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African Ungulates

A Comparative Review of Their Ethology
and Behavioral Ecology

With 55 Figures



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Threat and intimidation displays center on the head, with the ears playing an important role. Extending the ears sideways and erecting the anterior part of the body, sometimes enhanced by stepping on some elevated object (log, termite mound, etc., see Fig. 27), serve to increase the animal's apparent size and are commonly employed in both intra- and interspecific encounters. Other displays involve movements of the entire head (nodding, shaking) or of the trunk only, and a great variety of expressive nuances has been described; they are frequently combined with brief forward rushes. Agonistic encounters often include bursts of redirected aggression, such as thrashing and breaking of bushes and small trees. (Kühme, 1961, 1963; Hendrichs, 1971; Sikes, 1971; Douglas-Hamilton, 1972; Douglas-Hamilton and Douglas-Hamilton, 1975; pers. obs.).

Equidae. Being virtually the only ungulate group not possessing special weapons for intraspecific fighting, equids use primarily their teeth and hooves. I have already described fighting techniques of zebra briefly (see Fig. 24), and no further elaboration is needed here. The main points are that a considerable variety of methods is employed and that all of them show little or no ritualization (Backhaus, 1960; Klingel, 1967, 1972a; Hassenberg, 1971).

Rhinocerotidae. Agonistic encounters between rhinoceroses are characterized by a marked preponderance of various threat and intimidation displays, while actual serious fighting is relatively rare. The latter involves mainly clubbing with the head and "horns", wielded sideways, against the opponent's head and/or body. Jabbing with the anterior horn also occurs, but more often during pursuit of a fleeing antagonist. Many rhino bear wounds that could be attributed to horn jabs, but not all these are necessarily related to serious fighting; horn-jabbing also occurs fairly commonly in premating behavior. Some wounds may have causes unrelated to agonistic behavior (see Chap. 7, A, II).

Intimidation and threat displays include the following, in approximate order of increasing intensity of threat components: scraping with hindlegs (with or without defecation); head-high intimidation posture, presented frontally or laterally; stiff-legged approach and/or circling of opponents; frontal approach with the head stretched forward; forward rush with lowered head and vocalization (snorting, screaming), culminating in the two opponents standing directly opposite each other, with front horns almost touching, sometimes also accompanied by screaming. From this position, the antagonists may either proceed to fighting, as described above, or start withdrawing. During the withdrawal phase, ritualized urination and/or defecation (Chap. 5, C, IV) may occur.

This is clearly a case where relatively unrefined fighting techniques and crude, potentially lethal weapons are associated with pronounced displays that reduce the incidence of overt fighting. This description refers primarily to the black rhinoceros, but the behavior of the "white" (square-lipped) species appears to be very similar (Goddard, 1966, 1967; Schenkel and Schenkel-Hulliger, 1969; Owen-Smith, 1973, 1975).

Suidae. Of the African species, only the warthog has been studied sufficiently. However, while varying in some details, the agonistic behavior of bush pig and giant forest hog is said to resemble that of the warthog in its general

In plains zebra precopulatory behavior is most pronounced in matings with young mares, but much less elaborate, or even absent, in relation to adult mares.

Copulation involves frictional movements and is said to last from one to 3–4 min in plains zebra, but only a few seconds in Hartmann's zebra. It may be repeated at intervals of 1–3 h in peak estrus. During coitus the males of some species (e.g., Grévy's zebra in captivity) bite the female's neck or shoulders. There seems to be little or no postcopulatory interaction.

Estrous female equids may adopt a special "invitation" posture ("Präsentieren"): they turn the hindquarters toward the stallion, straddle the hindlegs and lift the tail sideways. This posture is especially pronounced in young female plains zebra, where it has strong visual signal value and attracts stallions who then try to abduct the young mare from her family group. In addition, females assume a characteristic facial expression while the male mounts ("Rossigkeitsgesicht"): the ears are laid back/down, the eyes half closed, the mouth is fairly wide open, with lips retracted upward, and may make slight chewing motions (Fig. 11 b in Klingel, 1974 a). The expression strongly resembles the equine threat; sometimes mares show biting intentions or actually bite the stallion during courtship (plains zebra: Trumler, 1958, 1959; Klingel, 1967, 1969 c; Hartmann's zebra: E. Joubert, 1972 b; Grévy's zebra: Zeeb and Kleinschmidt, 1963; Klingel, 1974 a. Reviews: Hassenberg, 1971; Klingel, 1972 a).

