

THE UNIVERSITY OF CALGARY

SOME ASPECTS OF SOCIAL BEHAVIOUR IN A POPULATION
OF FERAL GOATS (*Capra hircus* L.)

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGY

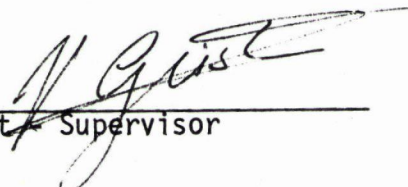
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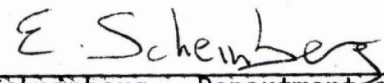
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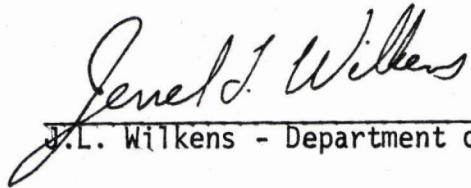
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "SOME ASPECTS OF SOCIAL BEHAVIOUR IN A POPULATION OF FERAL GOATS (*Capra hircus* L.)" submitted by Chris C. Shank in partial fulfillment of the requirements for the degree of Master of Science.


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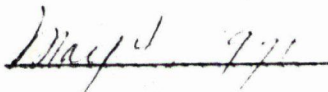

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ABSTRACT

Some aspects of the social behaviour of a population of feral goats were studied for 3 months in the fall of 1969 on Saturna Island, British Columbia. The goat population was subdivided into six size-sex classes. Social behavioural patterns were described, coded, and compared to those of other bovids. Social interactions were recorded by noting each pattern type performed and the size-sex classes of the initiator and the receiver. The data were analyzed with the aid of a digital computer. Models of goat social behaviour were developed and presented in the form of sociograms.

The constituent patterns of sexual behaviour were found to differ little from the sexual patterns of other bovids. Sexual behaviour was found to be expressed within two systems. The first, termed "formalized courtship", is characterized by one dominant male guarding a single female from nearby subdominant males and by his careful and prolonged courtship. The second, termed the "gang-bang", is characterized by large numbers of males simultaneously attempting to copulate with one estrous female with a corresponding breakdown of normal agonistic and sexual conventions.

Size-sex class variability in sexual behaviour was analyzed. Smaller males were found to direct less extensive courtship to females prior to copulation. Horned males were found to prefer adult females over female kids for courtship while hornless males exhibited the opposite trend. Only young males were found to treat kids in a qualitatively different manner than adult females. Females were observed to court only larger males.

Agonistic behaviour was described in terms of two associations. The first, the "rush association", is composed of patterns associated

with one antagonist running at his opponent with his head lowered. The second, the "clash association", is composed of patterns associated with head to head contact. Rush association behaviour is delivered by larger individuals to smaller ones while clash association behaviour is almost entirely restricted to equal-sized animals. It was hypothesized that clash association behaviour is instrumental in generation of the social hierarchy while rush association behaviour is the mechanism by which the hierarchy is reinforced.

ACKNOWLEDGEMENTS

This study was supported in part by National Research Council of Canada Grant 69-0625 awarded to my supervisor, Dr. V. Geist, and by equipment provided by Kananaskis Environmental Science Centre of the University of Calgary. I would like to express my appreciation to the Data Centre of the University of Calgary for making their facilities available and to the members of my committee for critically reading the manuscript. Dr. E. Scheinberg helped in the computer programming and Dr. V. Geist made the sketches and provided many stimulating ideas. The entire J.M. Campbell family helped to make my stay on Saturna Island very enjoyable.

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I. INTRODUCTION

Although the goat (*Capra hircus* L.) was probably the earliest ruminant to be domesticated (Zeuner, 1963), there has been surprisingly little critical information published on its behaviour. Stewart and Scott (1947), Scott (1948), and Ross and Scott (1949) considered the relationship between dominance and leadership in goats under penned conditions. Collias (1956) considered the socialization process of goats whereas Klopfer *et al.* (1964), Klopfer and Gamble (1966), and Klopfer and Klopfer (1968) studied "imprinting" in goats. Hafez and Scott (1969) compared the behaviour of sheep and goats and Rudge (1970) studied mother-young behaviour in the feral situation. In general, most of this information is not comparable to the precise investigations of ruminant behaviour that have been published in the past ten years.

The purpose of this study was a) to provide basic information on the social behaviour of domestic goats in natural situations, b) to compare their social behaviour to that of other bovids, and c) to generate a model of their social behaviour which is illustrative of social interaction preferences. Maternal behaviour is not treated extensively. This class of behaviour is covered by Rudge (1970).

1. Source of Data and Observational Procedures

A population of feral goats was observed from July 30 until November 6, 1969 on Saturna Island, British Columbia, Canada. The first few weeks of the study were spent in familiarizing myself with the study area, establishing techniques and describing and coding behavioural patterns. Individuals were classified by external characteristics into six size-sex classes as follows: 1) kids (defined as having no readily observable secondary sexual characteristics), 2) females, 3) hornless males, 4) small males (defined as having horns less than 20 cm in length), 5) medium males (defined as having horns 20-50 cm in length), and 6) large males (defined as having horns more than 50 cm long).

The presence of hornless males presents a problem in that they may represent either pseudo-hermaphrodites or functional males carrying a dominant gene for the polled condition. Eaton and Simmons (1939) report that the incidence of the pseudo-hermaphroditic condition may reach 11% in some breeds of goats. Pseudo-hermaphrodites are always hornless (Asdell, 1944) and have vestigial scrota (Short *et al.*, 1968). Since none of the Saturna Island hornless males were observed to possess other than normal scrota, it will be assumed that the hornless class is composed solely of functional, polled males.

Observations were made opportunistically since no schedule or systematic randomization of data collection could be instituted. This was due to problems in finding the animals in circumstances suitable to observation. Observations were made at distances of 50-800 meters using 7 x 35 binoculars or a 20x monocular spotting scope.

Data were recorded on sight with a portable tape recorder and were later transcribed into field notebooks. Data collection was discontinued as soon as it became apparent that any member of the group sensed my presence. Naturalistic observations were enhanced by watching Wodin, a tame male goat. He had been taken from the population when only a few days of age by the J.M. Campbell family and castrated at the age of one month.

A working definition of a "behavioural pattern" was adopted and considered to be any stereotyped, spatio-temporal sequence of movements and postures having constant and recognizable start and end points. No attempt was made to determine a single external releasing stimulus such as is implicit in the definitions of Lorenz and Tinbergen (Hinde, 1966). Only patterns deemed to have social significance were recorded. An "interaction" was considered to have begun with the exhibition of the first recognizable stereotyped, social behavioural pattern and to have ended with any period of diverted attention that I considered to be decisive. A distinct grouping of individuals was usually subjectively obvious. When in doubt, however, a distance of more than 100 meters separating the closest two individuals was used as a criterion for separation into two groups.

Data collection consisted primarily of three types; a) group composition, i.e., the number of individuals in each size-sex class present in the group being watched, b) the time (accurate to one minute) that an interaction was begun, and c) a description of the interaction in terms of the sequence of patterns observed and the size-sex class of the initiator and recipient of each pattern. More than one hundred and fifty observational hours were accumulated.

The interaction data, consisting of 3788 displays of patterns and 982 interactions, were punched onto BCD data cards.

2. The Study Area

Saturna Island is a small island, 3 miles in width and 7 miles in length (5 x 11.5 km), located in the southern portion of the Georgia Strait, British Columbia. A prominent ridge runs the length of the island and rises to an elevation of 1600 feet (490 m). About 200 persons live on the north side of this ridge whereas only one family lives on its south side. The study area consisted of the entire south side of this ridge. Figures 1 and 2 illustrate typical Saturna Island goat habitat.

The climate of the Gulf Islands is quite uniform and essentially Mediterranean in nature. The average annual rainfall is about 41 inches (101.6 cm) concentrated mainly in the winter months. The average annual temperature is 49°F (9.4°C). The coldest month is January with an average temperature of 37°F (2.8°C), while the warmest month is July with an average temperature of 62°F (16.7°C) (Anonymous, 1965).

Krajina (1965) classifies the Gulf Islands into the coastal douglas-fir biogeoclimatic zone. The most obvious plant associations on the south side of the island are Garry oak (*Quercus garryana*) - Douglas-fir (*Pseudotsuga menziesii*) complexes on dry, south slopes and madrono (*Arbutus menziesii*) - Douglas-fir complexes in wetter, more nearly level areas. Large areas of the level bench land between the ridge and the southern sea-cliffs have been cleared for pasture. The open south slopes are covered with goat paths, however, early

photographs show that goats have not significantly altered the gross ecology of the area.

