

TERRITORIALITY :
THE EXAMPLE OF THE WHITE RHINOCEROS
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ABSTRACT

The concept of territoriality needs review in the light of recent mammalian studies. Intensive behavioural observations were carried out on the white rhinoceros in Zululand, South Africa, and results on social organisation are summarised. Territoriality is exhibited by certain adult males and has the following features: (i) mutually exclusive ranges of 1–2 km²; (ii) a dominant assertiveness in interactions within the territory; (iii) specialised scent marking techniques using dung and urine; (iv) exclusive participation in reproduction. Territories may be shared with one or more subsidiary bulls. Territoriality in the white rhino may be characterised as a space-correlated dominance relationship with the function of ordering reproductive competition among males. It plays no significant role in population regulation. These conclusions are extended to other territorial ungulates. Methodological criteria for territoriality are suggested. Evidence is needed on (i) differing social classes; (ii) range utilisation patterns; (iii) spatial features of dominance relationships.

The term territory was first given precise meaning by students of avian behaviour. Classically, it referred to the area surrounding the nest site from which other conspecifics were driven away, usually by the male, though sometimes by both members, of a mated pair. The piece of space defended in this way was large enough to provide most or all of the life requirements of the pair and their dependent offspring. Subsequently, however, the concept has been widened by ornithologists to cover other defended areas, such as nest-only territories, mating-only territories, winter-feeding territories, group-defended territories, and even roosting territories (Nice 1941). Many possible advantageous functions of territoriality have been postulated (Hinde 1956), though rarely proven, among these the especially controversial one of population regulation (Wynne-Edwards 1962).

It has recently become evident that territoriality is also a widespread mammalian behavioural trait, notably among the African ungulates (Estes 1969). There has been, however, a variability in the interpretation of the term by mammalogists which tends to confuse the picture. Territoriality has sometimes been assumed, when all that has been demonstrated is site attachment (Talbot & Talbot 1963), or the setting of odoriferous marks (Hediger 1949). Some even allow for the existence of moving territories. Finally, the term territory has sometimes been applied loosely to the home range, which is simply the area normally used by an animal in the course of its routine activities, without any implications of exclusiveness (see Jewell 1966 for a discussion of home range concepts).

Part of the confusion results from the difficulty of mammalian observation under undisturbed natural conditions, another part is derived from the great behavioural complexity of mammals: simple threat-fight-flight types of interaction, which may easily be interpreted as "defence" of an area, are rarely witnessed. It has also now become evident that the expression of social behaviour (e.g. threats, amicable gestures, courtship) in terms of population organisation (group structure and stability, territoriality) is very sensitive to ecological influences (Crook 1970). Territoriality

may thus appear a striking feature of one population of a species, while in another population of the same species it may be only weakly expressed or absent (e.g. *vervet monkey Cercopithecus aethiops*, Gartlan quoted in Crook 1970b).

It is a cardinal principle in any scientific enquiry that we attempt, not to make nature fit into our arbitrarily chosen definitions, but rather to determine what features characterise those natural systems which seem to have something in common. In the light of recent mammalian field studies, some re-thinking regarding the implications of the term territoriality seems necessary.

Schenkel (1966) has already offered an excellent critical appraisal of the concept of territoriality as applied to mammals. He proposed three essential criteria: (i) intolerance of the presence of conspecifics, which (ii) is related to a fixed piece of space; (iii) the possibility of intercepting and driving away an intruder within a short time.

However these requirements are still not objection free. Why impose the need for direct interaction and driving away of an intruder upon the more olfactorily orientated mammals, in which the indirect technique of chemosensory communication may be equally effective in achieving the same end? His modification of "defence" to "intolerance" is also not an entirely satisfactory improvement. In certain circumstances, territory holders may tolerate other males within their territories. This occurs temporarily during the "challenge ritual" of the wildebeest *Connochaetes taurinus* (Estes 1969), and is a more permanent feature of territoriality in Grevy's zebra *Equus grevyi* (Klingel 1969).

Schenkel (*ibid*) reported as evidence for rejecting territoriality for the Tsavo black rhinoceroses (*Diceros bicornis*) the observations that (i) the animals shifted about irregularly (though largely in connection with movements to water); (ii) in any particular area, a number of different individuals were seen; and (iii) in encounters, even between bulls, aggression was only occasionally manifested. However, in certain situations, the same observations could also be made for the Umfolozi white or square-lipped rhinoceroses *Ceratotherium simum simum*, in which in fact there is very clearly expressed territorial behaviour by adult males (Owen-Smith 1971).