Rhinocerotidae. Whilst the black rhinoceros is generally solitary, apart from mother–young associations, a male may accompany an estrous female closely for several days. Initially the female tends to attack the approaching male, who then sometimes shows elements of agonistic displays but usually retreats; eventually the cow tolerates the male's presence, even in close proximity. Precopulatory behavior is comparatively simple, including mainly naso-genital contacts, the urination-Flehmen sequence, attempts by the male to lay his head onto the female's rump and mounting without erection. In the early stages, nose-to-nose contact and occasional bouts of mutual horning may occur, as well as horn jabs by the male against the female's hindquarters or flanks. The initial mountings without erection are characterized by the distance kept by the male, i.e., the lack of contact between his pelvic area and the female's body (cf. Fig. 6 in Goddard, 1966). These mountings may be repeated frequently, over a protracted period, and probably serve to test the cow's readiness to stand for actual copulation which is a rather prolonged affair, lasting from 20 to 40 min. During coitus, the bull shows certain rhythmic actions, such as changes in the position of his forelegs and the attitude of head and tail; these may be associated with a sequence of ejaculations. No postcopulatory behavior is reported; the two partners usually begin to feed or lie down after mating. Sexual behavior of the white rhinoceros appears to be largely identical (Goddard, 1966; Schenkel and Schenkel-Hulliger, 1969; Schenkel and Lang, 1969; Owen-Smith, 1973, 1975).

Suidae. Of the African suids only the warthog has been studied in sufficient detail. There is a pronounced driving phase, during which the male follows the female closely in a fast walk or trot, trying to establish and maintain naso-genital contact. Simultaneously he utters a series of low rhythmic grunts "resembling

hierarchy of the bachelor herd (without relinquishing his high status vis-à-vis the remaining bachelors) and re-enters the relative one of the territorial system. He enters, as it were, a different stratum in the overall social hierarchy; high rank in the bachelor herd is the "stepping stone" to establishing a territory. Behavior patterns associated with territoriality are exhibited with increasing frequency by males near the top of the bachelor hierarchy (M. V. Jarman, 1973).

Changes in territorial ownership are effected almost exclusively through fighting. Only rarely will a presumably "exhausted" male yield to another one without combat. Contests over territories are, in fact, the principal occasions on which serious fights occur (contrary to popular opinion, females are rarely the direct object of fighting). The victor in the fight will stay on the territory in question, the loser will have to leave and either join the bachelor herd (impala, kob, etc.) or set up a territory elsewhere (waterbuck). In a number of species the cycle outlined here may be repeated several times during a male's lifetime.

Interindividual relations in female groups may also be governed by an absolute hierarchy. Its expression is likely to be inversely related to herd size and cohesion, i. e., to be less pronounced in species commonly forming relatively large aggregations (e. g., impala, Uganda kob, Thomson's gazelle), but particularly well developed where groups tend to be relatively small and more stable in composition (e. g., sable, roan, Grant's gazelle). However, for most species insufficient information is available on this point.

In summary, we can say that there are probably as many variations of the basic pattern described here as there are species exhibiting this type of social organization. The range of variation is augmented even further by differences between local populations of the same species, related to environmental conditions (see Chap. 17). Nevertheless, three traits apply almost universally and thus characterize the pattern as a whole:

1. Territorial defense usually overrides sexual motivation in any given situation.
2. No female group is the exclusive property of any male, territorial or otherwise, i. e., males compete for possession of territories, not females.
3. Nonterritorial males are largely excluded from reproduction.

Some of these features will be discussed further in Chapter 18.