3. History and Description of Saturna Island Goats

According to Mr. E. Reed, a long-time resident of the island, the Saturna Island goats were introduced shortly after 1890 by a Mr. B. Dyne. Mr. Reed did not know the race of this original stock. Shortly thereafter, Mr. J. Pain may have introduced some goats as mentioned by Geist (1960). When Mr. Reed arrived on Saturna in 1919, the goats were well established in a feral state. During the 1920's many Saturna Islanders kept goats and, undoubtedly, many of these became feral. In 1921, Mr. L.C. Harris introduced several purebred hornless Toggenburg bucks, bought from a Mr. Bejornfeldts of Curlew Island. Geist (1960) mistook the name "Bejornfeldt's" for a breed of goats. Several erratic attempts have been made to exterminate the goats, but in general they are now well tolerated by islanders and considered to be a characteristic feature of the island.

At the present time, the goats' range is restricted to the entire length of the island's south coast up to the crest of the prominent ridge. Most of their time is spent on the open slopes but they were often seen to frequent the dense woods above and below the slopes and to occasionally come out onto the pastures of the bench and onto the sea-cliffs.

The goats appear suitably nourished and there is no evidence of unusual parasitic infestation (Geist, 1960). The major source of mortality is probably hunting pressure from man. Falls may kill goats as is evidenced by complete skeletons found at cliff bases.

Natural predators are few. Eagles may take some kids as Brandborg (1955) observed for Rocky Mountain goats (*Oreamnos americanus*). Ravens kill domestic lambs on Saturna Island indicating that they may also attack young goats (Campbell, pers. comm., 1969).

Morphologically, the Saturna Island goats exhibit a wide range of individual variability. The breeds are "quite undeterminable" (Geist, 1960), although Alpine, Toggenburg, and Saanen characteristics (Peglar, 1929) appear to be present. Individuals are quite diverse in colour with black, brown, red, white, grey and mottled types present. The horn shapes of the males are quite variable. Most common are the widely diverging, twisted, non-spiralling horns. Less common are horns forming a large, open spiral with little or no twisting, and those that are laterally compressed with no divergence, twisting, or spiralling. Gradations between these types occur.

Although no special techniques were employed to determine the number of goats inhabiting Saturna Island, a fair estimate of the population is between 125 and 175 individuals. Size-sex ratios, based on 178 observed groupings, are presented in Table I. More males were observed than females. This difference is significant (calculated $\chi^2 = 10.96$, tabular $\chi^2 = 6.63$, $p = .01$) and may be due to the fact that females have a tendency to form smaller and less observable groups. Equality in numbers of adult males and females has been reported for feral goats in Hawaii (Yocum, 1967), Barbary sheep (*Ammotragus lervia*) in New Mexico (Ogren, 1965), and Himalayan tahr (*Hemitragus jemlaicus*) in New Zealand (Anderson and Henderson, 1961). Several papers have presented sex ratios in feral goats or closely re-

lated species that differ significantly from equality. Williams and Rudge (1969) state that a population of feral goats in New Zealand had an adult male to adult female ratio of 1:1.8. Geist (1971) states that the adult ram to adult ewe ratio is 0.9:1.0 for bighorn sheep (*Ovis canadensis*) in Banff National Park and 0.88:1.0 for a Stone's sheep population in British Columbia, whereas Boyd *et al.* (1964) cite the case of feral domestic sheep (*Ovis aries*) on St. Kilda Island, Great Britain where the ram:ewe ratio fluctuates between 1:2.8 and 1:5.5.

Group size varied from 1 to more than 100. Figure 3 indicates that groups sizes are highly variable. The apparent increase in group size in October is not statistically significant at the 5% level of probability due to the high standard deviation (14.95) but does indicate that some larger groups began to form during this period. Group size data for the first two weeks of November are not available as almost all the goats on the island were aggregated into one large group numbering over 100 individuals which was impossible to record accurately. Geist (1960) states that the largest group he personally counted on Saturna was 37, but that he had reports of 54 and 75. Riney and Caughly (1959) recorded group sizes in New Zealand only as high as 14. Yocum (1967) states that in Hawaii groups larger than 20 were seldom seen. Figure 4 indicates that groups numbering between 4 and 6 were most common. This corresponds well with Yocum's (1967) data.

No quantitative analysis of grouping preferences between size-sex classes was performed due to limitations in the data. No obvious preferences were observed. There was no obvious colour preference in grouping evident from casual observations nor were there any ob-

vious individual attachments between known animals other than sibling and maternal attachments. Very little sexual segregation was noted during the period of the study. Large aggregations of females and kids were occasionally observed, but several adult males were always present. A female and her kids were often seen alone but the only solitary goats ever seen were males obviously searching for a group. Unisexual groups of more than 5 individuals were never seen. Geist [1960] reports observing one group of 7 males. According to the residents and Geist (pers. comm., 1970), no obvious sexual segregation occurs at any season.

This observation is contrary to reports on most bovid species; e.g., American bison (*Bison bison bison*) (McHugh, 1958), mountain sheep (Geist, 1968a), Alpine ibex (*Capra ibex ibex*) (Nievergelt, 1966, 1967), feral domestic sheep (Grubb and Jewell, 1966), Himalayan tahr (Christie and Anderson, 1964), and markhor (*Capra falconeri*) (Roberts, 1969). In feral goats, Riney and Caughley (1959) report a seasonal segregation of the sexes in New Zealand while Yocum (1967) reports that in Hawaii the males may be found with the females throughout the year. He attributes this to the fact that breeding occurs the year around. This is very likely the situation on Saturna Island where some breeding occurs the year around (Geist, 1960).

Data related explicitly to land tenure were not collected. Therefore, all conclusions about home range and territoriality are based solely upon impressions formed while in the field. All groups observed appeared to be fluid in composition and to range over the entire southern coast of the island. This indicates that during the months of the study, the Saturna goat population represents a single demic group with a home range of approximately 1 x 8 km. Therefore,

in following Burt's (1943) classic definition of territory as being any defended portion of the home range, no speculation is possible as to the existence of territoriality in Saturna Island goats.

Reports of other researchers indicate that feral goats may occupy a home range considerably smaller than was found in this study. Geist (1960) found the entire Walker Hook feral goat herd of Salt-spring Island, B.C. occupying a home range of 50 x 500 yards (45 x 457 m). Riney and Caughley (1959) report that female kid herds in New Zealand maintain a range of 1225 yards (1155 m) in diameter or less. Yocum (1967) reports groups in Hawaii using areas no larger than 0.5 miles (0.8 km) in diameter.

Territoriality is probably absent in the Caprinae. Banks (1964) described behaviour in domestic sheep under penned conditions that might be interpreted as territorial in nature. Pfeffer (1967) considers male mouflon to be territorial during the breeding season, however, this is questionable from his descriptions and may only reflect great loyalty of mouflons to seasonal home ranges as found for mountain sheep by Geist (1971). Territoriality is common among antelopes and is reviewed by Leuthold (1966).

II. DESCRIPTION AND COMPARISON OF BEHAVIOURAL PATTERNS

1. Alarm Behaviour

Goats exhibit a variety of alarm behaviours when faced with potential danger. In all cases, alarm is accompanied with an "alarm snort" produced by violently expelling air through the nostrils with an accompanying explosive, sneezing sound. In some cases, a fine spray of mucus is visible. Such a snort is common amongst bovids,

e.g., the Persian bezoar (*Capra aegagrus*) (Lydekker, 1898 in Rudge, 1970), mouflon (*Ovis musimon*) (Pfeffer, 1967), mountain goats (pers. observation) and impala (*Aepyceros melampus*) (Schenkel, 1966).

When the danger stimulus is intense, such as when I was seen after stalking very close, the discoverer immediately snorts and runs. Group flight is then general and immediate with no attempt to ascertain the nature of the danger. When the danger is not deemed so important however, such as when I was discovered while still at a considerable distance, the individual making the discovery will stand rigidly staring at the stimulus source and snorting frequently (Fig. 5). Group members will then approach him forming a tight bunch until they, in turn, discover the source of alarm at which time they also snort and stand rigidly. Tails of males, and occasionally females, are held up vertically as in markhor (Roberts, 1969) and a front foot may be stamped such as I observed in mountain goats and has been described in several Asian sheep by Walther (1961a) and mountain sheep (Geist, 1971). Females often showed approach-withdrawal conflict behaviour in response to me. They would often approach me for a few steps and then turn and run back to the group.

