. Estes (1969) accepts this explanation for the blue wildebeest. It applies likewise to the black wildebeest. When standing in *parallel position* it is evidently much more difficult to move away without being attacked. The *reverse-parallel* position affords a comparatively secure position for both contestants and it seems as if the males move purposely into it, and explanation already offered by Estes (1969).

(4) Head-Rump and Head-Head Rubbing

Both displays have been observed in the Challenge Rituals of the blue wildebeest (Estes 1969). Head-rump rubbing is conspicuously absent in the black wildebeest ritual as already remarked upon by Estes (1969). The horn figuration of a black wildebeest bull does not permit a head-rump rubbing, as discussed in more detail above.

Head-head rubbing, observed infrequently in the blue wildebeest, was only observed on two occasions in the black wildebeest and then it had more the appearance of sniffing or licking each other's heads. In both instances the animals stood in the *parallel position.* On the first occasion two sub-adult males performed the head sniff while on the second occasion the approaching male sniffed the other's head and then moved on. Estes (1969) discussed these displays and came to the conclusion that rubbing is essentially sociable as it is seldom performed in a high-intensity encounter and that it is sometimes displayed by a male who wants to avoid an encounter; this seems to be confirmed by observations on the black wildebeest.

The virtual absence of social grooming in the Challenge Ritual in the black wildebeest, is, however, also indicative of the general lack of social grooming in non-territorial black wildebeest. This is contrary to Walther's (1966) observation on a captive herd, where social grooming was prevalent, though only between animals judged to be on "friendly terms".

(5) Urination-Flehmen Sequence

Flehmen has been observed in every group of ungulates, except pigs (Schneider 1930/34). In the Alcelaphini it has not been reported in the blesbok (Lynch 1971), bontebok (David 1970) and the hartebeest (Estes 1969); it is, however, performed by both wildebeest species. The biological significance of Flehmen is now seen as a means by which males check the reproductive status of females. Walther (1963), however, reports that the dibatag female routinely displays Flehmen in response to male urine.

Flehmen by males in response to urine of conspecific males is much less common; both wildebeest species perform it during the Challenge Ritual, and Walther (in Estes 1969) saw captive eland males and dorcas gazelle males perform Flehmen as a response to other male's urine. Captive American and Malayan Tapir male and female frequently performed Flehmen at specific places where both sexes regularly urinated (von Richter 1966). In the Challenge Ritual both contestants stand in *reverse-parallel position.* One male urinates, while the other male lowers its head, sniffs at the urine and then displays Flehmen. The animals quite often reverse the position, whereby the other male urinates and the opponent displays Flehmen.

Estes (1969) reports that if a male failed to urinate spontaneously during an encounter, the other might solicit this by extending his nose under the other's belly. This behaviour has not yet been observed in black wildebeest. On two occasions bulls in the *reverse-parallel position* were seen, however, to perform anus-sniffing, which is not known in the Challenge Ritual of the blue wildebeest (Estes 1969), but is very prevalent in the Challenge Ritual of blesbok (Lynch 1971) and bontebok (David 1970).

Estes' (1969) observation and frequency figures in the blue wildebeest show an almost fixed link between urination and Flehmen. In the black wildebeest, however, there are indications that urination and Flehmen need not necessarily follow each other, *viz.* another display may be fitted into the sequence. In the majority of cases where one or both contestants urinated none of them performed Flehmen.

Estes (1969), discounted the possibility that the *urination-Flehmen* sequence might be sexually motivated as no sexual arousal ever occurred during a Challenge Ritual either in the blue or black wildebeest, although it has been reported from the blesbok (Lynch 1971), the Uganda kob (Buechner *et al.* 1965) and Grant's Gazelle (Walther 1965b). The significance of Flehmen in the Challenge Ritual may be seen as a means by which the concentration of male hormones in the urine is checked to gain information of the sexual and territorial status of the tested animal (Estes 1969).

(6) Angle-horn

While standing in *reverse-parallel position* or during the *urination-Flehmen* sequence one or both males may perform *angle-horn, viz.* tilt his head sideways so that the "near horn" is pointed towards himself and to the hindquarter of his opponent. During the *urination-Flehmen* sequence, the urinating male usually performs *angle-horn.* It is, however, also displayed by both contestants simultaneously, occasionally causing them to move in a circle around each other.

