



On the origin of sexual displays in caprids

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Abstract

Observations on the social behavior of Nilgiri tahr (*Hemitragus hylocrius*) indicated a close similarity in form between behaviors observed in mother-infant relations and sexual encounters. Specifically, the postures adopted by a Nilgiri tahr offspring toward its mother in giving behaviors termed side and rear bunts bore striking resemblance to the sexual displays termed side and rear twists. A hypothesis that the primary sexual displays of Nilgiri tahr (side and rear twist) have been derived from mother-infant behavior (side and rear bunt) yielded several predictions about the occurrence of comparable displays in related taxa, indicating that the low stretch and twists of *Capra* and *Ovis* have evolved through ritualization from behaviors similar to the side and rear twists of *Hemitragus*. This contrasts with many ungulate groups in which a close relationship between sexual and aggressive behaviors exists.

Introduction

Display behaviors are thought to arise from other already existing behaviors, often through the process of ritualization of the original behaviors or the intention movements to perform them (HUXLEY 1914; DAANJE 1950). These original behaviors may have no element of communication (such as locomotion), they may be social acts (such as fighting or copulation), or they may be displays themselves (such as threats).

WALTHER (1984) presented convincing evidence of the close relationship between courtship and aggressive behaviors in many ungulate species. This relationship is particularly evident in those ungulates considered to be primitive, where the behaviors involved in sexual and aggressive encounters may be indistinguishable. Increased specialization is evident in more advanced forms, but the connection between sexual and aggressive displays is still recognizable in many species. In some of the advanced forms however, some sexual displays show no obvious connection with aggressive behavior. On the basis of the pattern discernible in other species, WALTHER (1984) suggests some possible means by which these displays may have arisen from aggressive behaviors. One of the taxonomic groups in this category is the sheep, goats, and their relatives. This study offers an alternative explanation for the derivation of sexual displays in these species. Specifically, that some sexual displays derive from mother-infant behavior.

Material and methods

The material presented on Nilgiri tahr is based on observations made during a two-year study at Eravikulam National Park, Kerala, India (RICE 1984, 1988 a, b, c; 1989). For this study, one subpopulation of about 120 tahr were habituated to close observation. Remarks on other species are based on published material or personal communications. Nomenclature follows WILSON and REEDER (1993).

Results

The Hypothesis: Sexual displays of Nilgiri tahr are derived from mother-infant behavior

Nilgiri tahr sexual displays included the rear twist, side twist, the foreleg kick, and tongue flicking (RICE 1988 a). The latter were usually performed in combination with the first two. In the rear twist (Fig. 1), the male stood behind the female, extended his neck and muzzle forward, and twisted the head along the long axis. The display was directed between the hind legs of the female. Depending on the distance between male and female, it terminated behind her, or with the muzzle pushing between her legs. In the side twist, (Fig. 2) the male was located further forward and slightly beside the female, so that his head was approximately level with her lumbar region. He then lowered his head, and twisted the muzzle in, usually just anterior to the hind leg of the female.

Two mother-infant behaviors of Nilgiri tahr bore a strong resemblance to the rear twist and the side twist. Although Nilgiri tahr young performed the usual bunting movements while suckling, they also performed two behaviors independent of suckling which I termed the rear bunt and side bunt. In the rear bunt (Fig. 3) the young approached the female from the rear, reached up between her hind legs, and gave a quick jab with its muzzle at the udder of the female. The side bunt (Fig. 4) was similar, but performed from the side, usually with the body of the young oriented in the same general direction as that of the female. This contrasted with the orientation of the young when suckling, which was usually in reverse-parallel position.

It should be emphasized that these rear and side bunts occurred independently of suckling and were quite different from suckling attempts, as the young executed the bunt and then turned away from the female, regardless of her reaction. Possibly, these bunts served to provide reassurance for the young. It was also clear that young were not simply



Fig. 1. To perform a rear twist, a male Nilgiri tahr extended his head and muzzle forward, and pushed the muzzle between the hind legs of the female.