Flight results immediately from high intensity alarm and usually results eventually from low intensity alarm. If the flight is short, the bunched condition of the group is maintained. If, however, the distance covered is great, a single line is usually formed with a female in the lead. A male was never seen to lead such a procession as reported by Darling (1937), nor was there any suggestion that large horned males were followed preferentially by small males as was shown to be the case in mountain sheep by Geist (1971). Stewart and Scott

(1947) demonstrated that leadership of this sort in goats is not related to dominance while the same has been shown for domestic sheep (Scott, 1945), Barbary sheep (Katz, 1949) and dairy cows (*Bos taurus*) (Beilharz and Mylrea, 1963; Dickson *et al.*, 1967). Flight was usually no more than 150 to 250 metres but was occasionally seen to continue for more than a kilometer. The distance covered in flight appears to be dependent upon the intensity of alarm and the nature of the terrain.

Males are, in general, less vigilant than females and are rarely the first to detect danger. They are often ignored by other group members when they perform alarm behaviour. In addition, their attention span in alarm situations is shorter than that of females as they are often seen to intersperse alarm behaviour with sexual and agonistic patterns.

Kids seem to be more responsive to alarm snorts than are adults. The Campbells report that Wodin would fall flat on the floor and remain motionless whenever someone sneezed. This behaviour ceased at approximately one month of age. Hafez and Scott (1969) state that young kids remain "frozen in one spot" while the mother goes off and grazes. Rudge (1970) says that in the feral goats of New Zealand this behaviour is lost at one week of age.

2. Urination and Defecation

The position that the female assumes for urination is an exaggerated squat with the hind legs deeply bent and the front legs straight (Fig. 7). Urination is generally followed by defecation which is performed with no change in posture.

The manner of male urination is more complicated. Castrates and immature males do not extend their penis to urinate and the urine falls vertically from the body. No particular posture nor interruption of activity was associated and it was therefore quite inconspicuous. Normal adult males were never seen to urinate in this manner although this may be due to the fact that it was simply not observed.

Adult males were often seen to extend their penis, bend at the haunches or completely collapse one haunch and to extend the head back towards the penis so that, in some cases, all or part of the penis was in the individual's mouth. When the penis was not taken into the mouth, a fluid was occasionally seen to spurt out in phase with jerks of the penis in the sagittal plane. This fluid was seen to hit the individual in the side of the mouth and to cover his throat, face and beard. The fluid was emitted with sufficient force to extend several meters beyond the animal. Flehmen (see below) may follow.

I feel that the evidence indicates that this behaviour represents urination rather than ejaculation although it probably is not the only manner in which adult males urinate. Mockel (1937, in Asdell, 1964) found that the volume of ejaculate in dairy goats averages 0.57 cm^3 . Considerably more fluid than this appeared to be emitted suggesting that the fluid is urine. Other indications suggesting urination are the occasional occurrences of Flehmen. This behaviour will be termed "urine-marking".

Behaviour in which the male covers himself with his own urine is quite common among ungulates. The males of most cervid species impregnate themselves with their own urine (DeVos *et al.*, 1967) either by urinating on themselves or wallowing in a urine-

impregnated pit. The practise does not appear to be so universal in the Bovidae and there is still much uncertainty in differentiating urination from ejaculation in the caprids. Mountain goats might urinate into their rutting pits (Geist, 1965). Barbary sheep suck their own penises (Katz, 1949; Haas, 1959) and both authors feel that this evokes ejaculation. Ogren (1965) says that male Barbary sheep may urinate in a female-like squat. This is probably a reference to goat-like urine-marking behaviour. Walther (1961a), Krumbiegel (1954) and Geist (1971) mention behaviour in ibex that is identical to goat urine-marking. Krumbiegel feels that this is ejaculation while Walther is unclear as to just what this behaviour represents. Geist did not observe the emission of any fluid from this posture. Hediger (1950), however, states that during the rutting season, captive ibex males urinate in a manner apparently identical to goat urine-marking. He attributes this to hypersexuality resultant from captivity. Anderson and Henderson (1961) mention urine stains on the underbelly and neck-ruff of male tahr. Male chamois (*Rupicapra rupicapra*) occasionally shake while urinating causing their flanks and belly to become urine impregnated (Krämer, 1969). The presence of a long tassel of hair on the penis sheath facilitates this process.

3. Flehmen

Flehmen is a response by males to their own urine or that of females. In Flehmen, the muzzle is elevated and the upper lip curled back for a period of 5 to 15 seconds (Fig. 6). Upon cessation, the lips are licked vigorously and the actor may yawn. To evoke this response, urine must be taken into the mouth. For self-induced Flehmen, the manner of urine collection has been described. Collection

of female urine by the male is accomplished by placing the open mouth in the stream of urine at a point several centimeters below the female's perineum (Fig. 7). In those cases in which Flehmen did not follow, the male proceeded to bite and/or lick the ground where the urine had fallen. Flehmen almost always followed.

Flehmen was first described by Schneider (1930) and is termed "lip-curl" by Geist (1963). I feel that the former term is preferable since the homologous behaviour in some animals does not involve curling the upper lip; e.g., Thomson's and Grant's gazelles (*Gazella thomsoni* and *G. granti*) (Estes, 1967), American bison (McHugh, 1958) and wapiti (*Cervus canadensis*) (Struhsaker, 1967). Flehmen is performed by members of every group of ungulates except suids (Estes, 1969) and is apparently universal in the Bovidae (Ewer, 1968). In addition, it is present in such diverse orders as Chiroptera (Mann, 1961), Carnivora (Eaton, 1970, Verberne, 1970) and Marsupialia (Ewer, 1968). Its possible significance will be treated in a later section.

Female goats were never seen to exhibit Flehmen as were female mountain sheep (Geist, 1968a) and male goats were never seen to exhibit Flehmen to the urine of other males as were mountain sheep (Geist, 1968a, 1971), wildebeest (*Connochaetes taurinus*) (Estes, 1969), eland (*Taurotragus oryx*) (Estes, 1969), and *Gazella dorcas* (Walther, 1968). There is no overt aggression between males over spots of female urine although several males are often attracted. Geist (1969c) shows the same in mountain sheep. The Flehmen response becomes active in goats very early as a 4-week-old male was seen to exhibit Flehmen in response to his own urine collected from the ground.

4. Sexual Behaviour

a. Generalized Male Courtship

The courtship of the male goat appears to be typical of the Subfamily Caprinae in that the majority of displays are contact displays. The sexual interaction is typically initiated by the display of a "sexual approach" by the male toward the recipient individual. This pattern is characterized by the male walking directly towards the recipient in a slight suggestion of a crouch with the head slightly extended, ears stretched forward, the tail straight up and, often, the tongue extended.

This pattern is seen, often with slight variations, in mountain sheep (Geist, 1968a), three subspecies of ibex (*Capra ibex ibex*, *C. i. siberica*, *C. i. caucasia*) (Walther, 1961a), markhor (Roberts, 1969), impala (Schenkel, 1966), Uganda kob (*Adenota kob thomasi*) (Leuthold, 1966), greater kudu (*Tragelaphus strepsicero*) (Walther, 1961c), two species of waterbuck (*Kobus defassa* and *K. ellipsiprimus*) (Kiley-Worthington, 1964), and Grant's and Thomson's gazelles (Estes, 1967). In mountain goats, the crouch component is greatly pronounced (Geist, 1965; DeBock, 1970). Many names have been associated with this pattern, e.g., "low-stretch" (Geist, 1965), "Überstrecken" (Walther, 1961a), "overstretched posture" (Walther, 1961c), "nose-forward posture" (Schenkel, 1966), "sniffing posture" (Kiley-Worthington, 1964) and "stalking position" (Estes, 1967). Walther (1961c) feels that the pattern is derived from neck-wrestling while Kiley-Worthington (1964) remarks that it may be derived from suckling behaviour.

The courtship continues with the male delivering a series of "perineum sniffs" and "gobbles". The perineum sniff is performed by the male approaching the recipient from the rear and placing his rostrum against the recipient's perineum and licking or smelling the area. This pattern is performed by most mammalian species. Lindsay (1965) demonstrated that depriving domestic rams of their olfactory sense resulted in their inability to differentiate between estrous and non-estrous ewes by perineum sniffing, indicating that the pattern serves as an olfactory means of establishing the estrous condition of the receiver. Banks (1964) suggests that this pattern may be a mechanism of detecting temperature changes in the perineal region which might be associated with estrous.

