

Territoriality in the White Rhinoceros (*Ceratotherium simum*) Burchell

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The white rhinoceros maintains a territorial system based on a space-correlated dominance relationship in which breeding bulls defend individual areas against rivals, but may share them with subordinates.

THERE may be pronounced differences in social organization between closely related species, or even between different populations of the same species. For primates this variability has been correlated with environmental influences^{1,2}, but field data have been too scanty to demonstrate such a relationship for other mammalian taxa. There has, however, been much recent work on the ungulates, among which territoriality has been revealed as a conspicuous behavioural feature³. The rhinoceroses, being one of the most primitive ungulate families, are of special interest.

The Indian rhinoceros (*Rhinoceros unicornis*) in Kaziranga maintains separate grazing and sleeping territories defended by individuals of both sexes, while wallows and main pathways are communally shared⁴. Contradictory to previously held opinions^{5,6} Schenkel^{7,8} reported that the black rhinoceros (*Diceros bicornis*) in Tsavo, Kenya, did not exhibit territoriality. My observations indicate that the white or square-lipped rhinoceros (*Ceratotherium simum*) has a social system based on a very clearly delineated mosaic of adult male territories.

I have investigated intensively the ecology and ethology of the white rhinoceros in the Umfolozi-Corridor-Hluhluwe game reserve complex in Zululand, South Africa. Observations began in 1966, and since November 1968 have continued without interruption to January 1971. The white rhinoceros is an unusually favourable subject for a detailed study of social relationships. Because of their poor vision individuals or groups can be observed for long periods without disturbance. From variations in horn shape and other features, I have been able to recognize all the adults and several immature individuals in the main study population which includes nearly 200 animals.

The general ecology and conservation of the southern white rhinoceros (*C. s. simum*) have been described by Player and Feely⁹, and its current status has been reviewed by Vincent¹⁰. Backhaus¹¹ has reported some features of behaviour in the northern subspecies *C. s. cottoni*.

Territorial Behaviour

Territoriality is exhibited by only a segment (roughly two-thirds) of the adult male population. Their territorial behaviour may be characterized by the four following features.

(i) Range exclusiveness: the ranges of the territorial bulls, as plotted on the basis of numerous sight records, are mutually exclusive and non-overlapping, so that all suitable habitat is divided into a mosaic of territories, each typically about 2 km² in area. A territorial bull rarely leaves the confines of his territory, except when forced to make excursions to water during the dry season.

(ii) Ritualized encounters; two territorial bulls meeting at a common boundary, engage in a tense but silent confrontation. The bulls repeatedly advance towards each other with raised heads, touch horns (Fig. 1), then back apart to wipe the anterior horn over the ground. Occasionally, with lowered heads, they may clash horns momentarily, but otherwise attacking gestures are inhibited. On the rarely observed occasions on which one bull had intruded a short way into the territory of another, the trespasser backed steadily in the face of the territory owner's advance, until their common border was reached, whereupon the two bulls separated.

(iii) Confinement of oestrous cows: a territorial bull encountering a cow which is nearing oestrus, enters into a consort relationship with her which may last for 2–3 weeks. If this cow wanders towards a boundary region, the bull moves ahead, squealing softly, to stand in front of her, determinedly blocking her further advance. If the cow runs off in fright (for example, when disturbed by my presence), the bull does not pursue her more than 100–200 m beyond his boundary. As a consequence of the territorial system, courtship and mating proceed without interference from other bulls.

(iv) Scent marking: territorial bulls exhibit specialized techniques of defaecation and urination. Backwardly directed kicking movements are made before and after defaecation, so that the dung is broken up and scattered. Although defaecation is almost invariably carried out by territorial bulls at one of the numerous (twenty to thirty) dungheaps present on the territory, these dungheaps are also used by other rhinos, and they are distributed throughout the territory. Urination is effected in the form of a fine spray in three to five spasmodic bursts. It is usually preceded by a scraping action of the legs, and frequently also by a wiping motion of the anterior horn over a low bush or the ground. The fine droplets of urine coat the scrapemarks on the ground and the leaves of the bush if one is present. Urination is not related to any special "marking posts", but is carried out repeatedly whenever the bull moves

about and this probably saturates the territory with his characteristic odour. The existence of preputial scent glands has been reported¹², and there is evidence that rhinoceroses are able to recognize the location of territory boundaries by smell.