Angle-horn has been interpreted by Estes (1969) as the result of conflict between aggression and escape. The animal performing *angle-horn* is restrained from turning and facing the opponent; this is substantiated by observations on the blue wildebeest where the bull, performing *angle-horn,* actually moves his hindquarters away and his head closer to the opponent. This argument seems acceptable, as bulls circle while performing *angle-horn*. The bulls are reluctant to expose their unprotected flank but also do not dare to move away; by keeping their heads facing inward they may be able to view better what is going on behind them and are able to whirl around if the other bull feigns attack.

(7) Head-flagging

Estes (1969) describes this as alarm display and classifies it as a displacement activity, caused by strongly conflicting attack/escape desires. The contestants either stand parallel, head-up posture and face ostensibly outward or both bulls face each other with their heads turned sideways; sometimes the males will also stand at an angle to each other. When standing in the *reverse-parallel position* each animal's head is turned outward.

Head-flagging is most often resorted to after one male feigns attack, after an actual combat or during a break in a Challenge Ritual; from this position they may start to perform *agonistic grazing*. The slightest movement during *head-flagging* by one of the opponents results in immediate *cavorting*, feigning attack or actual interlocking of horns.

Walther (1968a) describes that topi perform *head-flagging* when facing each other, heads turned either in the same or opposite direction, during a Challenge Ritual and especially before they engage in horn-pushing. After the encounter the contestants will again perform *head-flagging* and withdraw, sometimes in *grazing attitude*. Gosling (1966) depicts a territorial Coke's hartebeest in the typical *head-flagging* posture, while the opponent is pawing. Territorial bontebok and blesbok males perform *head-flagging* ("looking about" in blesbok) when approaching each other and after *anus-smelling* in blesbok (David 1970; Lynch 1971). *Head-flagging* after an encounter is known in the Tragelaphini and also in the eland (Walther 1964a). In Thomson's and Grant's gazelle (Walther 1964b; 1965b) *head-flagging* terminates an agonistic encounter.

Walther (1964a; 1964b; 1965b) interprets *head-flagging* as an offer of peace, "Friedensangebot", which, however, does not indicate inferiority or submissiveness on the part of the performing animal. Elements of threat are prevalent, as the horns are still visible to each other. In Thomson's gazelle the encounter is actually renewed if the contestants do not groom their shoulders or move away (Walther 1964b). Walther (1964b; 1965b) speculates that *head-flagging* may have developed from the intentional movement of turning away while the horns are still visible to the opponent in head-high position – a threatening posture.

The close similarity of the *head-flagging* position in the gazelles and the Tragelaphini, as described by Walther, to the display performed by the wildebeest, as well as the situations in which it is performed, has convinced me that we are dealing with a display and not with a displacement of the alarm posture.

Estes (1969) in his discussion of the alarm display in the blue wildebeest refers to its close resemblance to the *head-up posture* and remarks that any sudden movement of one of the contestants leads to a renewed encounter or at least to combat readiness. He comes, however, to the conclusion that it is the alarm posture performed as a displacement activity, *viz.* they adopt *head-up posture* but do not dare to face each other directly, which would be the strongest form of challenge.

(8) Circling

Also when bulls circle around each other, a conflict between attack and escape is evident. The contestants, standing in *reverse-parallel position,* start to move around each other, the head always held close to the opponent's hindquarter. In contrast to threat-circling in oryx and in Grant's gazelle, where heads are raised high in both partners (Walther 1958; 1965b), both wildebeest species keep their heads low, displaying the *grazing attitude.* Circling again affords some protection, as a contestant can move away in *grazing attitude* without much fear of being attacked.

(9) Combat

Only in high-intensity encounters do the animals resort to interlocking and pushing with horns. The intensity and frequency of bodily encounters is highest just prior, during and after the rut. Serious fights are the exception to the rule and only very seldom does one of the contestants get hurt (Estes 1969). No serious fight could be observed in black wildebeest, although territorial bulls with horns broken off may be an indication of more serious encounters. Males engaged in a Challenge Ritual may interlock horns from almost every position described above.

Contestants standing parallel, circling each other or performing *head-flagging* will readily feign attack and in high intensity encounters interlock horns. Any movement, slightly depicting aggression, is immediately met by the opposing bull with a sudden whirl around to face the attacker. This can be observed very well when the contestants stand in the *parallel position;* immediately one male moves his head sidewards towards the other, the latter is ready to meet the challenge.

If *cavorting* is performed vigorously by one male his opponent whirls into a face-on position. The cavorting animal sometimes will lunge forwards from above, front legs off the ground. A direct approach without any "preliminaries" often results in immediate horn locking. In many cases, feigning attack is all the action seen in a Challenge Ritual, as the animals stop short of actual bodily contact. Interlocking and pushing while on the hoofs is quite common, while dropping on to the metacarpalia only takes place in high intensity encounters.