The basic courtship pattern of the male goat is the "gobble" (Fig. 8). It is synonymous with what Hafez and Scott (1969) term the "sexual call" and homologous to what Banks (1964) terms the "nudge" in domestic sheep and what Geist (1968a) terms the "twist" in mountain sheep. The pattern is quite plastic in nature and is composed of several distinct components. As in domestic sheep (Banks, 1964), not all these subacts are always performed. As the gobble is delivered, the male is typically behind and approximately parallel to the recipient. Fraser (1964) has demonstrated that in goats, deviation from the parallel alignment is related to male impotence. The gobble is initiated with a sudden lunge of the entire body toward the receiver which occasionally results in the male pushing the female forward with his chest. Alternatively, this lunge may consist of only a violent thrust of the head. This lunge or head thrust com-

ponent is usually accompanied by a deep, guttural moan. A flapping of the lips and/or a flickering of the tongue causes this moan to fluctuate in intensity at a rate of approximately 3 to 5 per second. The volume is highly variable but in some cases may be audible at distances approaching 3/4 km. It is from this sound that the onomatopoeic term "gobble" is derived. This pattern is apparently restricted to the Caprinae. The sudden lunge at the female accompanied by a tongue flicker and guttural vocalization has been described for mountain sheep (Geist, 1969c, 1971), markhor (Walther, 1961a), ibex (Walther, 1961a), Barbary sheep (Haas, 1959), and domestic sheep (McFarland and Clegg, 1960; Banks, 1964). The Marco Polo sheep apparently performs the lunge and the grunt but not the tongue flicker (Walther, 1961a).

The gobble is usually directed at the receiver's flank and is therefore, of necessity, accompanied with a twisting of the head. The gobble may, however, be directed towards any part of the recipient's body and from as far as 5 m away. In these cases, the head twist is occasionally seen and it is therefore probably a distinct component of the gobble and not only an exigency of the alignment of the bodies. The head twist is much more prominent in the behaviour of caprids such as mountain sheep (Geist, 1969a), Marco Polo sheep (Walther, 1961a), urials (*Ovis orientalis*) (Walther, 1961a), markhor (Walther, 1961a), mouflon (Pfeffer, 1967), domestic sheep (Banks, 1964), and Barbary sheep (Katz, 1949). It is not seen in mountain goats or ibex.

High intensity gobbles may be accompanied by from one to 4 kicks from a front leg (Fig. 8). The leg is bent at the juncture of the

cannon with the ulna and held stiffly during the kick. This pattern was termed "Laufeinschlag" by Walther (1958), later "Laufschlag" by him (1964a) and "front-kick" by Geist (1968a).

The front-kick is common in the Bovidae. Antelope commonly keep the leg perfectly straight during the front-kick. A review of the occurrence and non-occurrence of this pattern in antelope species is given in Buechner and Schloeth (1965).

In the Caprinae, the front-kick is present in urials (Walther, 1961a), markhor (Walther, 1961a), domestic sheep (Banks, 1964), mountain goats (Geist, 1965; DeBock, 1970), mouflon (Pfeffer, 1967) and mountain sheep (Geist, 1968a). The pattern is present in vestigial form in ibex which paw with a limp leg rather than delivering a definite kick (Walther, 1961a). To date, the front-kick has not been reported in Barbary sheep.

In both the goat and mountain sheep (Geist, 1969a, 1971) the displacer may kick so high that the leg rests upon the receiver's back. In such cases, the front-kick often becomes extended into a mount. This indicates that the front-kick and the mount may be closely related. However, Walther (1961b) feels that the front-kick is derived from fighting behaviour. Several theories have been forwarded as to the significance of the front-kick. Walther feels that it shows an intention to mount (1961c) or is a test of the female's readiness to be mounted (1964a). Buechner and Schloeth (1965) suggest that the front-kick may serve to habituate the female to contact. Between gobbles and perineum sniffs, the male stands with his tongue slightly extended, ears stretched forward, and tail straight up. Usually his nose is almost touching the flank of the

receiver. Occasionally, the chin may be resting on the receiver's back or he may very pointedly look away from the receiver. Resting the chin on the back is a pattern seen in many bovids and one that Walther (1958) feels is derived from neck-wrestling in ancestral species, and indicates an intention to mount (Walther, 1961a). The holding of the head close to the receiver is doubtless a derivative of this chin-resting. The staring away is similar to "bush-gazing" in caribou (*Rangifer tarandus*) (Lent, 1965) and probably indicates non-aggression. Like domestic sheep (Banks, 1964) and mountain sheep (Geist, 1971), goats exhibit no precise temporal arrangement of courtship patterns. Some bovids do exhibit sequences of courtship behaviour and courtship "reaction chain" analysis has been done for some wild species, e.g., waterbuck (Kiley-Worthington, 1964).

b. Anestrous female response to courtship

Reaction to courtship exhibited by the anestrous female goat is usually slight, as it is in most bovids. The recipient runs forward several steps at each gobble but continues grazing, and in general appears to ignore the male. The female's tail may be kept in a normal near-horizontal position or it may be clamped down tightly. No particular ear position is assumed. Often urination will be performed in response to a low-stretch, a perineum sniff, or a gobble. The male will test this urine, exhibit Flehmen, and generally terminate his courtship.

c. Courtship behaviour during estrous

Estrous females are typically presented with vigorous and persis-

tent courtship by the male. In response, the estrous female wags her tail and retreats. The tail wag probably serves to waft vaginal odours.

If the female is not yet ready to copulate, this courtship may be quite bothersome to her. Response may be of several types. She may simply run, in which case a "sexual chase" results with the courting male or males delivering gobbles and front-kicks toward her rear. It often appeared that the immediate cause of courtship was to force the female to run. Alternatively, the female may attempt to ward off the male by backing into cavities in the rocks and delivering low intensity horn threats to the male. This behaviour makes it impossible for the male to mount. In some cases, the courted female will turn on her suitor and vigorously horn threat, rush and butt him. There was no evidence that the female's aggressive behaviour was in the least successful in causing a termination of the courtship. This follows Rudge's (1970) observations and is in marked contrast to published reports on ibex (Burkhardt, 1961) and Barbary sheep (Haas, 1959; Ogren, 1965).

Female goats were occasionally observed to actively court males. Lindsay and Robinson (1961b) and Lindsay (1966) have indicated that the domestic ewe is very active in seeking and choosing a mate. Geist (1971) observed mountain sheep ewes courting rams that were exhausted from previous copulations. The condition of the courted male goat was, unfortunately, undetermined. In courting a male, the female goat rubs and horns the male's neck and shoulders while he stands rigidly. As soon as she stops rubbing, the male resumes normal courtship patterns. On two occasions a very masculine

appearing female was observed to mount Larges. This was mentioned by Hafez and Scott (1969) and considered to be female courtship. It has also been described for American bison (McHugh, 1958) and waterbuck (Spinage, 1969; Walther, 1964b). The female was never seen to nuzzle the male's inguinal area and no mutual circling ("Paarungskreisen" of Buechner and Schloeth, 1965) was observed such as is present in the behaviour of domestic sheep (Banks *et al.*, 1961; Banks, 1964) and Uganda kob (Buechner and Schloeth, 1965). There was no evidence that aggressive behaviour is contained in the courtship of the female or that it partakes of any typically male behaviour (other than the mount) such as is seen in Grant's gazelle (Walther, 1965a), mountain goats (Geist, 1965), mountain sheep (Geist, 1968a, 1971), black rhinoceros (*Diceros bicornis*) (Goddard, 1966), or some cervids (Geist, 1971).

Male behaviour towards a receptive female is not qualitatively different than that towards a non-receptive female with the exception of the "mount" pattern. The male typically approaches from the rear, extends his penis, and rears clasping the female with his front legs. The male's head is up in the mount as it is in all members of the Tribe Caprini. Most antelope mount with their heads up (Buechner and Schloeth, 1965). Wildebeest (Walther, 1965b) and kudu (Walther, 1964b) mount with their heads on the female's back. The mountain goat mounts with his nose buried in the female's dorsal hair ridge (Geist, 1965).

If the female is not ready to copulate, she will run forward several steps and the male will slip off. If she is receptive, she will stand still, lower her head slightly, and place her tail to one side. Once during a long, uninterrupted mount, the male's back sud-

denly straightened, his chin shot up and he fell off. This probably signifies ejaculation. No consistent differentiation could be made, however, between successful and unsuccessful mounts.

