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Agonistic and Sexual Behavior of Nilgiri Tahr (*Hemitragus hylocrius*)

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With 11 figures

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Abstract

Nilgiri tahr (*Hemitragus hylocrius*) were observed in the wild in Eravikulam National Park, Kerala, India. Agonistic and sexual behaviors were described and classified by social function.

The social behavior of Nilgiri tahr was compared with that of related species. Nilgiri tahr are thought to be evolutionary intermediates between the Rupicaprini and the Caprini; this was reflected in their behavior. While they used reverse parallel fighting and neckfighting, clashing with the horns was also well developed.

Introduction

The Nilgiri tahr (*Hemitragus hylocrius*) is found in scattered populations along the Western Ghats, a range of mountains situated along the west coast of South India. The total wild population consists of about 2 200 animals (DAVIDAR 1978, RICE in press a). Due to deleterious human impacts on these restricted populations, the Nilgiri tahr is classified as vulnerable by the International Union for the Conservation of Nature and Natural Resources (GOODWIN & HOLLOWAY 1972). Previous studies on Nilgiri tahr have included population surveys and notes on natural history by DAVIDAR (1963, 1971, 1976, 1978) and a short term investigation on behavior and ecology by SCHALLER (1971). Aspects of Nilgiri tahr biology pertaining to conservation and predator-prey interactions have been presented elsewhere (RICE 1986, in press a).

This paper presents an inventory of Nilgiri tahr social behavior and compares it with that of related species. Morphologically, particularly with regard to horn structure, tahr are intermediate between the Rupicaprini and *Ovis* and *Capra*. Therefore, the social behavior of tahr is of interest in evaluating the relationship between social organs such as horns and social behavior.

Study Area and Animals

This report is based upon observations made in Eravikulam National Park, Idukki District, Kerala (located at 10° N latitude, 77° E longitude). Much of the National Park consists of a high rolling plateau at about 2 000 m. Grassland, shrubland, and forests (locally known as sholas) occur within the park. As is typical for the region, terrain above about 2 000 m is covered primarily by grassland. There are numerous small patches of forests in hollows and gullies in these areas. The deeper valleys are extensively forested.

Eravikulam National Park sustains about 550 Nilgiri tahr, the largest wild population (RICE 1984, in press a). Most of the information contained in this report was obtained from one subpopulation of about 125 animals.

Male Nilgiri tahr grow to about 110 cm at the shoulder and weigh about 100 kg. Females are smaller, about 80 cm at the shoulder and weighing some 50 kg (RICE in press c). Males probably possess dermal shields (GEIST 1967) as has been shown to be true for Himalayan tahr (*Hemitragus jemlahicus*, RICE in press b).

Nilgiri tahr are primarily grazers, but also occasionally browse along the fringes of forest patches (RICE 1984).

The rutting season at Eravikulam was during the monsoon (Jul. and Aug.), and most young were born in Jan. and Feb. (RICE in press d).

Like many Caprini, Nilgiri tahr occurred in two main types of groups, mixed and male. Mixed groups were made up of adult females, their subadult offspring, and during the rut, adult males. Outside the rut, older males left the mixed groups and formed their own smaller, unstable groups. Mixed groups varied from 2 to 150 animals, with an average size of 42, and lone females were rare. Male groups ranged from 2 to 20, with an average size of 3, and lone males were not uncommon.

Methods

This study was carried out between 8 Aug. 1979 and 26 Sep. 1981. The primary means of study was direct observation of the animals in the wild. For this purpose, one sub-population was habituated to my presence, and about 60 tahr were marked with color-coded collars.

Observations

The conditions of observations varied considerably through the course of the study. This was a result of both weather and terrain. The rain and mist during the monsoon placed severe limitations on visibility, and whereas it was not difficult to keep an individual or group in sight on the open grassy plateau, this was not the case when the tahr moved into steep slabs or cliffs. The distance of observations varied from a maximum of about 800 m (through a 20—40 × spotting scope or 10 × binoculars) on flighty animals, to a minimum of a few m on habituated animals. Generally, I tried to maintain an intermediate distance of 50—200 m. Observations were recorded on tape in a stylized anecdotal manner, and later transcribed. Photographic records were made with 50 mm and 200 mm lenses, and 2 × tele-extender.

Habituation

During fair weather, the open grassy hills on which the tahr lived permitted extended observations from a considerable distance with the aid of spotting scope and binoculars. At the beginning of the study, closer approach was not possible as the tahr exhibited a flight distance of about 300 m. It became clear from the onset, however, that during the monsoon (which coincides with the rut) observations would be impossible due to the thick mist, heavy rain, and high winds. Consequently, I decided to habituate one subpopulation to my close proximity.

Habituation, however, proved to be a lengthy process and consisted of three stages. Initially (Stage 1, ca. 7 months), I allowed myself be plainly visible to the tahr from a distance greater than their flight distance. I did not keep detailed records of the tahrs' responses, but there seemed to be a distinct threshold before which flight and moving off distances remained long, and after which they dropped rapidly to about 50 m.

The consolidation of this greater tolerance was promoted by several strategies I employed at these closer distances (Stage 2, ca. 2 months). I was careful not to focus my attention too intently on

the tahr, and often kept my gaze averted, pretending to go about my own business. Also, since I found the fresh green sprouts in the burned areas as sweet as the tahr seemed to, I occasionally "grazed" by pulling the basal shoots, and munching on them, often making this readily visible to the tahr. In addition I was careful to move very slowly, never taking more than about one step every 2 s and frequently stopping to stand in a relaxed manner.

These tactics seemed to be effective in helping the tahr become more accustomed to my presence at close range. However, by this time the 1980 monsoon was fast approaching, and it was evident that the distance at which their behavior could be considered normal was still too great for observations during the weather conditions characteristic of the monsoon. Consequently, I began using salt in hopes of accelerating the process (Stage 3, 3 months).

As soon as the tahr were allowing me to approach within about 10 m, I stopped placing the salt in specific locations, but instead carried it with me and distributed it to the tahr. The general practice was to find the group, move slowly and steadily to a point close to some animals and upwind from them, where I sat down and distributed the salt. The tahrs' desire for salt was quite evident in their willingness to approach quite close despite considerable nervousness on their part.

I also found that nervous animals were much more tolerant of me if there was at least one other tahr between them and myself. In this respect, the relatively uninhibited approach by one particular male young encouraged the other animals to come closer. At the same time, the tahr became more accustomed to my proximity when salt was not being offered, and about a year after the commencement of the habituation program, grazing animals, seeing me come over a rise, looked up briefly, and then resumed their grazing unperturbed.

On the other hand, the tahr quickly learned that when I approached and sat down salt was often distributed, and before long this became a problem in making observations. If I sat within less than about 100 m from the group, they would alter their orientation and graze in my direction. Soon observations had to be terminated since all I was observing was a ring of animals standing around watching me, and waiting for salt to be put out. For this reason, once the tahr were satisfactorily habituated to my proximity, I refrained from distributing salt unless I had some specific objective (e. g. collaring). Salt also proved useful in introducing other humans to the tahr.