Body contacts seldom last more than one minute; usually much shorter. Combat during a Challenge Ritual is not necessarily the climax of an encounter or the termination of it. Frequently the opponents will separate from each other, engage in other displays and later again come into body contact.

(10) Displacement Activities

During a Challenge Ritual a number of motor behaviour patterns seemingly unrelated to an agonistic encounter can be observed, *viz.* maintenance or comfort movements, grazing and lying down. Performed during a Challenge Ritual, they are classified as displacement activities. The performing of displacement activities signifies that the animal is inhibited from performing the motor pattern appropriate to the situation; a single emotion may be blocked in its expression, but more often two diametrically opposed drives are aroused simultaneously (attack-escape for example), which inhibit each other (Tinbergen 1940). Van Iersel *et al.* (1958) advance the hypothesis that the mutual inhibition of conflicting drives "disinhibits" another non-conflicting one. The most readily "available" non-conflicting pattern is maintenance behaviour. Accordingly, maintenance behaviour, in the form of displacement activities in agonistic encounters, is quite common in both wildebeest species (Estes 1969).

Scratching the head with a hindfoot, usually when the head is held low, has been observed frequently in both the blue and the black wildebeest; grooming with the mouth or cheek on the shoulder is less common. Shaking all over, usually after the animal has rolled, chewing the cud and grooming with the horns rank very low as displacement activities in the blue wildebeest (Estes 1969), and were also infrequently observed in the black wildebeest. The most commonly displayed maintenance activities are, however, a fly-shooing movement *(head-and-tail-sweep)* and the *grazing attitude* (Estes 1969).

In the *head-and-tail-sweep* the animal brings his head near the flank and sweeps simultaneously with the tail across the face. It is a rather aggressive looking movement and is sometimes mistaken as such and can provoke an attack. A similar *head-to-flank* movement is well known from the hartebeest (Backhaus 1959; Gosling 1966), blesbok (Lynch 1971) and bontebok (David 1970), where it is performed with great vigour by territorial males after kneeling and horning but the tail-sweep is absent, as all the species mentioned lack the long-haired tail of the wildebeest. Black streaks of pre-orbital gland secretion have been reported on the shoulder, of the hartebeest, (Dowsett 1966), so marking cannot be ruled out completely in this species. As discussed earlier, marking with pre-orbital glands in the black wildebeest is improbable. Furthermore, if one assumes that the *head-and-tail sweep* originated from marking the shoulder, this would offer no explanation for the origin of the tail sweep (Estes 1969). The possibility that the *head-and-tail sweep* is still a fly-shooing movement can be discounted as it is performed even when no insects are active (Estes 1969), and in any case in the Willem Pretorius Game Reserve no biting varieties are present.

Estes (1969) draws attention to the fact that the head movement in the *head-and-tail sweep* has some resemblance to aggressive hooking in females, but is hardly ever seen in males. This could suggest that the *head-and-tail-sweep* is a substitute for inhibited hooking.

Agonistic Grazing

A territorial male will adopt the *grazing attitude* while in *reverse-parallel position,* circling each other, during a break in a Challenge Ritual or when approaching each other at close quarters and when withdrawing from a Challenge Ritual. It is performed equally frequently in low or high intensity encounters and has the highest incidence of all steps performed in a Challenge Ritual of the blue wildebeest (Estes 1969).

When performed while approaching another male, it implies that the *grazing attitude* will counteract the aggressive tendency of the approach, while during withdrawal it equally counteracts any impressions of fear. To be able to serve both these functions, *agonistic grazing* would have to be neither aggressive nor submissive.

Estes (1969) discusses these aspects in great detail and it is sufficient to say here that *agonistic grazing* is truly neutral. At the same time Estes elaborated on the question whether *agonistic grazing* should still be called a displacement activity or if it has been ritualized into a new display. Estes comes to the tentative conclusion that *agonistic grazing* is a display rather than a displacement activity.

