

# TERRITORIAL BEHAVIOUR IN CERTAIN HORNED UNGULATES, WITH SPECIAL REFERENCE TO THE EXAMPLES OF THOMSON'S AND GRANT'S GAZELLES

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## ABSTRACT

An attempt has been made to distinguish between action area, home range, and territory in the Bovidae. The establishing of subjective boundaries is considered to be the most important criterion of territoriality. The existence of such boundaries becomes evident from certain behavioural symptoms; "defence" or better, localized dominance which may lead to intolerance, is one of them.

Not all bovids are territorial. Within the territorial species, there seem to be at least two types: (a) The animals, usually in pairs, may, under favourable conditions, stay in their territories permanently; (b) Only the males are territorial and stay in temporary territories, usually for several weeks or months. This last type is obviously more common in horned ungulates than the first one. Within this second type (b), there are species-specific differences. For example, in Grant's gazelle (*Gazella granti*), under certain environmental conditions, this type of territoriality is combined with harem behaviour, but in the co-inhabiting Thomson's gazelle (*Gazella thomsoni*), the females roam through the territories of the males and stay together with the same buck only for a few hours per day.

Even within one and the same species, there can be variations, apparently linked with differences in environmental conditions. This is discussed, using the examples of the Uganda kob (*Adenota kob*), the wildebeest (*Connochaetes taurinus*), and Grant's gazelle. Finally, there can be differences in the territorial behaviour of the same individual according to the phases of territoriality (beginning, peak, end) which is shown by the example of Thomson's gazelle.

I intend to speak about three kinds of subjective space in horned ungulates: the territory, the home range, and the action area (Walther 1967). In this paper, I will discuss the latter two only so far as it is necessary to make a distinction from territories.

The action area (*Aktionsraum*) includes all seasonal territories and/or home ranges as well as the migration routes, which connect them, in short, every place on which an animal sets foot during its individual life. The same may be true for a closed group as long as it exists as such. Apparently some colleagues are concerned that this term "action area" could be confused with "activity range" used by certain authors for "home range". I feel, however, that a term covering all the places and routes mentioned above, is needed for the description of the life history of an individual or a group, and for the discussion of traditional space systems in certain species, etc. The term "action area" seems to me adequate for this purpose and sufficiently different from "activity range". Moreover, "home range" is a well-known and commonly used term. Thus, I do not see a need for a second, synonymous term ("activity range").

The home range means an area in which an animal, or (more commonly) a group of animals stay long enough to become familiar with this area and to establish a space-time system within it. Of course, a home range has an end, but it does not have boundaries. As a consequence, the home ranges of neighbouring groups may overlap one another in part, and, provided that the inhabiting groups are open societies, individuals which have belonged to a given herd in a given home range for some time are completely free to leave this herd and this home range and to join a neighbouring herd in a neighbouring home range.

A territory is a place in which an animal lives for a short or a long period, with a boundary

established by the animal itself. In principle, a whole group can also be territorial, however, such a case among bovids is not known to me. The existence of this subjective boundary becomes evident from certain behavioural symptoms such as intolerance, or at least dominance over conspecifics of the same sex within the boundaries (“defence”), loss of this dominance and a certain diminution of aggressiveness outside the territory, higher thresholds for flight (even from predators) inside the territory, efforts to herd back con-specifics of the other sex when they intend to leave the territory, sudden halting of the territorial animal when arriving at the boundary (for example, when pursuing a trespassing bachelor), appearance of conflict behaviour when the owner leaves his territory temporarily, establishing a marking system, the structure of which is related to that of the territory (marking the centre and/or the boundaries – of course, only in species which mark in the olfactorial way).

I wish to stress that I cannot consider, either from a theoretical or practical viewpoint that defence is the only, or the constitutive consideration, in a definition of territoriality. Practically speaking, it may happen for example in Grant’s gazelle, with their relatively very large territories, that one male may occupy the only suitable place in an area, for example, a clearing in a bush area. In such a case, there are no territorial neighbours present, and it may last weeks and months until a bachelor group happens to pass through this area, and it is very unlikely that an observer will be present during this half to one hour to record such an encounter. In short, it is often not possible to see territorial defence for a long period. On the other hand, within one day, one can usually observe one or several of the other symptoms listed above, which are as indicative of territoriality as defence is. Furthermore, as I shall discuss later, there is sometimes no true defence but only a moderate dominance over other males inside the territory.