Sex and Age Classifications

Nilgiri tahr were divided into 6 sex and age classes after SCHALLER (1971). For more detailed descriptions see RICE (1984).

Young: Age 0—1 years. Gray-brown or light brown coat.

Yearling: Age 1—2 years. Gray-brown coat. Intermediate in size between young and adult females.

Adult female: Age 2+ years. Gray-brown coat. Carpal patch black.

Light brown male: Age ca. 2—4 years. Similar in body and horn size and pelage to adult females. Horns slightly thicker with facial markings sometimes slightly more distinct.

Dark brown male: Age ca. 5 years. Gray-brown to dark brown coat. Larger and more robust than adult females and light brown males with larger horns and more distinct facial markings. Carpal patches white.

Saddleback (male): Age ca. 6+ years. Dark brown coat with an area of light brown, white, or silvery hair covering the lower back, rump and/or flanks. Carpal patches white.

Most adult males could be individually recognized by natural markings, but this was not generally possible with females. About three-fourths of the adult females in the intensive study subpopulation were marked with color coded collars, modeled after those used by CLARKE & HENDERSON (1978) and TAYLOR (1969).

Results and Discussion

Description of Social Behavior

The explicit social behavior of Nilgiri tahr falls into three functional categories: agonistic, sexual, and mother-infant behavior. Each of these categories can be divided into various subcategories (mother-infant relations in Nilgiri tahr

will be presented in a later report). These subdivisions are patterned after WALTHER's 1984 classification of expressive behaviors in ungulates. In most cases, the position of individual behaviors in this classification was obvious after repeatedly observing it and the response of the recipient. On the other hand, the function of a few behaviors remained obscure, and I have presented some information on the context of these behaviors, in an attempt to elucidate their function.

A categorization along these lines has both advantages and disadvantages. One of the main advantages is that it provides a conceptual framework in which to consider the individual behaviors. The major disadvantage is that it requires considerable interpretation as to the meaning and function of the various behavior patterns, and does not lend itself to the consideration of transitional or multi-functional behavior.

The social behavior of Nilgiri tahr has been described to some extent by SCHALLER (1971, 1977). I have followed SCHALLER's names for the various behavior patterns, but have deviated from his terminology on a few for which an alternate term seemed more appropriate. SCHALLER uses different terms for some of the behaviors in his 1971 and 1977 accounts, and these are referenced in parenthesis where they differ from mine.

In Nilgiri tahr, agonistic behavior consists of aggressive acts, aggressive displays, and submissive acts. I saw no indication of distinct postures or displays associated with submission. Therefore, there is no category of submissive displays. Aggressive actions usually involved physical contact between the oppo-



Fig. 1: In the classic side clash of Nilgiri tahr, the blow is simultaneously delivered and caught on the curved outside surface of the horns, but the alignment of the opponents is not always exact

nents, and physical contact, or the positioning for it, was the apparent intent of the action. These were unritualized acts used to change the behavior and/or location of another animal. The simplest of these was an *approach*, where the initiator moved towards its opponent with aggressive intent, either at a *walk* or a *rush*, but giving no clear display or posture. A tahr might approach another for any of a number of non-aggressive reasons, and it was not always possible to determine the exact motivational state. For this reason, approaches were only recorded when the aggressive motivation of the initiator was clear. There were, no doubt, other occasions upon when such an intention was present, but not noticed.

A *chase* simply refers to a tahr's pursuit of another according to the usual meaning of the word.

The simplest form of contact was in the *butt*, where one tahr swung his head down, bringing the front of the horns into contact with the body of another animal. Such a move was sometimes accompanied by a step forward, emphasizing the blow. Of 99 butts, 20 % were to the flank, 13 % to the shoulder, 10 % to the neck, 10 % to the muzzle, 7 % to the rump, 6 % to the horns, and 10 % to the head, side, chest or leg. For 23 % of the butts, the place butted was not recorded.

Sometimes the initiator pulled his chin in as he lowered his head and pulled it to one side, to make contact with the opponent with the tip of his horns as he swung his head back and/or across in a *horn jab*. 43 hornjabs were directed towards the hind leg (26 %), the flank (26 %), the shoulder (9 %), or the chest, foreleg, belly or rump (16 %). The place was not recorded in 23 % of the hornjabs.



Fig. 2: When reverse parallel fighting, Nilgiri tahr push against each other with the shoulders, while delivering blows against the flank and side of the opponent with upwards and sideways sweeps of the horns, as is shown by the blurred head of the male in the foreground

Aggressive contact was often horn to horn. In the *head-on clash* (head-on butt, SCHALLER 1971), both partners lowered their heads to make contact in a mutually frontal orientation with respect to their heads. Usually, the contact was in the form of a quick sharp blow, but occasionally tahr also sustained contact by pressing their horns together for about a s.

In the *side clash* (Fig. 1), tahr typically stood with an angle of about 45° between their body axes, and bending their necks, brought the rounded outside-front surface of the one horn on that side in contact with the opponent's horn. As was the case with the head-on clash, side clashing was also sometimes a sustained, pressing contact.

Tahr also uncommonly hooked their horns together (*hook horn*). This sometimes happened as two partners were reverse parallel fighting. As they swung back from the lateral blow at the same time, the tahr caught each other's horns. Hook horn also occurred in the course of sparring among younger males.

Much of the fighting and sparring in tahr was not in the form of horn to horn contact. When *reverse parallel fighting* (Fig. 2, shoulder push, SCHALLER 1971, head-to-tail, 1977) the opponents stood parallel to each other, but facing in the opposite direction. They stood roughly shoulder to shoulder, and thus each animal's head was about even with the flank of his opponent. The contact consisted of a combination of movements. These included pushing against the partner with the shoulder and, while turning the horns in towards the opponent's flank, pulling the head across, upwards and back, usually striking the opponent in the side. These movements were performed mutually, but not necessarily simul-