Lying down

Estes (1969) and Walther (1966) report that blue and black wildebeest will occasionally lie down during a low-intensity encounter. Going down on the knees is a prelude to the combat-position, horning the ground or rolling and lying down. Walther (1966) interprets lying down during the encounter as a specific case of displacement activity, where elements of one specific motor pattern, due to their identical performance, are slipped into another pattern. Estes (1969) concludes that lying down is not a displacement activity but rather "absent-mindedness" on the part of the performing bull. He bases his conclusion on the concept of the activating of an instinct which is caused by a transitional action (Lind 1959). The transitional action is kneeling; a male going down on his knees to horn the ground during a Challenge Ritual may in the absence of any strong motivation "forget" his intentions and lie down. The absence of any strong motivation towards the opponent is indicated by the low intensity or the "playfulness" (Walther 1966) of the encounter.

In addition to the behaviour patterns described under the heading Challenge Ritual, *cavorting, head-shaking,* and *head-throwing* are integral parts of a Challenge Ritual. The motor patterns described under demonstration-threat advertising will also be performed during a Challenge Ritual, but here they are termed as threat because they are performed for the express benefit of an onlooking rival.

DISCUSSION

In the foregoing description of the Challenge Ritual the agonistic feature of the encounter between territorial bulls has been stressed. Estes (1969) lists three principles of agonistic behaviour based on a review of major publications in this field. Most of the motor patterns performed during a Challenge Ritual fit into this concept. The first principle is that conflicting desires to attack and escape are present during any hostile encounter as we have seen in the discussion of the Challenge Ritual. If there was no escape tendency or fear during an agonistic encounter the animals would attack without any preliminaries. Further evidence for the first principle is that animals rather display than actually fight.

The second principle states that the goal of any agonistic behaviour is to reduce aggression and induce escape in the opponent. The opponent's aggression could also be reduced by appeasement behaviour but in territorial males this would very likely lead to the loss of the territory and, therefore, no submissive motor patterns are to be found in the Challenge Ritual.

A further principle governing an agonistic encounter is the level of internal motivation and external stimuli which determines the intensity of the encounter. This explains why certain motor patterns will not be displayed at all or only at low intensity in many observed Challenge Rituals and why it is so seldom possible to watch the full sequence.

A number of motor patterns performed during a Challenge Ritual, however, do not conform with these principles *viz.* they are not related to fear or aggression, but to the gregariousness of the species and perhaps to the territorial-sexual drive.

The possession of a territory is the prerequisite for reproduction in the wildebeest; accordingly territorial behaviour is at its peak during the rutting season. The overriding sexual-territorial drive dominates the social life of the wildebeest male during this period, but not so completely as to suppress entirely his need for social contact. In the daily Challenge Rituals with his neighbours, a bull can "satisfy" his social needs, release his aggression and maintain his territory for reproduction. The strong desire for social contact in territorial males is substantiated by the fact that males far removed from each other actively seek an encounter with either their distant neighbours or a trespassing bull; the Challenge Rituals also quite often do not take place along the presumed boundary but deep in one of the contestants' territories. Furthermore, a male trying to establish a territory will always do so in the neighbourhood of another territory, although he will encounter much more competition here than when further away from an established territorial network.

The complex relationship between territoriality and gregariousness is also borne out by the fact that territorial males loose some of their strong attachment to the once fiercely defended territory and band up together temporarily in a bachelor group with the declining sexual-territorial drive after the rut. In the bachelor group territorial-sexual drive is dormant and the males can "satisfy" their social needs without engaging in a Challenge Ritual.

Fisher (1954) advanced the "dear-enemy" concept stating that "the effect of the holding of territory . . . is to create "neighbourhoods" of individuals which are masters of their own definite and limited property, but which are bound firmly, and *socially*, to their next door neighbours . . . Which in bird terms should more safely be described as mutual stimulation". Fisher (1954) however qualifies this statement later on to say that the formal proof for the biological survival value of social stimulation is so far still outstanding.

Estes (1969) applies the "dear-enemy" concept to the territorial behaviour of the blue wildebeest. The proof for the survival value of social stimulation as requested by Fisher (1954) is seen by me in the fact that territorial bulls can satisfy their gregariousness in the daily encounters and the constant challenge to their territorial rights. As only territorial bulls can partake in the rut and the territory owners constantly are challenged by their neighbours and individuals from a bachelor group only the fittest bull can hold on to his territory. By this process it is assured that only the best bulls reproduce. Territoriality has, therefore, a definite survival value for the species. The biological significance of territoriality in the reproductive behaviour is not very obvious in the sedentary populations of the black wildebeest where no large scale aggregation of females exists and the competition by males for territories is less fierce than in the migratory populations of the blue wildebeest (Estes 1969; Watson 1969).