In theory, I think it is a mistake to make defence a constitutive consideration in a definition of territoriality. If we do, we would have to include all cases of parental defence of the space around offspring, and the case of a male defending the space around his female(s), as well as the defence of an individual distance, and the defence of a feeder in captivity etc. In short, this leads to an inflation of the term “territoriality” which loses its value and meaning in this way. Moreover, defence is only one possible indicator among others (see above) for the existence of a boundary established by the animal itself. In other words, the primary consideration is not the defence but the subjective boundary. Therefore, this aspect should be considered in a definition.

The territorial boundary does not necessarily have to be a precise line, although this happens frequently enough, but it may also be a zone, or in some species such as wildebeest, the animal apparently establishes only a fixed centre and the territorial boundaries are given by a certain distance from this centre. In regard to a definition, however, it does not make much difference what the boundary looks like in detail, or which factors determine it. The essential point is that every territory has a boundary, and that this boundary brings about easily-recognisable changes (symptoms) in behaviour. The behaviour of the same individual inside and outside the boundaries of his territory is different.

Before we embark upon a discussion of territorial behaviour in certain bovids, it is perhaps not out of place to stress the fact that there are species which are not territorial at all. This is true, for example, for the majority of the Bovinae and Caprinae. In the territorial species we have at least two, perhaps even three types of territoriality:

1. I have observed and confirmed the first type in the dikdik (*Rhynchotragus kirki*), but we have reason to assume that a similar pattern may exist in some other species of Neotraginae and Cephalophinae. Here a pair (plus the offspring until they reach maturity) live in a territory for a long time. If the ecological conditions do not change drastically, and if the animals are not disturbed very seriously, they may possibly stay in their territory for a lifetime.
2. According to Verheyen (1953) in the bushbuck (*Tragelaphus scriptus*), the males and females have separate territories, and the sexes may join each other in a no-man's land, or the male may leave his territory and enter the female's territory for mating. According to my rather casual observations on steenbok (*Raphicerus campestris*) in Serengeti, the situation seems to be similar in this species. I feel, however, that in both species more information is needed before a final conclusion can be made.
3. The third type of territoriality is obviously the most common one in horned ungulates. In this case only the males become territorial and stay in their territories for limited periods – usually several weeks or months. Extreme cases, when the animals are territorial for only a few days or even for only a few hours, do occur occasionally. The other extreme is when such an animal maintains its territory for a year or even longer. Both extremes occur, but only infrequently.

In certain species, the last type of territoriality can be combined with harem behaviour. This means that a relatively constant group of females, with their offspring, may stay together with a male more or less throughout the territorial period. This I found, for example, to be true for Grant's gazelle on the clearings (mbuga) in bush areas where the territories of this species have an average diameter of about 800 m (Walther 1968 and in press).

In Thomson's gazelle, even in precisely the same areas occupied by Grant's gazelle described above, the territorial males have no constant harems with them (Walther 1964; 1968; Estes 1967). The territories, which average about 200 m in diameter, are located within the home ranges of female herds and the single territorial males are visited by the roaming females during their daily circuit. This means that females are together with a given male in his territory for only a few hours per day.

Estes (1966; 1969) observed a very similar situation in the wildebeest, and he recorded that single territorial bulls kept their territories in the Ngorongoro Crater for months and even years. However, in the neighbouring Serengeti plains the wildebeest move permanently, and the bulls become territorial only during the rutting season and usually just for a few hours. The longest territorial period which I recorded for a wildebeest in Serengeti was three days, and this was very exceptional.

In the case of the Uganda kob Buechner (1961) described so-called arenas. The single territories (only about 30 m in diameter) are clustered together within an arena. According to Buechner, only females in oestrus enter the arenas. But, besides these very small territories within the arenas, Leuthold (1966) also found much larger territories outside the arenas.