A mount is the cause of great excitement among nearby males who immediately come running toward the copulating pair and surround them. If a larger male is present, he will usually butt the mounting male off of the female. If there are only a few males in the vicinity and the courting male is dominant, he will display "guarding" or "tending" behaviour in which he follows the female, never herding her as cited by Hafez and Scott (1969), and attempts to block the approach of other males with his body and by occasionally rushing and butting them. Satellite males typically display low intensity, long distance gobbles (often without vocalization) to the female when the dominant male is not looking at them. When the dominant male turns and stares in their direction, courtship patterns immediately cease and they look away from him. The stare is a well-known threat in rhesus monkeys (Altmann, 1962), whereas looking away is said to have an appeasing function in wolves (Schenkel, 1947), gulls (Cullen, 1957), and mountain sheep (Geist, 1971). Bold satellite males, usually Smalls, often run in and hurriedly attempt to mount the female with no previous courtship. Although kids were often the recipients of sexual behaviour, they were never seen to be guarded.

When there are many males in the area, social restraints imposed by the dominant male become ineffective, precipitating a seemingly disorganized series of highly intense sexual and agonistic encounters which may best be termed a "gang-bang". In a gang-bang, normal sexual and agonistic behaviours are completely subverted in a fren-

tic exhibition of gobbling, mounting, butting, chasing and clashing. I found that the entire activity of a gang-bang was impossible to describe as the number of actors is great and the activity is incredibly intense.

A gang-bang usually begins with a male mounting a female and thereby attracting a large group of nearby males. The courting male becomes unable to effectively guard his female and a group "sexual chase" occurs. When the female finally stops, she is immediately surrounded by males who mount her repeatedly with few or no preliminary courtship patterns. Group excitement builds rapidly and several males may attempt to mount simultaneously on different parts of the female's body and other may mount these males. Almost always a mounting male, even a highly dominant one, is butted off. Normal agonistic conventions are disregarded as smaller males mount larger ones and males of unequal size clash. Avoidance of natural hazards is lessened as entire groups were seen to fall over small cliffs. The female remains motionless except to occasionally run and evoke a group sexual chase. The gang-bang ends with a gradual loss of social momentum. The female is left standing motionless with her head lowered while the remaining males engage in steadily decreasing agonistic activity. The entire gang-bang may last over an hour.

Loss of dominance control over satellite males by the guarding male with resultant breeding by the subordinates, such as in the gang-bang, has been described in high density rutting congregations of mountain sheep (Geist, 1971). Although he described intense homosexual activity among satellite males, and attacks on the dominant, the degree of social disorder was less than that observed for

goats. The quantitative studies of Lindsay and Robinson (1961a) and of Hulet *et al.* (1962) on domestic sheep indicate that when the receptive female to attending male ratio is high, the dominant male can no longer curtail the breeding activity of his subordinates. The opposite situation, such as occurs in goats, has not been studied quantitatively nor has the high intensity and subversion of normal dominance relationships, such as observed in the gang-bang, been described.

5. Agonistic Behaviour

Agonistic behaviour was considered to be any behaviour involving physical conflict or the threat of conflict. This behaviour type will be considered in terms of two associations of behavioural patterns rarely seen to be intermingled; the "rush association" and the "clash association".

a. Rush association

The rush association consists of the "rush" and its extensions, the "butt" and the "agonistic chase". The rush is performed by lowering the head, tucking in the chin and running directly at the recipient. In all rushes observed, the recipient retreated or attempted to retreat; counter-attacks were never seen. If the recipient's retreat is not fast enough, the attacker crashes into him with his horns. This is termed the butt (Fig. 9). Occasionally, and more often in females than males, the butt is accompanied by an upward swing of the head. If the recipient succeeds in escaping the butt, the attacker usually halts the rush immediately, but if continued, the rush becomes an agonistic chase.

The intent of the rush, from subjective determinations, is rarely to physically punish the recipient but simply to intimidate him and drive him off without the necessity of physical contact. The rush, then, functions primarily as a threat. Rush association behaviour probably exists in similar form throughout the Ruminantia.

b. Clash association

The clash association is characterized by patterns involving or related to forceable contact of the adversaries' heads. An interaction in which clash association patterns occur will be termed a "clash fight". Clash fights may be considered to be of two general types. The first, termed "sparring" is usually of short duration and often involves more than two individuals. The general impression conveyed to the observer is that of "play-like" behaviour. The second, termed "dominance fight" for reasons stated later, involves only two individuals. A dominance fight has no characteristics of play, may last several hours, and is usually terminated with one participant displaying male sexual patterns towards the other who responds in a typically female manner. Dominance fights are relatively rare and were observed on only 4 occasions. The two clash types are not mutually exclusive and no differentiation between them was made during data analysis.

The mode of initiation of a dominance fight was never determined due to the rarity of this interaction type. In any case, the beginning of a dominance fight is characterized by many rapid, highly intense "normal clashes" and "rear clashes". The "normal clash" is performed by the two antagonists facing each other from a distance of from 1 to 2 m with their heads cocked; that is, with the head up,

neck arched, chin tucked in, and head slightly twisted. The ears are held behind the horns and the tail is either horizontal or straight up. In some short-haired individuals, a dorsal ridge of hair may be erected from the neck to the withers. Simultaneously, the antagonists strike forward and downwards with the head. Head to head contact is made with the horns interdigitated and with the heads almost on the ground. Upon striking, both usually wag their tails vigorously. The force of the blow creates a loud "crack". There was no evidence that this pattern is other than essentially frontal in orientation. Patterns identical to the normal clash are present in all members of the Tribe Caprini and absent in members of the Tribe Rupicaprini (see Geist, 1971).

The "rear-clash" is performed by the sudden rearing onto the hind legs by one antagonist. One hind leg is placed behind the other in line with the clash while the head and torso are twisted so the face is towards the receiver (Fig. 10A & B). The head is cocked at an angle and the chin is pulled towards the chest. The front legs are held high, bent and pulled in close to the body. The rearer remains balanced upon the hind legs until the receiver appears ready to take the blow. This readiness is identical to the normal clash position. If sufficient preparation is not shown, the rearer will drop back to all fours - this pattern is then termed the "rear". The rear-clash is completed by the rearer descending forcefully onto his front legs delivering a strike forwards and downwards with the head. The recipient strikes as in a normal clash with head to head contact occurring close to the ground. Again, both usually wag their tails. As Schaffer (1968) states, there is a sideways thrust of the head as contact is made and one combatant usually has his head thrust to the side

(Fig. 10C & D). Much of the force of the blow then is dissipated in a lateral torque. The opponents were never observed to back away from one another after the clash as observed in Caucasian tur (*Capra caucasica*), Barbary sheep (Haas, 1959) and mouflon (Geist, 1971).

All members of the Tribe Caprini, except Barbary sheep (Katz, 1949; Haas, 1959) and primitive *Ovis* species (Pfeffer, 1967; Hafez and Scott, 1969), clash bipedally (Nilgiri tahr, Schaller, in press: markhor, Walther, 1961a; Roberts, 1969: ibex, Walther, 1961a; Nievgelt, 1967: tur, Petzsch, 1957; bharal (*Pseudois nayaur*) Lydekker, 1898 in Schaffer, 1968 and Geist, 1971: mountain sheep, Geist, 1969b: Marco Polo sheep, Walther, 1961a). However, a major distinction in bipedal clash type might be made between the *Ovis* and *Capra* evolutionary lineages. As *Ovis* species rise onto their hind legs, they are oriented frontally to the recipient. There is no twisting of the torso and the feet are placed approximately perpendicular to the line of the clash. They are off-balance (see Walther, 1961a; Geist, 1969b). In contrast, *Capra* species are orientated laterally to their opponent with their feet placed in line with him. They balance on their hind legs (see Fig. 10, Petzsche, 1957; Walther, 1961a; Roberts, 1969). It appears that the *Ovis* type of bipedal clash is a sophistication of the running clash observed in all species of *Ovis* and in no species of *Capra* except possibly the tur (Lydekker, 1898 in Schaffer, 1968 and Geist, 1971), which has obvious morphological affinities to both the bharal (Lydekker, 1913) and Barbary sheep (Geist, 1971). The *Capra* style of clash would be of the form expected if the clash were to arise directly

from a broadside display. Broadside displays are not present in the *Ovis* line but are seen, in varying degrees of reduction, in the *Capra* line.

Occasionally rear-clashes are preceded by the prospective rearer circling his opponent on the downhill side and then moving uphill in a peculiar rocking canter. Throughout this manoeuvre, his head is averted from his opponent. The hair on the back of the neck, from the occiput to the withers, can be seen to be raised on some short-haired individuals. A similar behaviour is occasionally seen following a clash, with one antagonist freezing into a stiff, essentially broadside stance with the head up and slightly averted (Fig. 10F). The other performs a static horn threat or places his head against his opponent's shoulder. Walther (1961a) pointed out the tendency for ibex, markhor and chamois to circle uphill and attack from above as did Geist for mountain goats (1965) and bighorns (1969b).