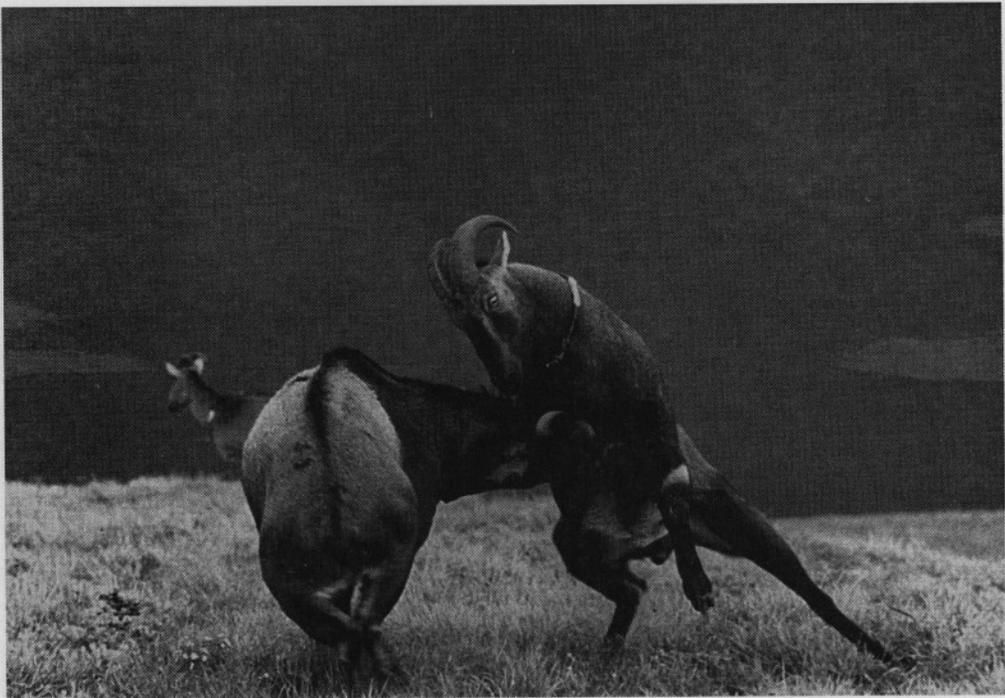


Fig. 3: When reverse parallel fighting, occasionally the horn tip of one male Nilgiri tahr lodged in the axial region of the opponent in the hook behind foreleg. Under such circumstances, the hooking male pulled back and up, making the utmost of this advantage

taneously (Fig. 2), as each tahr attempted to avoid the blows of the opponent by stepping away from them with his hind legs, while remaining in contact or at least close to the opponent at the shoulder. In this manner, reverse parallel fighting tahr usually circled rapidly about each other.

Several fighting techniques were also usually associated with fighting in a reverse parallel position. To *hook hoof*, a tahr lowered his head to catch his opponent's foreleg just above the hoof between his horns. The initiator then pulled his head up, raising the foreleg of the opponent.

A similar technique was sometimes directed towards the hind hoof in *hook hind hoof*.

Another fighting move, *hook behind foreleg* (Fig. 3) sometimes occurred during serious fights. As one tahr swung back when giving a blow in reverse parallel fighting, the horn tip caught behind the foreleg of the opponent, in the axillary region (the "armpit"). It was not my impression that the hook behind foreleg was performed intentionally, but once the horn tip was lodged in the axial region, the hooking animal usually took full advantage of the situation, and continued to pull back and up as his opponent tried to extricate himself.

When *neck fighting*, tahr adopted a variety of orientations, from frontal to nearly parallel. Most commonly the angle between the partners' body axes was more than 90° . The opponents pushed against each others' necks, usually emphasizing the basal portion. Tahr often made a smooth transition between neck fighting and reverse parallel fighting, and there was no clear line separating the two. Another type of contact was the *parallel shoulder push* in which the



Fig. 4: As the male Nilgiri tahr sprays urine, the urethral process flicks up and down, directing the urine flow onto the chin, neck, chest, belly, and back of the forelegs

opponents stood side by side and parallel to each other, and pushed and leaned against each other.

In contrast to the aggressive acts, aggressive displays did not involve bodily contact. Some occurred in situations of aggressive arousal, such as when a new male arrived during the rut. Aggressive displays indicating arousal have much in common with dominance displays (and might be considered a subcategory of them), but were not addressed or directed to a particular individual. Although a particular individual commonly elicited these behaviors, this was deduced from the context and sequencing only, and was not evident in the nature of the display. Several of these displays correspond to WALTHER'S (1984) "space claim" displays. To *spray urine* the male typically lowered his head and tucked his chin in, so that his forehead was a few cm off the ground. The penis was erected, and urine squirted or sprayed in a thin stream from the urethral process (Fig. 4). At the same time, the urethral process flicked up and down, directing the flow of urine onto the belly, chest, throat and chin. As a result, males had a distinct, strong odor. The site of a urine spray also had this odor, indicating the smell was the result of the contents of urine, rather than from chemical or biological changes taking place in the urine-impregnated hair. Although the distinctive posture adopted by the male in spraying urine probably had some display value, the resulting odor probably had a more significant effect as a long-lasting olfactory display.

Often while, or immediately after spraying urine, the male pressed his forehead against the grass one to several times in *bump forehead*. During



Fig. 5: In Nilgiri tahr most object aggression was directed at the grass and soil, as the tahr often knelt and dug its horn tips into the substrate. Several males frequently performed object aggression at the same site, leaving an area of bare ground and muddied grass

spraying, some of the urine ran down and around the outside of the muzzle, and it appeared that the bumping of the forehead served to work this urine into the facial hairs. It is worthy of note that the combination of spraying urine and bumping the forehead served to distribute the odiferous urine onto areas of the male's body which come in close proximity to another male's nostrils in the course of a fight. The experience of a fight is therefore likely associated with the smell of the opponent's urine, which in turn is probably correlated with the opponent's reproductive state, social status, and possibly individual identity.

Aggressively aroused tahr also resorted to *object aggression* (rub, SCHALLER 1971). In Nilgiri tahr, object aggression was most commonly directed at the grassy slope, or at a patch of dirt left by a previous animal. *Strobilanthes* or *Rhododendron* shrubs also were recipients of this behavior on occasion. Generally, a tahr lowered and turned its head sideways so that the side of the head lay approximately flat on the grass. The head was then swept across and back as the horn tips were dug into the ground (Fig. 5). At the completion of the sweep, the head was sometimes turned over, so that contact was on the other side for the sweep back, or the head was turned all or partially upright and the chin and/or cheek dragged back across the grass or dirt. Tahr often kneeled when performing this behavior, and in such cases the throat was also rubbed on the surface. When directed towards shrubs, object aggression was more similar to simple sparring with the branches.

Several other actions consistently took place in aggressive contexts, but were less clearly linked with other aggressive displays. These included *cavorting*, in



Fig. 6: As one saddleback male Nilgiri tahr ends his hunch with a head out display, the closer one turns to mouth his penis

which the animal ran a few strides with an exaggerated bucking, sometimes throwing the hind legs high in the air.

The *jump twist* took place as a tahr facing another reared up on his hind legs, and then twisted, first the head, followed by the rest of the body, to come down facing away from the other animal. The initiator then moved away.

A male also *mouthed* his *penis* in aggressive contexts, although the display value of this behavior was not clear (Fig. 6).