Related Elements

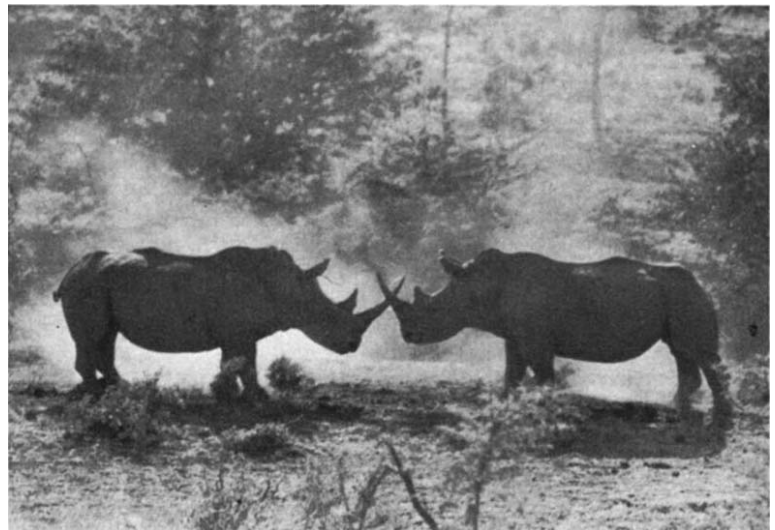
A territorial bull journeying to water attempts to avoid encounters with other rhinos, but, if accosted by a resident territorial bull, he adopts a subordinate defensive stance and bellows and shrieks. When off his territory he does not spray-urinate, but may still exhibit dung-kicking. His whole demeanour changes from confident assertiveness to nervous apprehension.

A bull occupies its territory apparently for several years, so that changes in territory ownership are rare events. From three such observed transitions, however, it is evident that the deposed territorial bull need not vacate his territory, but can remain on it as a subsidiary bull. Following defeat, he immediately ceases spray-urination, and more gradually abandons dung-scattering, initially decreasing the intensity and number of kicks.

Significance of Territoriality

The territoriality of the white rhinoceros is fundamentally a space-correlated dominance relationship between rivals. A territorial bull establishes himself as supremely dominant within the confines of his territory. Direct encounters are not necessary to prevent intrusions. The efficient scent marking system provides a bull with adequate evidence of the presence of others claiming dominance beyond his territorial limits and, in the absence of any motivation to challenge this dominance, a bull prefers to avoid the risk of a meeting. A subsidiary bull is analogous to what is frequently termed a bachelor male in other ungulates. Because all available habitat is divided up into territories, a subsidiary bull is forced to inhabit one of them, and it appears that the owner of the territory eventually becomes habituated to the other's presence. This arrangement may be a result of the relatively high white rhino population densities (about 5/km²) which have built up over much of Umfolozi Game Reserve and now threaten destruction of the habitat. The co-existence of subsidiary and territorial bulls probably represents the initial elements of a rank hierarchy within the territorial structure.

Fig. 1 The horn-touching posture adopted by two territorial bulls during a border confrontation.



Also present in the population are other solitary adult males which do not kick their dung or spray their urine, and which do not associate with cows for any length of time. Although lacking these characteristic features of territorial behaviour, each of these subsidiary bulls essentially confines his activities to the territory of a single territorial bull. A dominance-subordinance relationship exists between a subsidiary bull and the territory owner. If approached, the subsidiary bull exhibits nervousness, but stands his ground with defensive threats; the head is thrust forwards, the ears are flattened, and loud bellows and shrieks are uttered. A brief confrontation may ensue. Often, however, the territorial bull pays no attention to the presence of the other bull, and the two may graze in close proximity in apparent amity. A subsidiary bull sometimes remains nearby when a cow is being mated by the territorial bull, but does not interfere. Subsidiary bulls occasionally wander, but are accosted and sometimes attacked if they meet another territorial bull. Cases are known in which subsidiary bulls have moved elsewhere to become territory holders.

Cow-calf units have independent home ranges extending over 12–15 km², and encompassing seven to eight territories. There is extensive range overlap and they exhibit tolerance and sometimes amity towards other rhinos, with the exception of adult males. Sub-adults associate in pairs or occasionally in larger groups and some seem to wander erratically. The bond between a pair of young males can persist until both individuals are virtually adult in appearance. Cows, non-territorial males and immature animals do not scatter their dung or spray their urine.

A dominance relationship is a means of ordering competition for essential resources. One must therefore enquire in this case, which resource? Food is evidently of no great significance, because a territory owner will readily share his food reserves with a subordinate bull, and also, neither cows nor sub-adults show territorial behaviour. What a bull lacking a territory forgoes is the opportunity to reproduce. The territoriality of the white rhinoceros may thus be described as a system for ordering specifically reproductive competition among males. Its primary function within the population seems to be to increase the reproductive efficiency of prime bulls by reducing the incidence of injury-inflicting combat.

These statements can probably be broadened in scope to apply, with the exception of the Indian rhinoceros, to all other ungulates in which territoriality has been identified, and perhaps to any species in which territoriality is restricted to adult males. In evolutionary terms, territoriality of this type would be favoured over other possible systems for ordering reproductive competition, such as intra-group rank hierarchies (for example, Carmargue wild cattle¹³), or a moving dominance associated directly with a female harem (for example, caribou¹⁴). In this context, its favoured features are: (a), settled range occupancy as opposed to nomadism; (b), low aggregative tendencies; (c), a broadly defined mating season; (d), moderate population densities (low population densities lessen the likelihood of direct competition between rivals and therefore the need for territorial exclusion, high densities may result in the superimposition of a rank hierarchical system).