These behaviours are inconspicuous and probably represent a reduced and otherwise modified form of the broadside display of many bovid species. Interspecific comparisons will be made when treating threat behaviour.

Clash patterns are interspersed with occasional bouts of grazing, pawing with a front foot, and "head wrestling". Head wrestling involves interlocking the horns and attempting to twist the opponent's neck. Head wrestling proceeds from an essentially parallel head-to-head orientation but as the bout progresses any bodily orientation may be observed. The object appears to be to cause the opponent to lose control of his body movements by either pushing him down a hill,

twisting his neck, or pinning his head down with the plane of the face on the ground.

Pawing is usually interpreted as a threat and will be treated later. Feeding during conflict situations is observed in many animals and is usually interpreted as displacement or redirected behaviour. However, Estes' (1969) studies have shown that in wildebeest, grazing has been ritualized as an agonistic behaviour. Whether this situation is present in the behaviour of goats is uncertain due to the difficulty in differentiating between displacement and ritualized behaviours (Lorenz, 1952).

Head wrestling is a very common pattern in the Bovidae; particularly among the antelope. In the Caprini, head wrestling is performed by markhor (Roberts, 1969), Barbary sheep (Katz, 1949) mouflon (Pfeffer, 1967). It is absent from the repertoire of Nilgiri tahr (Schaller, in press) and ibex (Walther, 1961a). Shackleton (pers. comm., 1970) says that young mountain sheep will head wrestle during play but this pattern is very rudimentary in adults (Geist, 1971).

Clash patterns become less frequent and less intense as the dominance fight continues, whereas pawing with the front legs, feeding and head wrestling become more prominent. Haas (1959) mentions this tendency in Barbary sheep.

At the beginning of the dominance fight, head wrestling usually proceeds directly from the clash. However, as the fight continues, there is more of a tendency for the opponents to carefully interlock their horns by approaching one another slowly with their heads lowered until head-to-head contact is made.

At the termination of a dominance fight, one combatant typically directs a series of male sexual patterns such as gobbles, front kicks, perineum sniffs and mounts, exactly as he would to a female. The receiver responds exactly like a female; he retreats at each pattern, feeds cursorily, holds his tail in a horizontal position (typical of females) and even wags it. The receiver was never seen to respond aggressively. Presumably, the male role is played by the dominant and the female role by the subordinate as observed in mountain sheep (Geist, 1971), several species of primates (reviewed in Wickler, 1967), yellow-bellied marmot (*Marmota flaviventris*) (Armistage, 1962), and wolves (Schenkel, 1947). The combatants may continue their sexual role-playing for several days subsequent to the clash fight much as has been found in mountain sheep (Geist, 1971).

This close association between sexual and agonistic behaviours has been pointed out in some other species. Among the Bovidae, sexual behaviour has been observed in the ritualized fighting of mouflon (Pfeffer, 1967) and Nilgiri tahr (Schaller, in press). The observations of Walther (1961a) indicate that this association may occur in ibex. In mountain sheep, homosexual behaviour is observed not only following a dominance fight but also as a common expression of dominance (Geist, 1971).

Unfortunately, it was never apparent during the course of the dominance fight which combatant was "winning". This is a result of the stereotypic nature and nonlethality of this mode of combat and the usual equality in size and skill of the combatants. This uncertainty resulted in my inability to determine whether the dominant plays a primarily defensive role such as has been reported in mountain

sheep (Geist, 1971). However, trading of the rearing-up role in dominance fights and sparring matches was frequent enough to cast doubt on Reed's statement (in Schaffer, 1968) that, in goats, only the subordinate rears up.

"Sparring" matches are comprised of the same patterns as are dominance fights but the action is not so intense and extensive courtship was never seen to follow. On September 15 a sparring match was observed in which 4 Mediums stood in a circle with another Medium in the middle. The one in the middle rear-clashed and head wrestled in turn with each of those surrounding him. This is very similar to the "huddle" described by Geist (1971) in mountain sheep and behaviour types described for gazelles (Walther, 1964a & c, 1968) and ibex (Nievergelt, 1967).

Clash behaviour appears to cause little physical damage as goats are well endowed with physical defences. Schaffer (1968) showed that the large muscle masses of *Capra* which insert on the occiput and mastoid could counteract the enormous lateral torque developed in a clash. Geist (1971) presents skin thickness measurements for domestic male goats showing that they are well armoured frontally. Morphological adaptations to withstand heavy concussion are evident in the expanded frontal sinuses containing bony cross-struts which probably function to reduce brain compression and in the downbending of the braincase which probably functions in the prevention of "whiplash" brain injuries (Reed and Schaffer, 1966).

Some minor physical damages resultant from fighting were noted. A few males were observed to have their occipital regions superficially mutilated and bleeding. Many more males exhibited hairless-

ness in this area where old wounds had healed. Most of the larger males had ears that were mutilated to some extent. In the lesser extreme, this consisted of mere deformation (Fig. 8) while in the greater extreme, up to one-half of the ear was missing entirely. This is presumed to result from crushing the ears between the horns during a clash.

c. The abdomen lift

The "abdomen lift" was observed 11 times during playful agonistic interactions between kids. It consists of placing the head under the opponent's abdomen and lifting. The motion was not a "hook" or jab but rather a gentle but forceful lift. It appears to be similar to the "clinch" observed in dairy cows by Schein and Fohrman (1955) and the inguinal nuzzling seen in the sexual behaviour of waterbuck (Spinage, 1969). Adult tahr (Schaller, in press) and Barbary sheep (Haas, 1959) have been observed to utilize this pattern but in each case the purpose was to jab the opponent in the abdomen. This probably represents a hold-over from the front to rear parallel side-hooking form of combat seen in short-horned rupicaprids which are considered to be ancestral to the caprids on the basis of paleontological evidence (Thenius and Hofer, 1960). It cannot at present be decided if the abdomen lift of young goats is homologous to the fighting behaviour of rupicaprids or if it is closely associated with "udder bunting" during suckling.

d. Threat and appeasement behaviour

In the goat, one can differentiate 7 possible types of threat. These are the rush-threat, the horn-threat, the broad-side present threat, horning, pawing, staring and the urination-olfactory threat.

These will be treated in order.

The rush-threat of the goat has been described earlier. It was noted that this pattern functions both as a threat and as a prelude to the butt. The rush-threat is probably present in the behaviour of all ungulates.

The "horn-threat" of the goat is performed by conspicuously directing the horns toward an opponent. This pattern may be termed a "weapon threat" under Geist's (1965) classification of threat behaviours. The intensity of the display appears to be approximately proportional to the degree of dynamism exhibited. At low intensity, the horn-threat consists of simply lowering the head, tucking in the chin and holding the horns towards the receiver. At higher intensity it consists of a violent upward sweep of the horns.

As described earlier, horn-threats are often presented by the female to the courting male. In this context, however, it appears that the pattern may have a dual nature; either agonistic or sexual. If agonistic, the horn-threat consists of a violent sweep of the head. If sexual it consists of simply pointing the horns at the male, closing the eyes, and slowly shaking the head. This suggests nothing so much as "coyness".

The broadside display described earlier probably represents a "present threat" in Geist's (1965) terminology or a "display threat" in Lent's (1966). There were no definitive indications that this signifies threat, although it appears likely in view of the context in which it was observed and the many parallel interpretations in ruminant species; e.g., the bushbuck tribe (Walther, 1965b), cattle

(Schloeth, 1956), mountain goats (Geist, 1965), several antelope species (Walther, 1958, 1961b), chamois (Walther, 1961a), markhor (Walther, 1961a; Roberts, 1969), wildebeest (Estes, 1969), and tahr (Schaller, in press).

The state of display threats in the Capridae appears to be one of evolutionary transition. Geist (1966, 1971) has shown that the manner of display is correlated with the distribution of display organs. The evolutionary history of the Capridae has been characterized by a shift in this distribution of display organs, i.e., increase in horn size and reduction in body hair. Likewise, display threats have shifted from predominantly broadside threats to horn threats. The Nilgiri tahr a primitive caprid which displays broadside (Schaller, in press) has small horns and a large ruff. Highly evolved caprids, such as the ibex and the mountain sheep, exhibit no broadside displays (Walther, 1961a; Geist, 1971) and have no display hair. Both species have developed huge horns, however, which are likely to have display value. Forms representing an intermediate stage of evolution, such as the Barbary sheep, the goat and the markhor have horns of intermediate size and beards reduced to some extent. Broadside and horn displays are present to a variable degree. The broadside display of the goat, for example, has characteristics of the horn present of mountain sheep as described by Geist (1968a, 1971).