PROCEDURE

My study has involved an intensive investigation of the ecology and ethology of the white rhinoceros in the Umfolozi-Corridor-Hluhluwe game reserve complex in Zululand, South Africa. Observations were initiated over a six-month period in early 1966, and were then resumed in November 1968 and have since been continued without interruption up to June 1971, a time scale now encompassing 5½ years. The most detailed work has been done in an area, roughly 25km², in the western section of Umfolozi Game Reserve, where a relatively high white rhino concentration exists (population density about 5/km²). This has been supplemented by briefer observations from four additional study areas within the complex. The rhinos have been watched mainly by following them on foot. From variations in horn shape and other features, it has been possible to recognise all the adults and some of the subadults in the main study population, which includes nearly 200 different individuals. Thirty-five animals, mostly subadults, were marked with ear-tags. Ten radio transmitters were placed on cows and subadults to assist in the determination of range patterns.

RESULTS

In this report, I will merely summarise the essential features of the social system of the white rhinoceros and use it as a basis for making some suggestions regarding the nature of territoriality. A detailed analysis of data will be published later.

The individuals forming any local white rhino population can be classified into one of five social categories, which may be characterised by differences in age and sex, in their utilisation of space, in their direct and indirect interaction patterns with each other and by their role in reproduction: (i) calves; (ii) adolescents; (iii) cows; (iv) territorial bulls; (v) subsidiary bulls.

Age relationships

An individual still accompanying its mother is termed a calf. Separation takes place at an age of between two and three years upon the birth of a new calf, and the individual then enters a period of adolescence. Adolescence, as here used, is terminated in a female upon the birth of her first calf at an age of six to seven years, after which she is classified as a cow. In males adolescence lasts much longer, until virtually full weight is attained at an age of ten to twelve years and they become capable of challenging for a territory. Bulls which appear adult to a casual observer may thus remain functionally still adolescent. All mature males will be classed as either territorial bulls or subsidiary bulls; this distinction is independent of age.

Group structure

Most of the larger groupings which may be observed are merely temporary aggregations at grazing or resting areas. The cohesive groups consist mostly of twos, with some singletons and a few trios or larger groups of up to six individuals.

Most cows are associated only with their most recent offspring in the form of cow-calf pairs. A cow which has lost her calf will, however, accept the company of one or more adolescents, and the largest coherent groups are formed in this way. Two adult cows in this circumstance may also join together. Adolescents team up temporarily with a cow, or with one or more adolescents of about the same age; groups of two are however most stable. Adolescent bonds formed between males can persist until both individuals are almost adult in appearance. All mature males are solitary, except that territorial bulls will attach themselves to potentially oestrous cows and their companions encountered within the territory for periods of several days to two to three weeks.

Utilisation of space

The basic home range of a cow covers 10–15 km², with the animals favouring different sections during different periods. There are no seasonal shifts in basic home range, but towards the end of the dry season cows may be forced to wander further afield in order to obtain water. Such journeys are undertaken only every two to four days, and after drinking the animals return to their basic home ranges, though perhaps lingering to graze along the way. The basic home ranges of individual cows are unique and independent, and overlap extensively with the ranges of other cows and adolescents. They encompass some six to seven male territories.

The home range patterns of adolescents have yet to be clarified. It seems that some adolescent groups confine themselves to fixed home ranges of 4–10 km², while others move about erratically, appearing, remaining for a few months, then disappearing again.

Territorial bulls occupy ranges of 1–2 km² which are mutually exclusive. They do not wander beyond the borders of these territories as long as water supplies last. Drinking excursions when necessary are not prolonged more than a few hours, the maximum time necessary to make the return journey to the nearest water source.

The home range of each subsidiary bull is essentially restricted to the territory of one of the territorial bulls, though occasional wandering movements beyond these limits may take place. In some territories there may be no subsidiary bull, in others two or three subsidiary bulls cohabit the same territory, in addition to the territorial bull.

Direct interaction patterns

Cows are generally tolerant of the presence of other cows and of the presence of adolescents and calves. Approach to within a few metres by a stranger is usually resisted with snorts. However, on occasions two cows may come together to nudge horns amicably. Adolescents and calves show interest in other rhinos, and may engage in prolonged playful horn wrestling. Cows and adolescents react to an approach by any adult male with distance maintaining threats, using either snorts or a deep bellow which is coupled with a forward-thrust posture of the head and flattened ears. Occasionally they may clash horns briefly with the bull.

If two territorial bulls meet at a common boundary, there is a tense confrontation, with repeated advancing to touch horns with raised heads, followed by backing apart to wipe the anterior horn over the ground. There may occasionally be a momentary clash of horns with lowered heads, but actual attacks have not been witnessed. In the two observed instances in which one bull had penetrated a short way into the territory of a neighbour, the intruder backed away steadily in the face of the other bull, until the border was reached, whereupon the bulls separated in opposite directions.

