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Behaviour
Poster

Display and hyperbolization of signalizing symbols : Camels and Two Horned Rhinoceroses

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HYPERBOLIZATION OF SYMBOLS
SEXUAL SELECTION
HIERARCHIC RELATIONS
HORN-LIKE STRUCTURES
CAMEL HUMP
RHINO HORN

ABSTRACT – The theory of sexual selection and contemporary ethological theories on hierarchy and territoriality are in no contradiction, as may appear at first glance, and reflect the two sides of one and the same evolutionary phenomenon. Morphological structures, linked with the display behaviour are visual release stimuli, *i.e.* "symbols" through behavioural ritual significance. Their evolution follows the way of hyperdevelopment through :

- hypermorphosis,
- inclusion of additional structures,
- multiplication.

Structures with such a function are the humps of camels and rhinoceros horns, whose effect is hyperbolized through duplication, demonstrated at the lateral display.

THE HYPOTHESIS OF THE HYPERBOLIZATION OF SYMBOLS

Behavioural patterns and the related morphological patterns for intraspecific signalization play a major part in the life of mammals. Communication signals are not only related to the recognition of the species, the individual or the sex, but also the state of the specimen and its place in social interrelationships. Communication interrelationships are largely based on the behaviour of dominance and submission. Signalizing behavioural and structural patterns, linked with such a behaviour follow the law of sexual selection and intraspecific hierarchic relations, which actually are two sides of the one and the same evolutionary phenomenon. This approach to phenomena and structures linked with most of the manifestations of intraspecific aggression and competition, reconciles Darwin's theory of Sexual Selection (often underestimated and seen in oversimplified terms, as Davitashvilli, 1961, notes) and the more recent theories for social hierarchy and territoriality (Schjelderup-Ebbe, 1935, Wynn-Edwards, 1962, Lack, 1966).This has enriched the evolutionary theory of sexual selection with the concepts of ethology, which by no means do not exclude. The theory of sexual selection and the theories of hierarchy and territoriality do not contradict each other, as its appears, but rather supplement each other. Hierarchic relations and sexual selection follow the same way and develope the same patterns "used" in the struggle for females, as well as at the level of hierarchic competition. Morphological patterns (structures), evolved in connection with these phenomena and related to intraspecific display, have become visual releasers of a specific behaviour. In their impact we frequently see the manifestation of the principle of antipodal effect – the opposite influence on the different sexes. Frequently threatening patterns between males are those patterns through which the male wins over females.

The typical morphological display patterns become "symbols" with a specific behavioural ritual meaning. Their evolution usually follows a hyperbolization of their visual effect through their hyperdevelopment. This hyperdevelopment under certain condition changes can clash with the principal line of natural selection and can become, in spite of its positive intraspecific effect, eventually a negative structure. For instance the enormous horns of the Megaceros played an important significance for the realization of sexual selection and the survival of the most vigorous specimens. This hyperspecialization did not allow the species to adapt to the afforestation at the Pleistocene-Holocene boundary, and probably became a negative factor for its survival (Spassov, 1982). Patterns-symbols for instance became alaestethic structures (in Huxley's -1938- meaning of the term) with a perigamic significance (in the meaning of the term of Davatashvili, 1961) and with significance in a dominance behaviour. These are so called horn-like organs (Geist, 1966) (or more correctly horn-like structures), including horns, antlars, tusks, and other growths with a direct tournament and threatening intraspecific function. The structures which enhanced the threatening body contour are patterns-symbols too. Such structures are multifunctional in accordance with A.N. Severtsov's ideas on multi-functionality of organs. They have

a primary and secondary function(s) which do not always fit the main and minor functions. Frequently when such structure originated or developed there occurs a moment of re-adaptation : a number of canines which reach their large size in connection with food specialization hypertrophied under the influence of intraspecific competition. It is difficult to say whether horns for instance, have appeared firstly as a direct weapon for intraspecific struggle and later acquired the display function or *vice versa*. In the evolution of cervids, for example, it is clear that horns come to replace the tournament role of canine, which for this taxon turned out to be less suited (perhaps inhibiting the ruminant movement). Evidently the same laws of evolution were in force for different taxonomic groups which explains the convergence of similar structures in taxa so distant from one another. In such cases analogical behavioural patterns have had the leading role to result in morphological similarities.

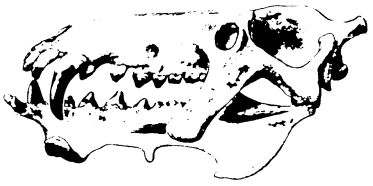
The ways of hyperdevelopment of morphological display patterns, leading to the effect of hyperbolization of the symbols are essentially three :

- hypermorphosis of the structure proper,
- accumulation of additional structures (behavioural patterns included),
- multiplication of structures.

Examples of the first evolutionary way are the hypertrophied and complex shaped horns of recent and fossil Cervidae and Bovidae, as well as the tusks of Proboscidea and Suiformes. As an example of the second way of evolution are the manes of lions and baboons, which enhance and underline the powerful front part of the body ; the bristling of the hairs of the chimpansee and many carnivores with a similar effect ; the development of dew-laps with a number of Bovidae and the bristling dorsal line of the Kudu, the enhanced additional lateral profile, ... I will deal with the third way in greater detail. The *Phacochoerus* is a suitable example. The two pairs of warts on the muzzle probably developed in order to protect the eyes from a rival blow from underneath. A similar supposition was made by Osborn, 1929, (on the origins of horns with early Titanotheres). These warts of the *Phacochoerus* also appear to have a visual impact. They repeat the shape of the tusks multiplying their threatening effect. Such a multiplication of facial growths with probably tournament significance is the case of the Permian *Estemmeosuchus*, (Therapsida), Eocene *Unitatherium* (Dinocerata), Oligocene Entelodonts (Suiformes), ... (fig. 1).