Goats of both sexes are often seen thrashing bushes, dead limbs, or other tough springy materials with their horns. In other species, this is commonly termed "horning" or "horn-thrashing". Horning was seen in what appeared to be purely comfort behaviour contexts and, among

males, in contexts bearing agonistic overtones. The latter usually occurred around a particular fallen tree upon which as many as 5 males would horn-thrash simultaneously. No fighting was associated although on one occasion homosexual behaviour was observed between two males that had been clash-fighting two days previously. If this horning does constitute threat behaviour, then it is of a very diffuse nature. In this context, the suggestion of redirected aggression does not seem appropriate. Alternatively, Leuthold (1966) suggests that horning may represent vacuum fighting behaviour.

Horn-thrashing is present in many bovid species. The behaviour is termed "Bodenhornen" by Schloeth (1961) and "Bodenforkeln" by Walther (1964b). It is conspicuous in species of the Alcelaphini (Estes, 1969), in cattle (Schloeth, 1961) and in mountain goats (Geist, 1965). In impala, Schenkel (1966) considers that "ground-horning" is a threat-display whereas "bush-horning" has no display value. Estes (1969) draws the same conclusion for wildebeest.

There was no evidence that the pawing observed during clash fights had any social significance. The only other context in which pawing was observed was immediately before lying down. This behaviour is performed very cursorily by both sexes.

Pawing is prominent in a threat context in the Bovidae occurring in the following tribes: Bovini, Caprini, Hippotragini, Antilopini, Alcelapheni (Walther, 1964a). Pawing is rare in bighorn sheep (Geist, 1971) but common in Marco Polo sheep (Walther, 1961a). In wildebeest (Estes, 1969) and impala (Schenkel, 1966) it constitutes a threat only when the actor is kneeling. Walther (1964a) feels that in the Alcelaphini, the behaviour is derived from the preparation of a rolling

place. Schloeth (1961) has suggested the same for cattle. In the Antilopini, Walther (1964a) thinks it is derived from the preparation of a dunging spot or from interdigital gland marking. Estes (1969) suggests that pawing may be ritualized from inhibited approach. In goats, it may be that the behaviour represents an evolutionary vestige.

The stare threat has been described in the section dealing with sexual behaviour. This threat is also functional when a highly dominant male displaces a subordinate from a bedding spot.

It is probable that the smell imparted to males by urination upon themselves may serve as an olfactory threat. This will be discussed in a later section.

No ritualized appeasement posture was observed such as is seen in the mouflon (Pfeffer, 1967), the wildebeest (Estes, 1969), or Grant's gazelle (Walther, 1965a), however, the assumption of female behaviour on the part of the loser of a dominance fight may indicate appeasement. Such behaviour would inhibit aggression by playing on the male's disinclination to direct agonistic acts to a female by keeping the rear-end to the dominant thereby pointing the horns away from him, and by channeling the dominant's aggressive behaviour into sexual behaviour. The same system of appeasement has been described for mountain sheep (Geist, 1968a) and many primate species (reviewed in Wickler, 1967).

Another action signalling subordination is the manner in which the satellite courting male looks away from the dominant and the courting male stares away from the female. This, of course, is the antithesis of the stare threat and would certainly indicate non-aggression if not appeasement.

III. ANALYSIS AND DISCUSSION OF BEHAVIOURAL DATA

1. Analytical Procedures

The method of analysis is derived from Altmann's (1968) study of the social behaviour of rhesus monkeys. The analysis of data of this type is complicated by the fact that the relative number of patterns is not a variable independent of population structure. For example, if the number of sexual patterns displayed by Larges was 5 times the number displayed by Hornlesses, then it would at first appear that, in general terms, Large males are more sexually active than are Hornless males. However, if Large males are present in the population in 5 times the number of Hornless males, such a conclusion must be abandoned and it must be expected that both exhibit about the same level of sexual activity. To overcome the effect of population structure, the data were transformed using a parameter termed "availability". All terms in the following discussion were taken from Altmann (1968) although the derivation is often different.

Availability may be thought of as the mean number of each size-sex class in a group weighted by the minutes of observation as follows:

$$A_i = \frac{\sum_{j=1}^Q (N_i)(T_j)}{\sum_{j=1}^Q T_j}$$

where A_i = the availability of the i^{th} size-sex class, Q = the number of groups, N_i = the number of members of the i^{th} size-sex class in the j^{th} group, and T_j = the number of minutes the j^{th} group was observed.

Availability then, is a relative index of the number of members of each size-sex class in view and represents the relative presence of interaction partners.

Utilizing this parameter, the number of dyadic interactions may be transformed into a constant which is independent of population structure. This constant is termed the "interaction constant" and is as follows:

$$C_{i,j} = \frac{I_{i,j}}{(A_i)(A_j)(M_{x,y})}$$

where $C_{i,j}$ = the interaction constant for patterns sent by the i^{th} size-sex class to the j^{th} class and is one element in the 6×6 $C_{i,j}$ matrix (Table II), $I_{i,j}$ = the number of patterns observed to be initiated by the i^{th} class and received by the j^{th} class, A_i = the availability of the receiver in the j^{th} class, and $M_{x,y}$ = the total number of patterns observed between all size-sex classes.

The interaction constants are somewhat ponderous and not easily comparable to each other. Interaction constants are therefore presented in terms of probability and termed "interaction indices" as follows:

$$P_{i,j} = \frac{C_{i,j}}{C}$$

where $P_{i,j}$ = the interaction index for patterns sent by the i^{th} class to the j^{th} class, and is one element in the $P_{i,j}$ matrix (Table II), $C_{i,j}$ = the interaction constant for patterns directed by the i^{th} class to the j^{th} class, and C = the summation of the 36 cells of the $C_{i,j}$ matrix.

As Altmann (1968) points out, the $C_{i,j}$ matrix has a bias along the main diagonal; that is, where $i=j$. This is because in such an intra-class interaction, there are N_i possible actors and N_i-1 possible receivers. Since many of the groups observed were small, such a bias would have a profound effect on the results.

Hence, an "intra-class availability" was calculated in the same manner as A_i but utilizing N_i-1 instead of N_i as follows:

$$B_i = \frac{\sum_{j=1}^Q (N_i-1)(T_j)}{\sum_{j=1}^Q T_j} = A_i - 1$$

where B_i = intra-class availability, Q = the number of groups, N_i = the number of members of the i^{th} size-sex class, T_j = the number of minutes the j^{th} group was observed and A_i = the inter-class availability of the i^{th} size-sex class. This value is then utilized for availability of the receiver in intra-class calculations of the interaction constant as follows:

$$C_{i,i} = \frac{I_{i,i}}{(A_i)(A_i-1)(M_{x,y})}$$

where $C_{i,i}$ = the intra-class interaction constant, $I_{i,i}$ = the number of patterns observed to be initiated by members of the i^{th} class, and likewise, received by the i^{th} size-sex class, A_i = the intra-class availability of the i^{th} class, and $M_{x,y}$ = the total number of patterns observed to occur between all size-sex classes. $P_{i,i}$ may be calculated from $C_{i,i}$ in the same way in which $P_{i,j}$ is calculated from $C_{i,j}$.

Interaction index matrices may be calculated for each individual behaviour pattern type, associations of patterns and the totality of patterns observed.

The sum of the columns of the interaction index matrix represents the probability that a member of each size-sex class will receive a pattern from all classes. These marginal totals are termed "reception indices". The sum of the rows of the interaction index matrix represents the probability that a member of each size-sex class will initiate a pattern towards all classes. These marginal totals are termed "action indices".

The "expected number of patterns" may be thought of as the number of patterns likely to be observed if interactions occurred at random. This value may be obtained by multiplying the product of the proportions of the total availability of the initiator and receiver by the number of patterns observed as follows:

$$E_{i,j} = \frac{A_i}{A} \frac{A_j}{A} M_{x,y}$$

where $E_{i,j}$ = the expected number of patterns directed by members of the i^{th} class towards members of the j^{th} size-sex class, A_i = the availability of the i^{th} class of actors, A_j = the availability of the j^{th} class of receivers, A = the sum of availabilities of all 6 size-sex classes, and $M_{x,y}$ = the total number of patterns observed.