Encounters between a territorial bull and the resident subsidiary bull of his territory follow one of two courses: (i) an approach by the territorial bull with the subsidiary bull standing his ground with defensive threats, the head being thrust forwards with the ears laid back and loud roaring bellows and shrieks uttered. The interaction may include a few brief clashes of horns. The territorial bull usually soon moves away. (ii) Ignoring by the territorial bull, with the subsidiary bull attentive to his movements and possibly making a few threat gestures. Following an encounter the two bulls may remain grazing or resting in close proximity.

If a territorial bull discovers a strange adult male on his territory, a more prolonged interaction is likely to ensue. There are repeated approaches by the territorial bull, which the intruder wards off with the defensive threat gestures described above. There may be repeated horn clashes, but attack is rarely carried any further, and it is again the territorial bull who eventually wanders away, leaving the other bull on the territory. Adolescent males may be accosted by the territorial bull, but are usually not molested, though occasional chases may be witnessed. A territorial bull off his territory during a journey to water, if confronted by a resident territorial bull, adopts the same defensive threat gestures as a wandering subsidiary bull.

A territorial bull investigates any cow that he encounters on his territory. The approach is frontal and is resisted by the cow with threat gestures. In most cases the bull thereupon wanders away. A persistent association between a bull and a cow indicates that the cow will come into oestrus shortly. Subsidiary bulls may approach cows but do so with greater hesitancy. They do not

form persistent attachments, apparently because of the presence of the territorial bull with any potentially oestrous cow.

Indirect communication by marks

Ritualised forms of defecation and urination which function in olfactory marking of the territories are restricted to the territorial bulls.

A territorial bull makes kicking movements with the hind legs before and after defecation, so that his dung is broken up and scattered over the dungheap upon which it is deposited. The complete urination ritual includes a wiping action of the horn over a low bush or the ground, then the front and hind feet are dragged forwards past this site. Finally, urination is effected in three to five spasmodic bursts in the form of a fine spray which coats the scrapemarks on the ground and the leaves of any bush present. A territorial bull off his territory does not spray-urinate, though he may still deliver a few kicks should he defecate.

Cows, calves, adolescents and subsidiary bulls may use the same dungheaps, but very rarely make any kicking motions with the hind legs. Urination is carried out by them in a directly functional manner in a continuous stream. Rhinos of both sexes direct olfactory attention to dung and to urination sites. There may be as many as thirty dungheaps scattered throughout a territory. Urination is not orientated to any special marking sites.

Reproduction

Reproduction is not seasonally restricted. However, the onset of oestrus is apparently stimulated by a flush of green grass, so that there is a mating peak in spring and subsequent calving peak in autumn following the gestation period of sixteen months.

A territorial bull forms a temporary consort relationship with the cow five to twenty days before she is ready to accept mating. This involves simply accompanying the cow on her movements. Should the cow wander towards a territory boundary region, the bull moves between her and the boundary with soft squeals, and turns her back. The cow is thus confined within the territory until she becomes receptive. True oestrus lasts one day only. The bull makes repeated advances behind the cow. Eventually after several hours, he is permitted to place his chin on her rump, and after several mounting attempts intromission is achieved. Copulation lasts twenty to thirty minutes. The cow offers no apparent stimulation, other than by standing to accept the bull.

A subsidiary bull may remain in the vicinity during a mating, but does not interfere. The strict observance of territorial limits prevents attendance by more than one territorial bull.

DISCUSSION

The territorial system of the white rhinoceros

Territorial behaviour in the white rhinoceros thus exhibits the following features: (i) restriction to certain adult males; (ii) mutually exclusive ranges; (iii) a dominant assertiveness in interactions; (iv) specialised scent marking techniques; (v) exclusive participation in reproduction.

Cows and adolescents do not exhibit territoriality and their home ranges overlap extensively. For adult males the impression is given that a system of partly overlapping ranges exists, until detailed behavioural observations reveal the differences between territorial and non-territorial

males. Once this distinction is made, it becomes clear that the dominant males occupy home ranges which are mutually exclusive and can be termed true territories, but that these territories may be shared with one or more subordinate males. Occasional excursions out of the normally used range, for the purpose of seeking water or perhaps exploration, must also be recognised as such in examining range relationships.

A territorial bull is clearly the dominant animal in interactions with other males within his territory, once the seemingly intimidating bellows and shrieks of a subsidiary bull are recognised by the observer as defensive threats, implying only that he will defend himself if attacked. Once he leaves his territory, however, a territorial bull loses this dominance, and reacts with avoidance or defensive threats should he then encounter any other white rhino.