While the aggressive displays listed so far had display value, that is, they communicated to other animals something of the motivational state of the displaying animal, they were not truly directed in that no particular conspecific was indicated as a consequence of the display. On the other hand, threats and dominance displays usually definitely did indicate a recipient. I have followed WALTHER'S (1974) formulations in categorizing threats and dominance displays. Threats are those aggressive displays which indicate "the readiness to fight", often by the use of intention movements towards fighting. For this reason, weapons, horns in the case of tahr, are often brought into play. Dominance displays, on the other hand, do not specifically incorporate the weapons, but rather they seem aimed at impressing the recipient by emphasizing certain characteristics of the displaying animal, such as his size or conspicuous markings.

Nilgiri tahr use three threats. One is the *horn present*, in which (in the typical case), the initiator oriented towards the recipient, lowered the head and pulled in the chin, directing the front of the horns towards the other animal. This was quite clearly an intention movement to clash or butt, and in some cases (e. g. when the recipient returned the threat), the initial threat was followed through with just that. The orientation for the horn present was generally with the head only, and could be directed in any direction relative to the body axis of the initiator. The extreme case of this was the horn present given by a resting female when courted by a male standing behind her, in which the female raised her chin, thus displaying her horns over her back.

The *lunge* consisted of a horn present combined with a rapid rush at the opponent. Some question exists as to whether the lunge is truly a threat, or might be considered an aggressive act, or attack. The movement of the initiator generally continued to or past the location of the recipient at the start of the interaction, and only the movement of the recipient away from the initiator accounted for the lack of physical contact. However, the consistency with which the lunge-retreat interaction lacked physical contact, and the somewhat standardized intensity with which the interaction took place, suggest that this behavior was primarily of display value. On the other hand, with some lunges it was quite evident that the initiator was making an attempt at bodily contact, and that only the rapid retreat of the recipient prevented this.

The third threat, the *hunch-side* was given in parallel orientation. The initiator hunched the back, twisted the head so that the muzzle pointed towards the opponent (and the horns away), and stepped sideways towards the opponent (Fig. 7). This display contained elements of both dominance and threat. The dominance element was evident in the hunched posture, while the angling of the horns away may be construed as a "swing out" movement (WALTHER 1984) in

preparation to side clash. As the hunch-side was frequently the last display given before the commencement of a fight, I considered it more of a threat than a dominance display.

Dominance displays serve to emphasize the size, maturational stage, vigor, and aggressive motivation of an animal. In the *hunch* (head-down, SCHALLER 1977) the animal arched its back and lowered the head, often pulling the chin in slightly. Hunches varied considerably in intensity. At the lowest intensity, the animal arched the back only slightly, and angled the neck downward keeping the chin extended, while moving with near normal gait. This graded to the opposite extreme, in which the back was very rounded, the neck lowered and the chin tucked in so as to place the muzzle in the vicinity of the forelegs (Fig. 8). At the same time, the tahr moved with a distinctive stiff-legged mincing gait, often moving in an arc around the recipient. The mane was erected, and flipped back and forth with each step. The hunch was given while moving, generally in more or less broadside orientation to the opponent, particularly in the more intense displays. Sometimes, however, a tahr hunched while approaching another, or even during flight. Having observed apparently the same display in Himalayan tahr, SCHALLER (1977) considered this a separate display, the humped approach. However, since the essential posture was not different, I have included these as hunches, although such hunches were usually of lower intensity. WALTHER (1974) considers the similar hunched posture of mountain goat (*Oreamnos americanus*) as a threat, since mountain goats fight in a similar posture in a reverse parallel position, and thus the broadside hunched posture signals a readiness to fight.



Fig. 7: In the hunch-side, Nilgiri tahr stepped sideways towards its opponent, and turned its muzzle towards the other, usually to a greater extent than shown here

Nilgiri tahr also fought in reverse parallel position, but serious fights never followed directly after hunching. Rather there was a bout of side clashing, and the tahr changed to reverse parallel fighting after a number of clashes. Consequently the hunch is not considered a threat in this species.

Unlike the hunch which was performed while moving, the *head out* (broad-side of Himalayan tahr, SCHALLER 1977) was given while standing still. While the rest of the body was not maintained in any particular posture, the neck was lowered to slightly below horizontal, and the chin was extended slightly (Fig. 6). This display was often given in broadside orientation, particularly if it followed a hunch (as was often the case). The otherwise rather unobtrusive posture was made more striking by the practice of holding the pose for a few s.

Another dominance display was to *stare* at another animal. It was not always possible to distinguish mere visual attention from a stare, but in other cases, the stare was obvious in the nature of the fixed steady gaze. After observing similar interactions between tahr, the importance of this display was demonstrated quite effectively in my own interaction with a newly arrived, and only partially habituated male. During the transition from unhabituated to habituation, such males tended to treat me like a dominant conspecific. To encourage them to relax, I tried to focus as little attention on them as possible. On the other hand, I was eager to record any individual markings, and this required close scrutiny. In this particular case, I moved diagonally up the slope, eyes to the ground, and closer to the male whom I could see watching me out of the corner of his eye. Then as I stopped, raised my binoculars and directed my gaze at him, he turned away and grazed — both submissive responses (see below). By being linked sequentially



Fig. 8: In Nilgiri tahr the hunch is often accompanied by short mincing steps

with other less specifically addressed displays, such as object aggression and spraying urine, the stare also served to impart an addressing to these displays.

Three displays occurred in aggressive contexts, but it was not quite clear if they were threats or patterns which merely indicated aggressive arousal. A tahr rarely gave a *nod*, a quick pull in of the chin. The nod differed from the horn presentation in that the head itself was not lowered. 7 out of 12 nods were directed towards an animal of the same class, and the other five were by females to males in the context of courtship. Perhaps the nod might best be considered as a hesitant and quickly retracted horn presentation.

The *headshake* was a quick lateral twisting of the whole head, without any other appreciable change in posture. Of a total of 185 headshakes, 64 were young-young interactions. The vast majority of these occurred after aggressive acts in young-young sparring bouts. After headshaking, either the sequence ended, or the young resumed sparring. Young also gave the headshake to females (33 times). Most of these were after the female terminated a suckling bout, and the headshake usually ended the sequence. Most of the remainder of headshakes were either intraclass, or to an older or larger class. It was my impression when young gave the headshake after the female terminated the suckling, that it served to vent their frustration at not being able to continue suckling. This venting of frustration may have also played a role when smaller or younger tahr were inhibited from responding aggressively to those larger or older. This does not explain the occurrence of the headshake in young-young sparring interactions, but it may be that in the somewhat disorganized sparring of young, it had no particular significance.

In the *thrust*, the muzzle and neck were thrust towards the recipient, and then withdrawn. The thrust was recorded only four times, all by females to saddlebacks. Three of these were after the female rose in response to courtship, and once after a rear twist. Thrusting then, was a rarely used way of objecting to courtship.