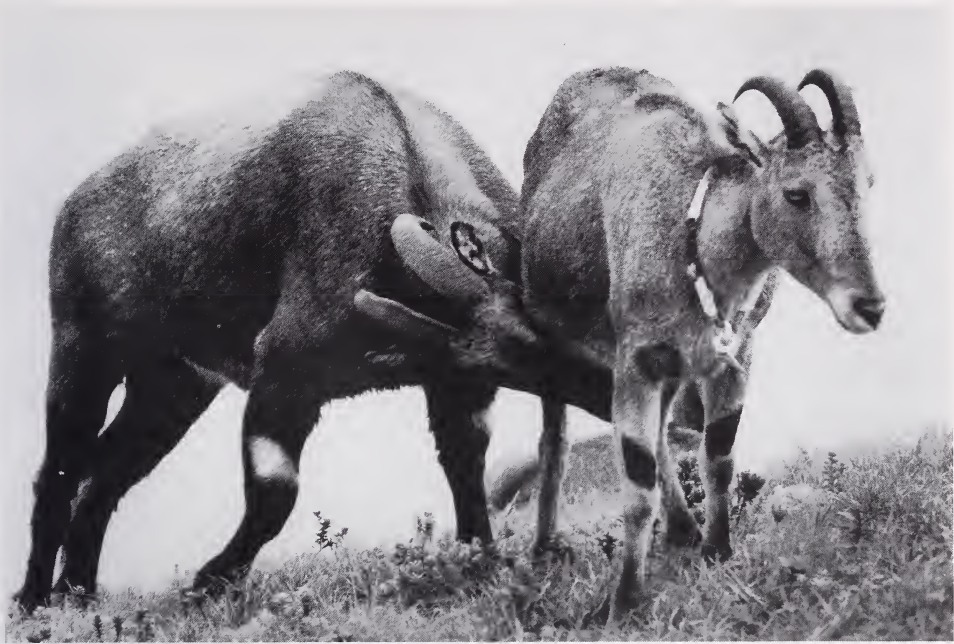


Fig. 2. In the side twist, the male turned his head just anterior to the hind leg of the female.



Fig. 3. The rear bunt was a quick poke at the udder from behind, with no apparent attempt at suckling.



Fig. 4. In the side bunt, the young turned his head in sideways to jab the udder of the female.



Fig. 5. The general orientation towards the inguinal region of the female was maintained when displays were performed in unusual positions or when the female was resting.

addressing courtship displays to females, as they showed themselves capable of normal rear and side twists in sexual play. The close similarity in form between these mother-infant and sexual behaviors suggests that the latter have derived from the former. Such a hypothesis yielded several predictions:

Prediction 1: Key elements of side and rear bunts will be evident in side and rear twists

The direction of the display in both the rear and side twists was toward the female's udder, not toward her perineum as might be expected in a posteriorly oriented sexual display. Also, when males gave corresponding displays to females which were reclining or in an unusual position, the orientation toward the udder was maintained (Fig. 5), and the neck extension and twisting were sometimes lacking. In addition, when giving the rear twist the male sometimes pushed his muzzle between the hind legs of the female to jab her udder. The orientation of both the side and rear twists toward the udder and the occasional jabbing of the udder during rear twists (as in rear bunts) is a clear indication of a close connection between these two sets of behaviors.

Prediction 2: Differences between the side and rear bunts and side and rear twists should be accountable by standard processes of behavioral evolution

There were several differences in the postures adopted by young and males in performing their respective behaviors. While the rear and side twists were oriented generally toward the udder of the female, the orientation was more specific in the rear and side bunts. That is, rear and side bunts invariably made contact with the udder, whereas the rear and side twists rarely did. Consequently, as it twisted sideways when giving the side bunt, the young had to turn its head back and in around the hind leg of the female, (Fig. 4), whereas the male merely extended his muzzle across in front of her hind leg. In the rear bunt, the young simply reached up to jab the udder (Fig. 3). An adult male, being much larger, would have to kneel or lie down to perform the same movement, but this would present obvious difficulties when displaying to a moving female. Instead, the male twisted his head sideways while lowering it slightly to achieve the orientation toward the udder of the female (Fig. 1). Also, the rear twisting male did not usually make contact with the udder, but pointed his muzzle at it, particularly if the female was moving. I made incidental note of contact in 1.5% of 2,399 rear twists. The rear and side twists of males therefore incorporated the same objective as do the rear and side bunts of the young, but the males do not usually follow through to make actual contact. The twists seem to be, in short, intention movements to the bunts, allowing for the great difference in size between young tahr and adult males.