Territorial behaviour, however, also serves a number of non-reproductive functions as discussed in more detail elsewhere (von Richter 1971a) territorial males cut out the yearlings, mainly males, from the female herds. Yearlings of both sexes have a strong attachment to their cows and interfere with the care of the newborn calf. As a cow will not tolerate such interference the yearling is constantly harassed, this attracts the attention of the attending territorial bull and it is eventually chased out and forced to join a bachelor group, especially in the case of male yearlings.

The separation of cows and calves, an important mortality factor in newborn calves, is counteracted by the cutting-out of yearlings which reduces the turmoil in the female herds. The resulting segregation of bachelor groups and female herds may also be beneficial to the species, as the bachelor herds are removed from direct competition for grazing (Estes 1969). However, no evidence could be found in the Willem Pretorius Game Reserve that bachelors inhabit a less suitable habitat than females as Estes (1969) reports for the Ngorongoro populations.

TABLE 1
COMPARISON OF SOME BEHAVIOUR PATTERNS IN THE TRIBE ALCELAPHINI

	CONNOCHAETES		ALCELAPHUS			DAMALISCUS		
Behaviour pattern	*taurinus*	*gnou*	*b. lelwel*	*b. cokei*	*lichtensteini*	*korrigum*	*d. dorcas*	*d. phillipsi*
Marking with pre-orbital gland	—	—	?	++	?	++	+	++
Glandular weaving	—	—	?	?	?	?	++	++
Pawing	+++	+++	++	++	?	++	—	+
Rolling	++	+++	—	—	—	—	—	—
Ground-horning	+++	+++	++	++	++	++	++	++
Cavorting	++	+++	?	++	?	++	+++	++
Head-shaking	+++	+++	?	?	?	?	+++	+
Head-nodding	+	++	?	+	?	++	++	+++
Neck-wrestling	—	—	?	++	?	?	—	+[2]
Submissive posture	+	+++	++	?	?	?	—	—
Lateral presentation	+++	+++	++	++	?	?	+++	+++
Reverse-parallel position	+++	+++	?	?	?	+++	+++	+++
Head-rump, head-head rubbing	++	+	?	+[1]	?	?	—	—
Urination-flehmen sequence	+++	++	—	—	—	—	—	—
Angle-horn	+++	+++	?	?	?	?	+	+
Head-flagging (alarm display)	++	++	++	++	?	++	+++	++
Circling	+++	+++	?	?	?	?	+	+++
Agonistic grazing	+++	+++	?	+++	?	++	+	++
Head-to-flank-sweep	—	—	++	++	++	—	+++	++
Head-and-tail-sweep	+++	++	—	—	—	—	—	—
Combat position on knees	+++	+++	++	++	++	++	+	++
	Walther (1966) Estes (1969)	Walther (1966) Estes (1969) This report	Backhaus (1959)	Gosling (1966)	Dowsett (1966)	Gosling (1966) Walther (1968a)	David (1970)	Lynch (1971)

[1] side-head [2] calves only +++ = very common, ++ = common, + = uncommon, — = absent

Large aggregations of blue wildebeest are immediately broken up by territorial males, who thereby help to space the population more evenly (Estes 1969; Watson 1969). In doing so the damage to the range, due to grazing and trampling, is probably reduced. Again this function is much more clearly visible in large migratory populations and does not show up to any extent in the sedentary populations we are here dealing with.

COMPARISON OF TERRITORIAL BEHAVIOUR AND THE CHALLENGE RITUAL IN THE ALCELAPHINI TRIBE

(Table 1)

In the Alcelaphini tribe the closest resemblance to territorial behaviour and related motor patterns is to be found in the behaviour of the two wildebeest species. *Head-head rubbing* and *head-rump rubbing* is conspicuously absent in the black wildebeest, and only the black wildebeest displays a very stereotyped and elaborate submissive posture (Walther 1966; Estes 1969; unpublished observations). The large and strongly curved horns of the species precludes using these for social grooming. The extreme and stereotyped appeasement behaviour counteracts the tendency of the black wildebeest to attack conspecifics, especially females from the side.

In the genus *Alcelaphus,* pawing and horning the ground is very conspicuous and has an intimidatory effect. It is commonly displayed before an encounter. Rolling after pawing and horning is absent. Very conspicuous however, is a *head-to-flank* movement, whereby the head is rubbed against the shoulder. The *head-to-flank* movement is found in both wildebeest species as well. Here however, the tail is swept across the face in the *head-to-flank* movement *(head-and-tail-sweep).* The omission of the tail sweep can be attributed to the shorter tail in the genus *Alcelaphus.*

Head-flagging is also performed by Coke's hartebeest during encounters between territorial males. Although their pre-orbital glands are not too well developed, kongonis actively mark the ends of twigs with the pre-orbital glands and also mark while rubbing their faces on the ground during horning sessions.