When they did not release responses, aggressive actions and displays often resulted in a submissive action on the part of the recipient. The simplest of these was to *stop* the "offensive act". For example, a subordinate male might stop his approach or courting of a female upon receiving the stare or approach of a dominant male. No other postures or movements were necessary in some cases to signal his subordinate status, and the dominant did not pursue the interaction further.

A slightly more definite response was for the submissive tahr to *turn away*. The submissive attitude was made more emphatic by *moving away*, or *scooting away*, that is, moving away rapidly. Depending on their mutual orientation, the submissive animal could also *back away*.

Another submissive action was for the tahr to turn in from the parallel orientation, and cut back, passing behind the dominant animal (*turn and cut behind*). This action was often noted in the context of conflict while grazing. Unlike other submissive actions, in the turn and cut the submissive animal turned its horns towards, rather than away from the dominant animal while turning back to pass behind. However, this action gave the dominant animal the option to

graze at the location at which the conflict took place. On the other hand, turning or moving away would give the dominant animal the same prerogative. It may be that the turn and cut is a defense tactic used by the submissive animal so it does not have to expose its side to the dominant animal.

To *graze* was also a submissive response in some circumstances. This was particularly evident in interactions between males in the context of courting females during the rut. In such instances the subordinate male's approach or courting of a female was interrupted by the approach or display of a dominant male. As was the case with staring, the motivational state of the grazing animal was not always easy to judge, but in some cases the connection between the subordinate's grazing and the actions of the dominant male was quite evident. The onset of grazing coincided with the latter's approach or display, and the grazing ceased as the dominant's attention turned elsewhere (to the female in question, or back to the female the dominant male was initially tending). In one case the subordinate dark brown male did not graze, but simply lowered the tip of his muzzle to the grass and stood still, suggesting that grazing has considerable signal value.

To *dribble urine* from a non-erect penis was also interpreted as an indication of subordination. This occurred in contexts similar to that of the urine spray, except that the close proximity of a dominant animal seemed to inhibit its full expression. Consequently, the penis was not erected, nor was any particular posture adopted as urine trickled from the penis. The submissive nature of dribbling urine was evident, not so much in the actions and reactions of the tahr, as in the context in which it took place. All urine dribbling was done by males of equal or younger class than they were interacting with. Three of six urine dribbles followed a method of deferral by the same animal, two followed object aggression and bump forehead, and one occurred spontaneously.

Flight was the submissive complement to being chased. I grouped the submissive behaviors of stopping the "offensive act", turning away, grazing, turning and cutting, moving away, scooting away, and backing away together under the category of *deferring*.

Sexual behaviors consisted of acts and displays by the males, and responses by the females. The *mount* was, of course, a sexual act. In mounting, tahr often clasped the mounted animal with the forelegs just anterior to its hindquarters. The head was usually held up in an approximately normal position, but on a few occasions the mounting animal lowered its muzzle onto the back of the mounted one. Mounts were sometimes accompanied by rapid pelvic thrusting, and some were terminated by a thrust of greater amplitude and/or a groan. In the terminal thrusts, the mounter's hindquarters were brought quickly forward against the hindquarters of the mounted animal, and the body was raised and straightened, but these acts were much smaller in amplitude than the terminal thrusts observed in some cervids (STRUHSAKER 1967; BLAKESLEE et. al. 1979), where the hind legs sometimes even left the ground. Terminal thrusts and the accompanying groan were presumed to coincide with ejaculation. On the basis of these behaviors and the response of the mounted animal, mounts were scored as to where copulation was considered very likely, possible, or not likely to have occurred.

Cases where the mounted animal disrupted the mount by moving forward before the action was successfully completed were considered as a *mount attempt*, and if the recipient moved before physical contact was established, this was called a *mount intention*. The distinction between mounts, mount attempts, and mount intentions was determined more by the reaction of the mounted animal than the actions of the mounter, and as such were a useful indication of the receptive state of the one being mounted.

Males also simply placed their muzzle near to the perineum of the female in the *perineum sniff*.

Flehmen was performed after placing the muzzle in a stream of falling urine. In Nilgiri tahr, flehmen did not differ markedly from the usual ungulate pattern (SCHNEIDER 1930). In giving the flehmen response, the head was typically held in the normal position and the chin elevated only slightly. Sometimes the head was turned slowly back and forth.

Sexual or courtship displays by males are all variations and elaborations on a common theme, in which the muzzle of the male is projected towards the inguinal region of the female. In the *rear twist*, the male stood behind the female and twisting his head sideways, extended his neck and muzzle forward, in the direction of, or to the udder of the female (Fig. 9). In some cases this move was so pronounced that he literally jabbed the udder with his muzzle.

The typical *side twist* was performed from further forward, with the male's shoulders beside and level with, or just behind the female's hindquarters (Fig. 10). The male then lowered his head, twisting it axially, and moved his head towards



Fig. 9: When giving the rear twist, the male Nilgiri tahr extends his muzzle and neck forward toward or between the hind legs of the female, and turns the head sideways. Rear (and side) twists were often accompanied by a foreleg kick

the female so that his muzzle pointed at or touched her belly, just anterior to the hind leg. Some side twists were from further forward, the muzzle being directed along the female's side, just behind her foreleg, just anterior to her foreleg (towards her chest), or even against her throat or chin. Both rear and side twists were also given from other than a parallel orientation. In this connection, any twist which was oriented at a part of the female's body anterior to the hind legs was considered a side twist. In some side twists, the male also leaned or pushed against the female's hindquarters with his shoulder.

Displays to resting females were similar in orientation, but not in form, since the resting female's inguinal region was much lower. I called the comparable versions of these displays the side and rear sniff. As with the twists, the *rear sniff* was from the rear of the female. The male lowered his head and extended it towards her. The *side sniff* was basically the same, except that the male stood to the side of the female. The amplitude of the twisting movement in these displays was dependent largely on the position of the male. For instance, a side sniffing male standing essentially behind the female, but far enough forward so that the display was directed anterior to the female's hind legs, lowered his head almost straight down, and twisted only very slightly towards the female's inguinal region. On the other hand, if he was standing off to the side, the twisting movement was much more pronounced to achieve the same orientation with respect to the male's muzzle and the female's inguinal region. These differences emphasized the importance of the orientation of the display over the actual form they took. As was the case with twists, side sniffs were also sometimes directed towards anterior portions of the female's body.