The question arises, to what extent are these territories defended? Interactions in which an intruding territorial bull has steadily retreated in the face of the territory holder's advance may readily be interpreted as defence of the territorial space. However, I have observed only two such incidents in over three years of concentrated field observation. The bulls prefer not to leave the confines of their territories, with the consequent loss of dominant status. The scent marking system is of importance in indicating the limits of the territories and the continued presence of the territory owners, without the need for direct encounters. A territorial bull does not defend so much the territorial space, but rather maintains his dominance within that space. Another adult male is permitted to remain on the territory, providing he demonstrates his subordinance when tested. The behaviour of a deposed territorial bull is of significance in this connection. Following defeat by another bull the former territory owner immediately ceases spray-urination, more gradually eliminates dung-kicking, and no longer attaches himself to cows. However, he need not vacate the territory, but may remain there, adopting the status of a subsidiary bull.

A dominance relationship gives the superior animal access to a desired resource without the need for direct agonistic interaction whenever the resource is available. The significant resource in the case of the white rhinoceros is clearly reproductive opportunity, since a territorial bull will readily share his food reserves with other males, and since neither cows nor adolescents are territorial. However, only the resident territorial bull can mate with an oestrous cow present within that territory. Territoriality as exhibited by the white rhinoceros thus has the prime functional role of ordering reproductive competition among adult males. The incidence of injury-inflicting combat is reduced, while courtship and copulation, which are drawn-out affairs, can proceed without interference.

The territorial system does provide some pressure for surplus males to shift elsewhere in order to claim a territory. But there is no reason to believe that the population density of cows is influenced by the territoriality of the males, or that the reproductive performance of adult females is limited by the availability of territorial males. Hence, territoriality does not appear to be playing any significant role in checking population growth, despite the habitat deterioration currently taking place in the Umfolozi Game Reserve.

Comparisons with other ungulates

Territoriality as shown by the white rhinoceros appears analogous with that exhibited by other territorial ungulates upon which sufficient information is currently available in the literature. This list includes Grant's gazelle *Gazella granti* (Walther 1965), Thomson's gazelle *Gazella thomsoni*

(Walther 1964), hartebeest *Alcelaphus lichtensteini* (Dowsett 1966), impala *Aepyceros melampus* (Leuthold 1970), kob *Adenota kob* (Leuthold 1966), puku *Kobus vardoni* (De Vos 1965), waterbuck *Kobus defassa* (Spinage 1969), wildebeest *Connochaetes taurinus* (Estes 1969), chamois *Rupicapra rupicapra* (Krämer 1969), pronghorn *Antilocapra americana* (Bromley 1969), vicuna *Vicugna vicugna* (Koford 1957), and Grevy's zebra *Equus grevyi* (Klingel 1969). In all these species (i) territorial behaviour is restricted to adult males, and (ii) possession of a territory gives a male exclusive rights to mate with any female present within its limits. It seems justifiable to generalise that territoriality as seen in the ungulates has evolved primarily as a system for ordering reproductive competition among males.

Other types of territorial system may be related to food as the essential resource, for example in carnivores such as the hyaena *Crocuta crocata* (Kruuk 1966). In birds, territoriality can limit the density of settlement of breeding pairs, for example in the Red Grouse *Lagopus lagopus* (Watson and Jenkins 1968). In such cases territoriality may play a role in population regulation.

Methodological criteria for territoriality

Territoriality is, in essence, a spatially localised dominance relationship among rivals for some essential resource. Its characteristic expression is the exclusion of certain conspecifics from a fixed piece of space, by whatever means this is achieved. Such exclusion may be activity specific, it may be only temporary, and it will be related only to those conspecifics which are rivals for the critical resource. There may also be variation in the efficiency with which rivals are excluded, giving a flexibility of expression which may be correlated with population levels.

To prove or disprove the existence of territoriality in a population, the following evidence is thus required:— (i) observations must be sufficiently intensive to distinguish between different social classes of individuals within the population; (ii) ample information must be available on range utilisation by the seemingly dominant individuals, considering spatial and temporal features and activity relationships; (iii) the spatial features of dominance relationships between potential rivals must be analysed in relation to competition for various essential resources.

It must be recognised however that strict territoriality is only one possible way of socially regulating competition for an essential resource. Its degree of expression may be profoundly modified by existing ecological circumstances, such as the degree to which each resource is limited, population density levels and population mobility. An alternative and perhaps preferable approach is to examine, for any particular population, the manner in which competition is organised among constituent individuals in relation to each resource of possible significance. In addition to material resources such as food which affect individual survival, there must also be considered individual opportunity to make a reproductive contribution to the next generation, which is of vital evolutionary importance.

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