Backhaus (1959) reports that Lelwel's hartebeest will resort to lying down as a submissive gesture, as does the black wildebeest. Neck-wrestling (Halskampf) is performed by the kongoni and fights which result in the wounding of the contestants, especially when one takes flight, are also prevalent. These features are generally considered to be more archaic behaviour patterns (Geist 1966; Walther 1968b).

The topi (genus *Damaliscus*) paws and horns the ground in a kneeling position but the *head-to-flank* movement which follows in the other genera is absent, as is any sign of rolling. During an encounter between territorial males the contestants may stay in a *parallel* or *reverse-parallel* position or face each other, *head-flagging* is displayed prior to and after an encounter. Scratching and grooming the shoulder while confronting each other has been observed, as in *Connochaetes* and *Alcelaphus.* Marking grass stems with the pre-orbital glands has been reported by Gosling (1966) for the topi and for the tsessebe by Huntley (1970).

Bontebok (David 1970) and blesbok (Lynch 1971) have been the objects of detailed studies of territoriality. Pawing and rolling is absent in bontebok, while blesbok paw very infrequently. Horning the ground in a kneeling position is frequently performed during a Challenge Ritual by both subspecies. The *head-to-flank* movement is performed while both species horn the ground or face each other in combat position on the knees.

The blesbok has fairly well-developed pre-orbital glands while bontebok only show minimal secretion. In both species, territorial males deposit the secretion carefully on grass stalks and subsequently move their horns across the stalks *(glandular weaving)*. David discounts *glandular weaving* as a means of demarcating a territory in bontebok while Lynch accepts it for the blesbok. David interprets the *head-to-flank* movement as a displacement activity derived from flyshooing movements, while Lynch assumes a marking effect, although no secretion is visibly deposited on the shoulder or flank of either species.

Territorial bontebok and blesbok approaching each other will display *head-flagging*. David assumes that it serves as appeasement, while Lynch interprets it as a displacement activity similar to Estes' (1969) alarm displacement in the blue wildebeest.

The very pronounced *urination-Flehmen sequence* of the genus *Connochaetes* has not been reported in either *Alcelaphus* or *Damaliscus* during a Challenge Ritual, or in any other context. *Anus-sniffing,* however, is very pronounced in the Challenge Ritual of both blesbok and bontebok. In the other members of the Alcelaphini it has only occasionally been reported in the black wildebeest. Neck-wrestling was reported occasionally in blesbok calves by Lynch, but has not been reported in the bontebok.

The differences and similarities in the various behaviour patterns cut across the taxonomic separations of the species. The behaviour patterns reflect the adaptations of the various species to different habitat requirements, in the evolution from hypothetical forest dwelling ancestors to savanna-inhabiting species. The genus *Connochaetes* has to be considered the most advanced of all the Alcelaphini, having adopted a nomadic mode of life in response to the drastic seasonal changes of the savanna habitat. Demarcating a territory by means of pre-orbital or interdigital glands has disappeared. In contrast, the genera *Alcelaphus* and *Damaliscus* show less pronounced nomadism and all perform pre-orbital gland demarcation. Intra-specific encounters have been least ritualized in *Alcelaphus*, resulting in serious injuries to combatants. Accordingly the genus has a well-developed submissive posture. In the black wildebeest intra-specific encounters between territorial bulls are highly ritualized and serious injuries are almost absent. However, a very stereotyped submissive posture is displayed by non-territorial animals, as especially females try to hook and gore each other in intra-specific encounters. The tendency to jab is also still occasionally seen in territorial bulls.

Neck-wrestling has so far only been reported in Coke's hartebeest and in blesbok calves. The aggressive hooking by females of both wildebeest species, and during the pre-mating behaviour by black wildebeest males could be considered as an archaic behaviour pattern.

The occurrence of neck-wrestling in blesbok calves and hooking in the females of the wildebeest and during pre-mating behaviour seems to indicate that both patterns were once present in all Alcelaphini but have been lost during the evolution of the genera *Connochaetes* and *Damaliscus,* where it only appears in the females or in the calves. The appearance of more primitive behaviour patterns in the mating behaviour, in the encounters of females and in juveniles is known in other ungulate species as well. (Walther 1968b).

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