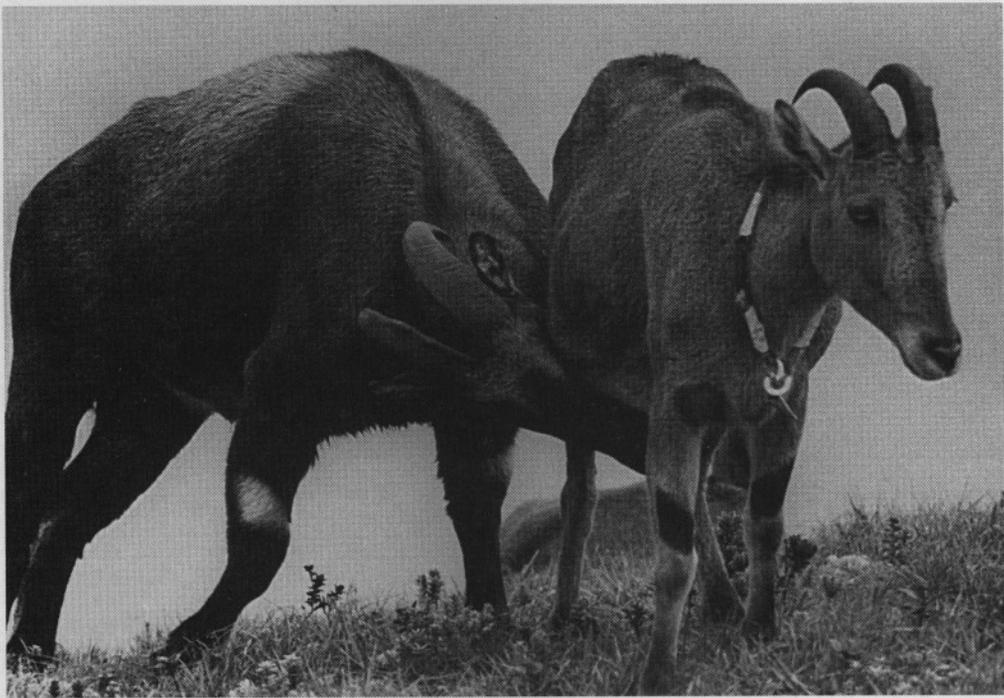


Fig. 10: In the side twist, the male Nilgiri tahr usually approached from the rear, and turned his muzzle sideways usually toward the inguinal region of the female, just anterior to her hind leg

Both twists and sniffs were often embellished with other displays performed at the same time. In the *foreleg kick*, the male raised and lowered one foreleg 10—20 cm and dropped it back to the ground. Usually this action was repeated a few times in succession. In Nilgiri tahr, the foreleg is held straight, but not necessarily rigid, and emphasis is placed on the downward stroke, so that the kicking produced a rhythmic thumping.

In the *tongue flick*, the male rapidly flicked his tongue in and out. This also produced a rhythmic "flapping" noise. Both the foreleg kick and tongue flick generally occurred in connection with twists or sniffs, but sometimes they were performed by themselves. The *whoosh* was a rapid expellation of air, apparently through the mouth. When combined with the tongue flick, this produced a broken slurping sound. Males also sometimes accompanied sexual displays with a *hum*, a soft, closed mouth vocalization of about 1—2 s duration.

Female tahr reacted to the attentions of males in various ways. The *flinch* was a quick movement which seemed to indicate that they were startled or uneasy. Females also moved quickly a few paces to *scoot away*, or they kept going to *run* off. A response of resting females was to *rise*. Mounted females sometimes *struggled* in an attempt to break the clasping hold of the male.

In reaction to the approach or courting of a male, females frequently urinated. Their posture in doing so did not differ noticeably from the normal, slightly crouched urination posture. The usual response of the male was to place his muzzle in the falling urine and perform flehmen.

Severely harassed females also gave a series of whistles. These were quite similar to those given by alarmed tahr, but had a more breathy quality (had more of a hissing sound). This appeared to be related more to the fact that they were usually running at the time, than that they occurred in a sexual context (running alarmed tahr gave a whistle that sounded virtually the same).

Several higher order behavioral categories also proved useful in describing the actions of Nilgiri tahr. These categories incorporated one or more of the behavioral units described above, and gave an indication of the motivational state of the animal involved. Extended sequences of aggressive acts fell into two categories, *fighting*, and *sparring*. Fighting and sparring both involved the same aggressive behavior patterns, but differed in the context, intensity, course and outcome. Fights occurred at moments of conflict, particularly when two males simultaneously attempted to court the same female. They were of high intensity, as each tahr appeared to use all its strength to damage its opponent, and they ran their course from beginning to end without pause or interruption. In fights there never was any question as to which was the winner, and which was the loser (since the loser was usually chased out of the group by the winner). Sparring, on the other hand, took place during general daily activity. The same behaviors used in fighting occurred, but they were of much lower intensity, and the possibility of injury seemed remote. There were often pauses in the proceedings as one or both of the partners stood or groomed, and changes in partner were not uncommon. Lastly, it was usually impossible to designate a winner or loser, instead it appeared as if one of the partners just lost interest and turned away.

Comparisons with Other Species

Published information on the behavior of Himalayan tahr is limited to a few observations by SCHALLER (1973, 1977), and incidental observations on a captive group by HASSENBERG (1981). I know of no published information on the social behavior of the Arabian tahr (*Hemitragus jayakari*), but I did have the opportunity to observe a small captive group for a few hours. Consequently, the lack of a certain behavior having been described for these species does not preclude it from the species repertoire.

All three tahr species use horn present (jerk, SCHALLER 1977), and lunge. This is not surprising, as these moves are common to most horned ungulates (WALTHER 1979).

Apparently the only other Caprinae which performs the hunch-sidle is the mountain goat (GEIST pers. comm.).

Both Nilgiri and Himalayan tahr give a hunch, and the Arabian species may do so too. Himalayan tahr erect the hairs of their mane during hunches, and the erected neck hairs often frame the black face with an apron or ruff, and the tail is raised. Nilgiri tahr erected their manes when hunching, but the tail remained in the normal position. Similar, sometimes less conspicuous, postures are also given by other caprines such as wild goat (*Capra aegagrus*), domestic goat (*C. hircus*, SHANK 1972), Punjab urial (*Ovis orientalis*), bharal (*Pseudois nayaur*), or takin (*Budorcas taxicolor*), musk oxen (*Ovibos moschatus*, SCHALLER 1977), mountain goat (GEIST 1965), and north-eastern chamois (*Rupicapra rupicapra*, KRÄMER 1969). However, whether these postures are completely homologous to those found in tahr is not clear. Most of these species reach the extremity of their display with the head held low, and stretched forward. Nilgiri tahr, however, pull the chin back, partially inverting the head in the full expression of the display. Mountain goat also have a similarly extreme form of hunch, and like Nilgiri tahr they turn the head slightly when doing so (GEIST 1965). As previously mentioned, WALTHER (1974) considered the hunch as a threat in mountain goat, since in hunching the animal adopts the posture for reverse parallel fighting.

As Nilgiri and Himalayan tahr fight in reverse parallel position, we may also conclude that this was originally the case with these species. However, in Nilgiri tahr, serious fights commence with side clashing, not reverse parallel fighting, and thus the hunch does not signal immediate readiness to fight in this species, but rather it indicates the status and general motivational state of the sender. This would seem to indicate a change in the meaning of the display, not on the basis of changes in its own form (e. g. through ritualization or modification), but on the basis of changes in the social context in which it occurs.