I have already mentioned that in Grant's gazelle, the single territorial males are together with relatively small but approximately constant harem groups (usually 10 to 20 members) in the bush areas. In the same species, the situation is different in the open plains (Walther, in press). Here, too, certain males may become territorial. Nevertheless, their territories are within the home ranges of large mixed herds (in Serengeti 40 to 400 members). These herds are composed of females, juveniles of both sexes, and fully adult, non-territorial males. Similarly to the female

herds in Thomson's gazelle, these mixed herds enter the territories in the course of their daily circuit. However, a territorial Thomson's gazelle ram (at least at the peak of his territorial period, see below) as well as a territorial Grant's gazelle ram in the bush area drives away every other adult or subadult male which happens to enter his territory. The territorial Grant's gazelle ram in the open plains do not do so. They show a moderate dominance over the non-territorial males as long as the latter are in their territories, but they do not fight them and usually they do not chase them away. They show dominance displays (Walther 1965; 1968; Estes 1967) during encounters with them, and it is always the territorial male which is clearly superior in these encounters. Furthermore, the territorial male interferes as soon as one of the non-territorial males tries to approach a female. As long as the herd is inside the territory, only the territorial ram has the right to copulate. When the mixed herd leaves his territory, he may remain solitary or may even leave together with the herd. But now – outside his territory – he does not behave differently from any other adult male bachelor until the herd returns to his territory where he regains dominance over the other adult males, and the exclusive right for sexual activity.

In closing I would like to mention the differences and variations which may occur in the same individual in relation to different phases of territoriality. I have studied this phenomenon mainly in Thomson's gazelle.

During the beginning phases of territoriality, not always but frequently, the male Thomson's gazelle are extremely aggressive. In exceptional circumstances a territorial male will chase even females out of his territory in the same manner as he would chase other males. Furthermore, a very high marking activity was typical of this phase. Obviously, the rams were not yet sure of the exact position of the territorial boundaries. Heavy fighting took place, and sometimes one of the opponents was completely defeated and fled for miles, relinquishing his territorial status in this way. Before, during, or after these encounters, "displacement activities", predominantly grooming and scratching, were not uncommon. According to various circumstantial conditions, this phase may last from a few hours to several days.

After about one week, at the latest, the territorial male reaches a stage which may be called the peak of territoriality. The boundaries of the territory have been established, often to the nearest metre. The territory is well-marked. The buck refreshes or enriches the marks every day. Thus marking activity is still high but not as hectic as in the initial phase. Fights between the territorial neighbours are common, but they are not very intense, and usually they do not last long. Only in relatively rare cases do these fights result in changes of the boundaries. Usually they serve to re-affirm the position of the boundaries, and none of the opponents is defeated during these encounters. Consequently, these fights do not end with the flight of one of the rivals, and none of them loses territorial status. Bachelor males are chased away without any fight, as soon as they happen to enter a territory. Females are welcome, and when they leave the territory, the ram tries to stop them. Usually he is not very successful in doing so. This stage may range from about one week up to four or five months.

When a male continues to stay in his territory the local conditions usually change drastically. The country has become dry, the originally short grass has grown high, the majority of the females and bachelors, and even many territorial males, have left the area. Now, the male is often alone in his territory for days and weeks. If there is still an occasional territorial neighbour around, they may engage in a few encounters over the boundaries. The marking activity dwindles. If some

females enter the territory, the male herds them for a short while but he usually does not make much effort to retain them. If bachelors enter the territory, the territorial ram is dominant over them, but he does not chase them away. Often they are in his territory for hours. When the females or the bachelors move ahead, the territorial male may leave his territory together with them. After half a mile or so, he may stop and return. Even when alone, he sometimes makes excursions outside his territory. Altogether, it seems as if he is not quite sure about his territorial status and the position of the territorial boundaries during this end phase. I might add that the longest territorial period which I recorded for Thomson's gazelle in Serengeti was about one year.

Not all territorial Thomson's gazelle go through these three phases. Many of them leave their territories after two to eight weeks, right in the middle of the phase which I have described as the peak of territoriality. Others leave their territories even during the initial phase, that is without having established a true territory.

In the literature, I did not find many references to these phases, but they definitely do exist, and the entire concept of territoriality can be drastically altered by them. Sometimes I wonder if certain controversies in the literature on territorial behaviour are not simply due to misunderstanding these phases. In any event, the territorial behaviour of bovids can vary according to species-specific differences, within the same species according to different environmental conditions, and within the same individual according to the particular phase of territoriality.

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