An example of the third way of hyperdevelopment of display-structures appears to be humps of camels and horns of rhinoceroses. Their doubling with some species may be explained with the lateral display of the body.

a *Phacochoerus*



b *Entelodon* skull (see the paired prominences on the mandible and on the zygomatic archs)

c *Unitatherium* head

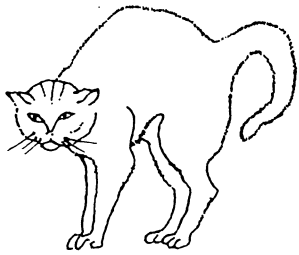
d *Estemmeosuchus* skull (by Tchudinov, 1983).

Figure 1 : Multiplication of the tournament display structures

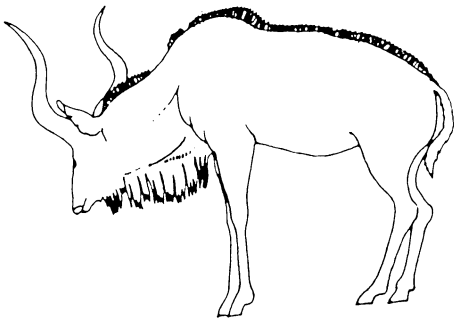
LATERAL DISPLAY

Lateral display as a form of intraspecific competitive relations is quite frequent in the animal world, mammals included. The humped lateral threat posture is typical for a number of

Felidae (Leyhausen, 1975). Lateral demonstration is also typical for many ungulates (Geist, 1966 ; Walter, 1971) (fig. 21). Lateral display is related to the challenging of the rival, by the powerful body profile to whom demonstrated. Probably this display originates from the blocking of the way of the rival (Walter, 1971). The effect of the enhancement of body was achieved through bristling of hairs, development of dew-laps and manes, humps, ..., related to enhancement and underlining of the profile, *i.e.* hyperbolization of the threatening effect.



a A cat in a humped posture. The tail follows the shape of the back



b Male *Tragelaphus strepsiceros*. The mane, the humped posture and the mid dorsal strip enhance the profile (by Walther, 1974)

c Parallel "march" in *Cervus elaphus* (after Clutton-Brock & Albon, 1979, stylized).

Figure 2 : Lateral display in mammals

HORNS OF RHINOCEROSES

Horns of rhinoceroses, besides their supplement use as a defensive intraspecific weapon, should be seen in the context of horn-like structures : tournement intraspecific weapons with an important ritual significance. There is ground to suppose, that in two-horned rhinoceroses the display role of the front horn is duplicated. This is particularly effective in lateral demonstrations, which exist in rhinoceroses (Schenkel & Schenkel-Hulliger, 1969). In this case the entire contour of the back appears to be visually important, in particular in *Ceratotherium simum* : at the neck of the adult a growth of connective tissue and horny hardened skin appears, which is enhanced like a hump when the head is straightened in display posture (fig. 3). There also appears to be sexual (dimorphism, without sufficient data for the present to back the claim).

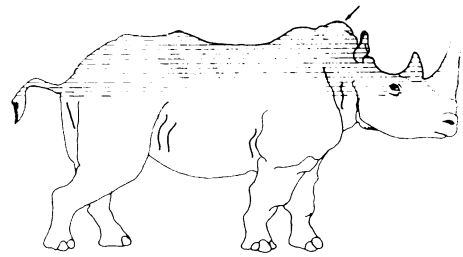


Figure 3 : *Ceratotherium simum*
A bull in display posture

HUMPS OF CAMELS

The functions of humps of camels remain an enigma. The supposition expressed some time ago that fats in the hump serve to ensure survival without water, has been rejected in recent literature. Other physiological adaptations are considered the cause of the great endurance of the camel to thirst (Schmidt-Nielson, 1979). The fats in the hump have a certain role as a energy depot in times of food shortage, however this does not explain their shape and position on the body. The supposition put forth (Grzimek, 1969) that the hump was a shield against the sun rays also fails to explain the shape and position, neither does it explain their number in the *bactrianus*.

Nevertheless lateral display is known with Camelidae. It exists in lamas (Koford, 1959). In camels the dominant male leader of the harem demonstrates his profile against the other males up to a distance of 3 km. (Baskin, Inst. Evol. Morphol. and Ecol., Moscow, personal communication). Evidently the hump has the function to raise the body profile. The double hump has developed as a consequence of the evolutionary

trend of multiplication of display structures and hyperbolization of their effect (fig. 4).

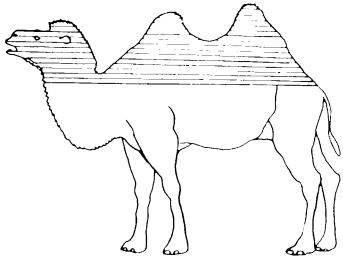


Figure 4 : *Camelus bactrianus*
Profile of a male in lateral display

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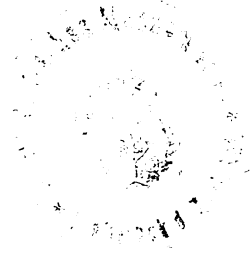

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