The courting male performed his displays numerous times in succession, in contrast to the rear and side bunts which were given by the young one at a time (unlike normal bunts given during suckling). Consequently, the rear and side twists of males can be considered to have arisen through ritualization (by repetition of the intention movements) from the rear and side bunts of young.

Our understanding of the function and meaning of sexual displays in ungulates is incomplete, but probably the male gained an increased tolerance of his proximity to the female by performing actions similar to those employed by young. At the same time, courtship that was too enthusiastic was disadvantageous to the male because such courtship usually caused the female to move away. This incurred energetic costs in following and attracted the attention of other males, thereby promoting competition (and incurring further energetic costs) and risking loss of access to the female (GEIST 1971). The response of female Nilgiri tahr to being jabbed in the udder by a male was invariably to scoot away, and this explains the low frequency with which this aspect of rear twisting was

Table 1. Occurrence of the low stretch and twist in selected ungulates (see text for references)

Species	low-stretch	twist
Tribe Caprini		
<i>Hemitragus hylocrius</i>	—	+
<i>Hemitragus jemlahicus</i>	+	+
<i>Ovis</i> spp.	+	+
<i>Capra</i> spp.	+	+
<i>Pseudois nayaur</i>	+	+
<i>Ammotragus lervia</i>	+	+
Tribe Rupicapriini		
<i>Oreamnos americanus</i>	+	—
<i>Rupicapra rupicapra</i>	+	—
<i>Rupicapra pyrenaica</i>	+	—
<i>Naemorhedus crispus</i>	—	—
Family Cervidae		
<i>Rangifer tarandus</i>	+	—
<i>Cervus elaphus</i>	+	—
<i>Cervus eldi</i>	+	—
<i>Cervus unicolor</i>	+	—

employed, and the advantage of performing the intention movement rather than the complete display.

Prediction 3: If these sexual behaviors arose before Caprini diverged from the Rupicapriini, but before tahr diverged from other Caprini, more primitive related taxa will lack comparable behaviors while they will be exhibited by more advanced forms

Within the Caprinae, Nilgiri tahr belong to the tribe Caprini. This tribe also includes two other tahr, the Himalayan tahr (*H. jemlahicus*) and the Arabian tahr (*H. jayakari*), as well as sheep (*Ovis* spp.), ibex and wild goats (*Capra* spp.), bharal (*Pseudois nayaur*), and aoudad (*Ammotragus lervia*). The sexual displays of the Arabian tahr have not been described, but with this exception all of these species share two displays which have a bearing on the discussion. These are the low-stretch and the twist (Tab. 1,

WALTHER 1961; GEIST 1971; SCHALLER 1973, 1977). To perform a low-stretch, the animal extends the neck and muzzle forward, so that the throat and the base of mandibles form a straight line, near or above horizontal. The twist is given by rotating the head, horns away from the female, while maintaining the low-stretch.

Nilgiri tahr did not give a low-stretch, but occasionally a male did not completely return to a normal posture between rear twists. Instead he left his neck lowered and muzzle extended. This posture resembled a low intensity low-stretch. The advantages of a cautious courtship have already been mentioned, and it seems reasonable that the low-stretch in other Caprini has arisen through further ritualization by intensification and 'freezing', of this interim intention movement to perform a rear twist. The twisting motion has evidently persisted, but it is done with the muzzle extended. Thus, in the parallel position, the orientation toward the udder is lost completely and the muzzle remains pointing forward.