SCHALLER's (1973) description of a broadside display in Himalayan tahr is quite like the head-out I observed in the Nilgiri species. While many other caprines give broadside displays, none maintain a posture similar to this while doing so.

The stare has been reported in Japanese serow (*Capricornis crispus*, KISHIMOTO pers. comm.), south-western chamois (*Rupicapra pyrenaica*, LOVARI 1985), and bighorn sheep (*Ovis canadensis*, GEIST 1971).

Within the Caprinae, spraying urine occurs in takin (SCHALLER 1977) and north-eastern chamois (KRÄMER 1969), in many *Capra* species (WALTHER 1961; SCHALLER 1977; SHANK 1972), and in all three tahr species. Unlike the Nilgiri tahr, which sprays urine onto and between its forelegs, the Arabian tahr male turns his head sideways and arcs his body laterally to spray the urine beside one foreleg onto the side of his face (USHER-SMITH pers. comm.). This is not surprising considering the thick "leggings" of long hair adorning the forelegs of Arabian tahr. These leggings would block most of the urine spray directed between the forelegs. Bumping the forehead in connection with spraying urine seems to be another unique aspect of Nilgiri tahr behavior, although the method of spraying by Himalayan tahr has not been described.

In bumping the forehead, a Nilgiri tahr male distributes the urine scent around his head and face. The lateral whiskers of Arabian tahr (HARRISON 1968) and the beards of goats (*Capra*, SCHALLER 1977) may have a scent bearing function. Interestingly, male bighorn and Dall's (*Ovis dalli*) sheep rub the secretions of preorbital glands of dominant males on their faces as opposed to displaying their own scent.

Object aggression is widely employed by Caprini, and probably all species perform it in some manner (horn vegetation, SCHALLER 1977). In Nilgiri tahr and Arabian tahr, however, object aggression seemed to serve a somewhat specialized function. This function was closely related to the "object" involved. Although Nilgiri tahr did sometimes direct their object aggression towards shrubs, the most common recipient was the grass and the underlying earth as well. Extensive or recurrent bouts of object aggression at the same site (as was frequently the case), left an earth colored patch up to 1 m in diameter, where the digging of the horn tips and rubbing of the neck and head dug up and soiled the vegetation. In Nilgiri tahr, both object aggression and spraying urine occurred in the same context of aggressive arousal, and as a result, these sites often bore the typical male scent. In addition, the male's face often became covered with mud. Thus, object aggression not only served the usual functions of providing a (redirected) outlet for aggressive intentions and displaying the vigor and strength of the animal, it also served as a visual and olfactory mark, and enhanced the maturational appearance of the male by darkening his facial area.

Object aggression seems to have a quite different function in Arabian tahr. Like Nilgiri tahr, Arabian tahr evidently do perform object aggression against plants, but the majority of the few displays I witnessed in the captive group were directed at the ground. Certain sites with dry loose sandy soil were favored. As with Nilgiri tahr, the display incorporated the digging of the horns into the earth, but in this case, the back and forth movement with the head turned sideways served to slice into the sand with the relatively flat horns. The display terminated by raising the head as the Arabian tahr continued to hold its head sideways, and the flat inner margin of the horns thus lifted a quantity of sand. The head was usually brought up sharply, and this motion threw the sand onto the back of the animal. As a result, the coats of the Arabian tahr were impregnated with dust and sand, as was amply evident whenever they shook. Although this behavior has not

been observed in the wild, the resulting shallow sandy pits are quite evident in areas Arabian tahr occupy (MUNTON 1979).

Mouthing the penis has been reported in Himalayan tahr, several species of *Capra*, aoudad (*Ammotragus lervia*), and bharal (SCHALLER 1977).

In horned ungulates, the forms of fighting are often closely related to horn types. Within the Caprinae, the horns of tahr are intermediate between the short, sharp, often dagger like horns of the more primitive members of this subfamily (*Nemorhaedus*, *Capricornus*, *Rupicapra*, and *Oreamnos*), and the long, curved or twisted horns of other caprines such as the sheep and the goats. With the exception of the chamois which has a hook shaped horn, the relatively straight, sharp horns of the rupicaprines are most suited for poking, jabbing, or stabbing with the tips. Unfortunately, the fighting methods of many of these species have not been described. However, the mountain goat is typical of this group with regards to horn shape, and its major method of fighting is in a reverse parallel position. Although rupicaprines may make horn to horn contact, this is likely to be more of a head to head mutual butt, since the rounded horn surface is not suitable for catching a blow.

The sheep and goats represent the other end of the spectrum. In adult males of these species, the horns are massive, long, and curled or twisted in such a manner as to make the tips virtually useless as weapons. Rather, it is the frontal surface of the horns (near the base) which is the point of contact. In addition, this contact is not horn to body, but horn to horn. At this area of contact, two basic types of horn surface can be distinguished in the sheep and goats. The first is a broad, more or less flat surface typical of sheep and the Alpine ibex. The second is a projecting rib along the anterior edge of the horn, exemplified by the other *Capra* species. In both types, the significance of these structures is evidenced by the well developed fighting techniques of these species which strongly emphasize frontal contact. In sheep this is seen in the bipedal charge leading to mutual frontal ramming, and the corresponding rearing to clash in the goats.

In tahr, the males' horns are heavier and more curved than those of rupicaprines, but they are nevertheless lighter and much shorter than those of the sheep and goats. However, although one might say there is a continuum in horn shape and size, the same cannot be said about the respective fighting behaviors as there is not a fighting style "half way" between reverse parallel fighting and frontal clashing. Rather, in tahr, as exemplified by Nilgiri tahr, both fighting techniques are used. Furthermore, both fighting techniques are used in an intermediate way. When Nilgiri tahr reverse parallel fight, for instance, the curvature of the horns is too great to allow the horntips to jab directly into the body of the opponent, yet the blow is still delivered with the most distal portion of the outside surface of the horns. This means that although the tip itself does not dig into the opponent, the impact of the blow is still concentrated on a relatively small surface. Furthermore, the horntips can still play an important role in some circumstances, such as in the hook behind foreleg.

On the other hand, clashing with the horns is also an important fighting method in Nilgiri tahr, with two basic types of clashing occurring. In head-on clashing, the flat frontal surface(s) of the horn(s) accepts and delivers the blow, as

is the case in sheep and alpine ibex. However, such clashing is not as well developed in Nilgiri tahr, as they usually remain stationary while clashing. In one fight I observed, the males backed away from each other and then rushed forward on all fours to clash. I never observed rearing to clash as HUTTON (1947) reported for this species. In contrast to head-on clashing, side clashing Nilgiri tahr make contact with the outside of one horn. The configuration and shape of Nilgiri tahr horns are particularly suited to this type of clash. As the horns do not diverge markedly, the sides can be brought together as the opponents stand parallel to one another, and the rounded cross section gives a relatively flat surface to catch and deliver the blows. Side clashing has not been reported to date in either of the other tahr species, and considering their horn configuration, it seems unlikely that it occurs. This is because the horns of the other two species diverge, and are more oblong in cross section. Thus, there is not a surface to deliver or accept this form of clashing.