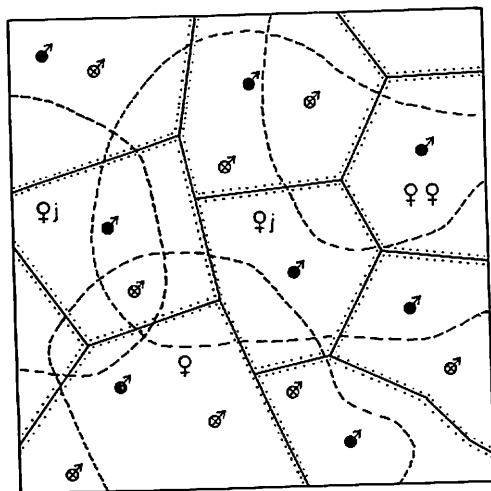
F. Territory and Absolute Hierarchy Combined

SO-type 6. Exclusive home ranges in a portion of the adult males, with other adult males resident as subordinate "satellites" on some of the territories (Fig. 54). Social units are (1) adult territorial males, (2) adult-satellite males, and (3) small female/young groups.

This interesting social system has only recently been discovered in the white (square-lipped) rhinoceros in South Africa (Owen-Smith, 1971, 1972, 1973, 1974, 1975).

Fig. 54. Male territories combined with absolute hierarchy.

♂: dominant territorial male; ♂: subordinate territorial male ("satellite"); ---: boundary of male territory/home range; ----: boundary of female home range



About two thirds of the adult males occupy territories incorporating their entire home ranges (areas of about 2 km^2). Small groups of one or two females with their most recent offspring (up to six animals) inhabit overlapping home ranges of $10\text{--}12 \text{ km}^2$, covering parts or all of six to eight male territories. Temporary groups of two to five adolescent animals use similar home ranges, but some also range farther afield. So far, the system corresponds closely to our SO-type 4 (gerenuk). The important, and characteristic, difference lies in the behavior of the remaining one-third of adult males. Also living solitarily, each of them remains within the territory of another bull whom he accepts as dominant by either simply avoiding encounters, or by exhibiting specific submissive behavior. Up to three of these "satellite" bulls (Owen-Smith calls them "subsidiary" or β -males) may live on one territory. They exist as "social castrates," i.e., access to females in estrus is denied to them by the dominant territory owner; they can be regarded as the social equivalent of the bachelor herd in SO-type 5. This parallel is suggested by the fact that, occasionally, a satellite bull moves elsewhere to become territorial. Conversely, territorial bulls defeated by a rival may remain on their former territory but assume the role of satellite to the new occupant.

Of particular interest are some behavior patterns associated with different social status, suggesting important psychic changes accompanying the step from satellite to dominant bull, or vice versa. Dominant bulls urinate in a characteristic manner, emitting urine "in the form of a fine spray in three to five spasmodic bursts" (Owen-Smith, 1971, p. 297). They also scatter their dung, deposited at fixed sites, by kicking movements with their hindlegs. Satellite bulls neither spray their urine nor scatter their dung. Also, "a defeated territorial bull immediately ceases spray urination, and more gradually eliminates dung scattering" (Owen-Smith, 1974, p. 346). Such clear-cut behavioral correlates to social status have, to my knowledge, been recognized only rarely.

The white rhinoceros' social organization, although having various attributes in common with that of many other ungulates, nevertheless appears to be unique

in its combination of well-defined relative dominance (territorial male vs other territorial males) and absolute dominance (a given territorial vs his satellite male).

For the black rhinoceros, results and interpretations of several field studies are at variance. Goddard (1967), working mainly in Ngorongoro Crater, Tanzania, found male home ranges (see Table 3) overlapping widely, with no evidence for territoriality. Schenkel (1966b; also Schenkel and Schenkel-Hulliger, 1969) concluded from studies in Kenya that the black rhino was not territorial. More recently, however, Hitchins (1971) presented observations from South Africa which suggest that the black rhino has a social organization closely resembling that of the white rhino. The existence of satellite males would have obscured actual territorial relationships to observers not aware of this possibility. Patterns of ritualized urination and defecation of the two species appear to be virtually identical, but it is not yet known how they are distributed among different social classes in the black rhinoceros.

There is a certain similarity between the social system of the white rhinoceros and that of Grévy's zebra. However, an important difference is that, in the latter species, the territorial male may tolerate virtually any other—nonterritorial—males on his territory, not just one or two specific individuals. The reason for this tolerance may lie in the large size of the territories (up to 10 km²: Klingel, 1974a, b), which makes it impractical to defend them against all other males.