The remainder of the Caprinae includes two tribes, the Ovibovini and the Rupicapriini, of which the Rupicapriini, with their primitive goat-like features are of primary interest. If the early stages of the low-stretch and twist are manifested in the displays of Nilgiri tahr, one would not expect to see such displays in more primitive species. The twist is indeed lacking in those species which have been studied (mountain goat, *Oreamnos americanus*, GEIST 1964, 1975; north-eastern chamois, *Rupicapra rupicapra*, KRÄMER 1969; south-western chamois, *R. pyrenaica*, LOVARI 1985; and Japanese serow, *Naemorhedus crispus*, AKASAKA and MARUYAMA 1977; J. BERG pers. comm.), but the same cannot be said for the low-stretch. Although it is apparently lacking in the Japanese serow, it is given by both the mountain goat and chamois. In these species, the low-stretch is considered to be a submissive or appeasement posture (GEIST 1964, 1971; KRÄMER 1969; LOVARI 1985), but it is also used in courtship as the male approaches the female, especially when combined with a crouch. LOVARI (1985) shows the great similarity between the extreme form of the low-stretch in south-western chamois and suckling postures of the young, and further demonstrates the relationship between the low-stretch and suckling behavior by his observation

of a behavior termed the mock-suck. In the mock-suck, the courting male “inserts his muzzle under the female’s udder area and delivers 2–3 blows like kids do to stimulate lactation.” Therefore, it may be that the low-stretch originated in the Rupicaprini, being nevertheless derived from mother-infant relations.

Prediction 4: Comparable sexual displays will be lacking in less related taxonomic groups

The low-stretch also occurs in ungulate species outside the Caprinae (WALTHER 1984). This seems to contradict this prediction unless the low-stretch has arisen independently in several groups. However, this is not unlikely for the following reasons:

(1) Although it is widespread, the low-stretch is not universal (WALTHER 1984). Consequently, it may make as much sense to suggest separate origins for this display, as it would to suggest a common origin.

(2) In some groups, the connection between the low-stretch used in sexual contexts with aggressive displays is obvious. This is particularly true in the cervids, many of which perform a low-stretch in approaching and driving females in courtship. This is exemplified by caribou (*Rangifer tarandus*, DE VOS et al. 1967), elk (*Cervus elaphus*, GEIST 1966; STRUHSACKER 1967), Eld’s deer (*Cervus eldi*, BLAKESLEE et al. 1979), and sambar (*Cervus unicolor*, SCHALLER 1967). Sambar also use the low-stretch as a threat (pers. observ.).

(3) WALTHER (1984) suggested that the low-stretch may have arisen from an intention movement to lick the perineal region of the female in some species. Such a separate origin would imply independent evolution of this display for those species.

Unlike the low-stretch, the twist is confined almost entirely to the Caprini, and in the few cases where it does occur in other ungulates, it is as an “aberrant or strongly reduced performance” (WALTHER 1984). Therefore, it seems likely that twisting has a single origin common to all Caprini. However, according to the hypothesis being suggested here, the twist and the low-stretch are closely connected. So, unless the twist was somehow “added on” to the low-stretch, this connection may indicate that both the low-stretch and the twist developed together in the manner being proposed.

Prediction 5: Comparable parallel links between mother-infant and sexual behaviors will occur in other lineages

Similar connections between sexual and mother-infant behaviors have been reported by other authors. In Indian rhinoceros (*Rhinoceros unicornis*), SCHENKEL and LANG (1969) interpreted the female’s act of placing her muzzle in the inguinal region of the male during courtship as symbolic suckling. However, LAURIE (1978) considered that she was merely sniffing his penis. DUBOST (1975) reported courting African water chevrotain (*Hymoschus aquaticus*) males licking the females’ udder, and this was occasionally observed by ROBIN (1979) in lesser Malayan mouse deer (*Tragulus javanicus*). In mule deer (*Odocoileus hemionus*), GEIST (1981) suggested that the vocalizations employed by mule deer in courtship simulate the vocalizations of infants. HORWICH (pers. comm. 1983) considers the lip smacking of macaques (*Macaca* spp.) and tonguing of black howler monkeys (*Alouatta pigra*), which are used in courtship, as being derived from suckling. EWER (1968) cites several studies reporting infantile vocalizations being used in courtship by males (i. e. in field mouse (*Microtus arvalis*), the European red squirrel (*Sciurus vulgaris*), hamsters (*Cricetus* sp.), and the raccoon dog (*Nyctereutes procyonoides*)).