Alone among the territorial ungulates studied so far, the

Indian rhinoceros, with its system of food territories, seems exceptional. As it also has a peculiar mating system¹⁵ this species warrants a more detailed investigation. The reported lack of territoriality in the black rhinoceros^{7,8} is open to question. As this study has indicated, intensive observations are necessary to distinguish non-territorial and territorial males, which, if they inhabit the same range, can obscure the spatial pattern expected of territoriality.

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- ¹ Crook, J. H., and Gartlan, J. S., *Nature*, **210**, 1200 (1966).
- ² Gartlan, J. S., *Folia Primatol.*, **8**, 89 (1968).
- ³ Estes, R. D., *Z. Tierpsychol.*, **26**, 284 (1969).
- ⁴ Ullrich, W., *D. Zool. Garten*, **28**, 225 (1964).
- ⁵ Hediger, H., *Bijdr. t.d. Dierkunde*, **28**, 172 (1949).
- ⁶ Ripley, S. Dillon, *Ecology*, **39**, 172 (1958).
- ⁷ Schenkel, R., *Z. Tierpsychol.*, **23**, 593 (1966).
- ⁸ Schenkel, R., and Schenkel-Hullinger, L. M., *Ecology and Behaviour of the Black Rhinoceros* (Paul Parey, Berlin, 1969).
- ⁹ Player, I. C., and Feely, J. M., *Lammergeyer*, **1**, 3 (1960).
- ¹⁰ Vincent, J., *Lammergeyer*, **10**, 12 (1969).
- ¹¹ Backhaus, D., *D. Zool. Garten*, **29**, 93 (1964).
- ¹² Cave, A. J. E., *Mammalia*, **30**, 153 (1966).
- ¹³ Schloeth, R., *Z. Tierpsychol.*, **18**, 574 (1961).
- ¹⁴ Lent, P. C., *Anim. Behav.*, **13**, 259 (1965).
- ¹⁵ Ripley, S. Dillon, *Ecology*, **33**, 570 (1952).

Trophic Interaction between Cloned Tissue Culture Lines of Nerve and Muscle

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Tissue culture of neural tumour cells with skeletal muscle provides a model for the early stages of synapse formation. Functional synaptic transmission, however, has not yet been seen.

AN important generalization underlying present understanding of the development and function of the nervous system is the great orderliness and specificity of interneuronal and neurone-endorgan connexions. Little is known of the physiology of formation of these connexions, either in developing embryos or during regeneration of cut nerves in adults. One indication of how a cell signals its willingness or unwillingness to accept innervation comes from work on muscle by Miledi, who described a striking correlation between the distribution of chemoreceptors on a presumptive postsynaptic cell surface, and the ability of that cell to accept a new synapse^{1,2}. Thus damaging a muscle fibre at a discrete point, which causes a local hypersensitivity to acetylcholine³, also locally removes the barrier to hyperinnervation of that muscle fibre, so that a new synapse can be formed at the hypersensitive area². Recent studies of regenerating synapses on parasympathetic nerve cells in the frog heart⁴ provide a similar correlation between chemosensitivity of a neuronal surface and the receptivity of that neurone to innervation, showing that this relationship is not unique to muscle.

Briefly summarized, the phenomena that seem common to synapse formation both on skeletal muscle and parasympathetic nerve cells¹⁻⁴ are as follows: (a) the noninnervated post-

synaptic cell is more or less uniformly sensitive to neural transmitter; (b) contact with an ingrowing nerve is followed by removal of this generalized sensitivity and the development of local sensitivity at the point of contact, probably before there is any functional synaptic transmission¹; (c) other nerve fibres are now unable to make synapses on the insensitive region of that cell; and, finally, the synaptic contact is enlarged and normal function becomes possible.

Our aim has been to develop a simple system in which synapse formation can be studied under controlled conditions *in vitro*. It has long been known that synaptic connexions can be induced to form within primary cultures of tissue explants or disaggregates⁴⁻⁸, but there are still many cell types in such cultures, making it difficult to undertake the detailed biochemical studies necessary to define the molecular events responsible for the formation and observed specificity of synapses. We have chosen to study the interaction between pure (cloned) continuous tissue culture lines of nerve and muscle. The nerve cells are from the C 1300 mouse neuroblastoma, clone C1A⁹, and the muscle cells from a cell line of rat skeletal myoblasts, clone L-6¹⁰, given us by Dr D. Yaffe.

The nerve-like properties of the neuroblastoma have been described in moderate detail^{9,10-13}, but the physiological properties of the muscle cell line have not been described. A detailed description of these cells will be presented elsewhere; briefly, the cell line is carried in the form of myoblasts, which grow in a monolayer on tissue culture dishes. After becoming confluent the cells begin to fuse, forming multinucleate myotubes which later develop into striated muscle fibres. The fibres begin to beat spontaneously late in the myotube stage, before striations appear. The development of electrical excitability is similar in many respects to that recently described in developing tunicate muscle¹⁴. Individual myoblasts have resting potentials of about -70 mV, and behave in an electrically passive manner when depolarizing or hyperpolarizing

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