Most caprines probably show submissive behaviors similar to those of Nilgiri tahr, although they may not be classified in exactly the same way. The turn and cut of Nilgiri tahr, however, appears to be a unique method of indicating inferiority. This may be because of the particular relevance of turning and cutting to conflict between animals standing in a parallel position. As noted above, this is a more important orientation for Nilgiri tahr than most other related species. It comes into play in the hunch sidle and the side clash, two forms of aggression which are unique or particularly well developed in Nilgiri tahr. These two aggressive behaviors and the horn presentation (which is also often given in parallel orientation) elicited most of the turning and cutting. Thus this particular mode of indicating submission employed by Nilgiri tahr is specific to the unique forms of aggression they emphasize.

The four most common sexual displays I have described for Nilgiri tahr, the rear twist, side twist, rear sniff, and side sniff are essentially variations on a single type of display. This twisting movement, often combined with the foreleg kick or tongue flicking, are widespread, in fact nearly universal among Caprinae (WALTHER 1979, SCHALLER 1977). However, unlike most of these species, including the Himalayan tahr (SCHALLER 1973), Nilgiri tahr do not perform the accompanying low stretch. Nilgiri tahr do adopt the position corresponding to the low stretch at the full extension of the rear twist, and sometimes a male displaying to a resting female from a short distance maintained a similar attitude between side sniffs. However, in the first case, the posture is not maintained. Instead it is momentary, attained at the extremity of the display. In the second case, the posture is adopted more as a stance of less than complete withdrawal from the side sniff than as a display in its own right. This contrasts markedly with the rigid stereotyped posture of mountain sheep (GEIST 1968) or Alpine ibex.

Conclusions

Based on his formulations on the evolution of caprines, GEIST (1971) made several predictions about aggressive behavior in *Hemitragus*. Although GEIST's remarks refer to Himalayan tahr, most apply to Nilgiri tahr as well. GEIST

correctly predicted that tahr would fight in reverse parallel orientation, but that a number of components would be added. These are the various forms of hooking and clashing. However, neck fighting is not as well developed (in adults) as he suggested, and Nilgiri tahr do not "dive under the the opponent's belly and hook him with the horns, attempting to throw him backward" (p. 318). Although Nilgiri tahr do occupy an intermediate evolutionary position between the Rupicaprini and Caprini, they seem to be somewhat more advanced than GEIST predicted.

A behavioral phylogeny for the Caprini can be constructed starting with the primitive rupicaprid features (exemplified by *Oreamnos*) of fighting in reverse parallel stance and use of the hunch as a threat. Cladistic analysis by the method of SWOFFORD (1984) based on the occurrence of these and 7 other agonistic behavior patterns (SCHALLER 1977) resulted in the groupings shown in Fig. 11. In assigning the character states, the clear-cut occurrence of a behavior pattern in any representative of a genus was considered appropriate for that genus.

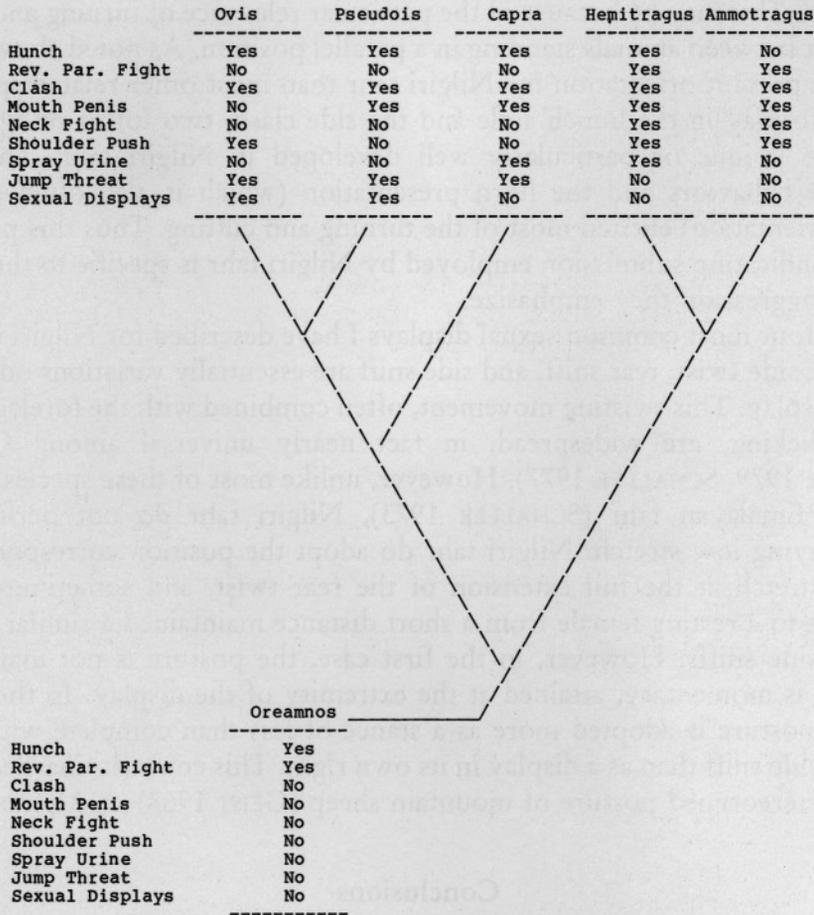


Fig. 11: Cladogram of Caprini based on aggressive behavior with *Oreamnos* as the out group. Rev. Par. Fight = Reverse Parallel Fight. Sexual displays refers to the use of sexual displays in aggressive encounters between males

This phylogeny is not in keeping with others that have proposed for this group (and there are many, SCHALLER 1977). Chromosomal and electrophoretic evidence (NADLER et. al. 1974, SCHMITT 1963) indicate a closer affinity between *Ammotragus* and *Ovis* than between *Ammotragus* and *Capra*. SCHALLER (1977) considered *Pseudois* more closely related to *Capra* than *Ovis*. He argued that the similarity in social behavior between *Pseudois* and *Ovis* was a result of environmental, rather than phylogenetic influences. The position of *Hemitragus* (along with *Ammotragus*) as an early departure from the *Ovis-Capra* lineage is in near agreement with SCHALLER's depiction (1977: 333). The practice of spraying urine links *Hemitragus* with *Capra*, but other similarities (Fig. 11) suggest a stronger affinity between *Hemitragus* and *Ammotragus*. Therefore, relationships within the Caprini remain ambiguous. The assessment of chromosomal G-band patterns in *Hemitragus* and *Pseudois* would be helpful in understanding the evolution of behavior in this group.

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