One further comparison is of interest. In humans, manual and oral contact with the female’s mammary glands is, in a number of cultures, a conspicuous and important component of courtship and pre-copulatory behavior. Human infants may also seek reassurance through manual and oral contact with its mother’s breast. This transition from sucking to contact for reassurance to sexual behavior is directly parallel to the transition from suck-

ling to side and rear bunts to courtship displays in Nilgiri tahr. Consequently, a relationship between mother-infant behavior and sexual behavior seems to occur in a wide diversity of mammal species.

Discussion

This study has suggested an explanation for the development of two common sexual displays in the Caprini, the low-stretch and the twist. The low-stretch occurs in many ungulate species outside the Caprini, and this is not surprising as lowering the neck and extending the muzzle is the simplest way for an animal to get its mouth or nose close to another animal. Therefore this posture may be adopted in unritualized form in all types of social interaction, be it aggression (to bite), mother-infant relations (to suckle), or sexual behavior (to sniff falling urine or the perineum of a female). In Caprini, the ritualized low-stretch has probably not developed from aggressive behavior, as biting is virtually absent in these species. Also, as the most unritualized forms of this display (mock-suck in chamois and rear and side twist in Nilgiri tahr) are directed toward the udder of the female, not toward here perineal region, the development of the low-stretch from mother-infant behaviors is strongly indicated.

There is some question as to whether the low-stretch in Caprini has its origin in the low-stretch of Rupicaprini or whether it has developed from displays similar to the rear and side twist of Nilgiri tahr. Tahr are considered evolutionary intermediaries between the Rupicaprini and the Caprini, and one would therefore expect tahr to low-stretch if this display can be traced to the Rupicaprini. Himalayan tahr do low-stretch, but Nilgiri tahr do not. On the other hand, tahr, bharal, sheep, and goats all perform a twisting courtship display, while rupicaprines do not. The close combination of the low-stretch and twist in most Caprini can be explained by considering the rear and side twist of Nilgiri tahr as precursors to these displays. One can, therefore, conclude that the low-stretch and twist employed in courtship by various members of the tribe Caprini has evolved through ritualization from behaviors similar to the rear and side twist of Nilgiri tahr. It also appears likely that the rear and side twists of Nilgiri tahr have their origins in the rear and side bunts which Nilgiri tahr young direct toward their mothers. Therefore, these sexual displays have their origin in mother-infant relations.

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Zusammenfassung

Zum Ursprung einiger sexueller Verhaltensweisen bei Capriden

Aufgrund von Beobachtungen am Nilgiritahr wird aus der Ähnlichkeit des Twists (Drehung des vorgestreckten Kopfes um seine Längsachse) – von der Seite und von hinten – als männlicher Werbegeste im Paarungszeremoniell mit einer Haltung, in der Jungtiere mitunter – von der Seite oder von hinten – zum Euter der Mutter hin vorstoßen, auf eine Verbindung in der stammesgeschichtlichen Entwicklung geschlossen. Diese Hypothese führt zu mehreren Voraussagen über die Formen dieser Verhaltensweisen und ihr Auftreten in taxonomisch verwandten Gruppen: (1) Gemeinsame Grundkomponenten sind in der besagten Werbehaltung des Bockes wie im Vorstoß des Jungtiers zur Mutter erkennbar. (2) Unterschiede der beiden sollten sich aus Vorgängen bei der phylogenetischen Verhaltensentwicklung erklären lassen. (3) Falls sich das besagte Werbeverhalten herausgebildet hat, bevor sich Caprini und

Rupicaprini voneinander schieden und auch bevor sich die Tahre von den anderen Caprini abgespalteten, werden vergleichbare Werbegebärden bei primitiveren Verwandten fehlen, während fortgeschrittenere Formen sie zeigen werden. (4) Vergleichbare sexuelle Verhaltensweisen werden bei taxonomisch ferner stehenden Gruppen fehlen. (5) Vergleichbare Parallelen zwischen Verhaltensweisen in den Mutter-Kind-Beziehungen und im Paarungszeremoniell werden auch in anderen taxonomischen Einheiten auftauchen. Eine Durchsicht der verfügbaren Informationen ergab eine starke, wenn auch keine unanfechtbare Unterstützung für die hier vertretene Hypothese.

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