A value, termed the "relative deviation", was calculated as an index of how far the number of patterns actually observed varies from the number that is expected if interactions were to occur at random.

$$R_{i,j} = \frac{O_{i,j} - E_{i,j}}{E_{i,j}}$$

where $R_{i,j}$ = the relative deviation from expectation of the number of patterns sent by the i^{th} class and received by the j^{th} class, $O_{i,j}$ = the observed number of patterns initiated by the i^{th} class and received by the j^{th} class, and $E_{i,j}$ = the expected number of patterns sent by the i^{th} class to the j^{th} class. This index varies from -1 to $+\infty$.

2. Analysis of Total Behaviour

General behavioural trends evident from the totality of behavioural patterns recorded will be examined first. Only the most general conclusions may be drawn from this treatment since behavioural syndromes of different social direction and intensity are represented as an aggregate. More detailed treatment of behavioural types will follow.

A chi-square test was employed to determine if the social behaviour of the goat is a stochastic system. Comparison of the observed and expected numbers of patterns yields a χ^2 value of 6999.125 with 25 degrees of freedom indicating decisively that interaction is not at random - that is, attractions and repulsions do exist in choice of interaction partners. The magnitude of these attractions and repulsions is evident in Figure 11 which represents relative deviation from expectation. The greatest attractions in goat society are, in general, males for females and males for their own size-sex class. Essentially the same has been described for cattle (Schloeth, 1961) and mountain sheep (Geist, 1968b). The greatest disinclination to

initiate social interaction are evident in males for size-sex classes larger than themselves and in kids, females and Hornlesses for almost all classes.

The sociogram of total goat behaviour (Fig. 12) constitutes a general model for the totality of social behaviour in the Saturna Island herd during the months of the study. The high interaction index for Small x Small interaction is a result of chance observations of several extended intra-class clash fights which are magnified by the low availability of the Small male class. The sociogram shows that females and Smalls are preferred as receivers while Larges are the most likely to deliver a pattern. It also shows that Hornless males are, to some extent, social outcasts; i.e., they receive and initiate very few patterns. Subsequent analysis will isolate these and other trends.

3. Sexual Behaviour

Figure 13 is a sociogram representing total sexual behaviour and offers a generalized overview of all sexual behaviour by presenting interaction, action and reception indices and the number of patterns observed. The particular patterns represented in this sociogram are the following: mount, gobble, gobble with front kick, front kick, sexual approach, perineum sniff, and sexual chase. It is evident from this figure that very real differences exist in the sexual behaviour of the male size-sex classes.

a. Male size-sex class variability in level of sexual activity

Figure 15 shows that the number of sexual patterns directed by

a male towards a female is positively related to the size of that male's horns. This might be interpreted in one of three ways: 1) larger males may engage in more sexual interactions than smaller males, 2) they may deliver substantially more sexual patterns per sexual interaction, or 3) both situations may occur. Figure 14 verifies the first supposition by presenting the ratio of the observed number of sexual interactions shown by each male class towards females to the expected number. The relation between horn size and sexual activity is striking. Figure 15 verifies the validity of the second supposition by representing the average number of sexual patterns per sexual interaction delivered by males of each class. Only those sexual interactions that showed definite start and end points are included. Figure 15 indicates that the values for Hornlesses and Smalls are essentially the same whereas the much higher values for Mediums and Larges are also approximately equal. The general conclusion drawn from Figures 14 and 15 is, then, that the larger the male's horns, the greater is his sexual activity towards females.

When kids are the subject of the male's sexual attention, the situation is essentially the same. With reference to kids as sexual objects, Figure 13 shows the same correlation between horn size and sexual activity with the exception of the Smalls which show a disinclination in choosing kids as sexual receivers. Figure 14 shows a surprisingly high value for Hornlesses indicating that they initiate many sexual interactions towards kids. In Figure 15, the curve representing kids as sexual receivers is almost identical to that for females with the exception of the value for Smalls which was based on a sample of only 5 interactions and should, therefore, be disregarded.

The general conclusion, then, is that regardless of the receiver type, the level of sexual activity is proportional to horn size with the exceptions that Smalls have a disinclination to interact sexually with kids and that Hornlesses initiate numerous short sexual interactions with kids.

b. Male size-sex class variability in selection of sexual object

The sociogram (Fig. 13) indicates that kid sexual activity is almost entirely intra-class. The ratio of the heterosexual receptivity indices of female:kid ($0.55:0.27 = 2.04$) indicates that males in general prefer females as sexual objects over kids by a factor of more than 2 times.

However, it was my impression that males rarely, if ever, directed sexual patterns to male kids. This was, however, not verified due to the difficulty of determining the sex of kids at great distance. If adult males do exclude male kids as sexual partners, then the above preference ratio of female:kid underestimates the kid as an object of sexual attention. Discrimination by the goats themselves probably presents no difficulty since Saturna Island males develop the characteristic male musky smell at 3 to 4 weeks of age. This conclusion is based on personal observations of a captured kid and Mr. J.M. Campbell's observations of Wodin. Peglar (1929), however, states that the smell is not apparent until 6 months of age. This probably does not apply to Saturna Island goats.

Given the assumption, then, that males select only the female kids as sexual objects and that the sex ratio of kids is 50:50 (Rudge,

1969, Williams and Rudge, 1969) a recalculation of the interaction index matrix is possible by partitioning the availability of kids into 2 equal parts and generating a 7 x 7 matrix. Such a manipulation results in a ratio of heterosexual receptivity indices of adult females: female kid of 1.48; that is, males prefer adult females over female kids by a factor of only 1.5 times. Figure 16 represents this value separated into size-sex classes of male actors and indicates that all horned males exhibit approximately the same preference ratio for adult females over female kids whereas Hornlesses prefer female kids almost twice as much as they do adult females. This analysis, of course, would only apply during the months in which the study was conducted when most kids were between 6 and 10 months of age.

This surprisingly high use of kids as sexual objects is understandable with reference to the great sexual precocity of goats. Peglar (1929) cites the case of an unweaned female 3 months of age being successfully bred. Yocum (1967) mentions a 5-month-old female carrying a fetus. Geist (pers. comm., 1970) shot a female kid on Saturna Island which was less than 30 pounds and carried twin fetuses. Rudge (1969) states that both the male and female feral goats of the New Zealand mainland are fertile at 6 months, however, Williams and Rudge (1969) write that on the small islands off New Zealand, sexual maturity is not reached until one year of age.

Such precocity is undoubtedly the result of artificial selection for low breeding age since few such signs of early maturity are shown in wild caprids. The female minimum breeding age of ibex is either 2 1/2 years (Couturier, 1961) or 1 1/2 years (Nievergelt,

1967; Heptner, 1961), of markhor 3 years (Heptner, 1961); of bighorn sheep 2 1/2 to 3 years (Smith, 1954), or 1 1/2 years under exceptional feeding conditions (Geist, 1971); of the Rocky Mountain goat 2 1/2 years (Lentfer, 1955), of chamois (Couturier, 1961) and of Himalayan tahr 1 1/2 years (Anderson and Henderson, 1961). In contrast, domestic ewes first breed at 7 months on the average (McKenzie and Terrill, 1937).

Since males appear to prefer adult females over female kids only slightly, the question is whether males treat adult females and kids in a similar manner. Such a comparison may be made by compiling the number of several pattern types offered by members of each male class to members of female and kid classes and then calculating the correlation coefficient for each combination. These values are shown in Table III and indicate the Larges, Mediums, and Hornlesses treat females and kids almost identically. Smalls, on the other hand, treat females and kids quite differently and treat both females and kids differently than do other males. Geist (1968b, 1971) has shown that mountain sheep rams treat ewes and lambs in a similar manner.

c. Male size-sex variability in the relationship of courtship to copulatory behaviour

The totality of sexual behaviour may be subdivided into mount patterns and courtship patterns. Courtship patterns are defined as all sexual patterns other than the mount. Figure 17 represents the ratios of the number of mount to the number of courtship patterns delivered by each male size-sex class. Hornlesses exhibit a great tendency to mount kids with little prior courtship. Kids showed a

very low intra-class mount to courtship ratio of only 2.1; that is, kids 6 to 10 months of age exhibit about twice as many mounts as courtship patterns.

d. Maturation of male sexual behaviour

Since the horns of bovids continue growth throughout the life of the animal, the classes of horned males represent a gradation not only in size, but also in age. Variations in sexual behaviour between the size-sex classes, may be largely a function of maturation. Maturation manifests itself in males of greater age and size becoming increasingly sexually active (Fig. 14) and being likely to direct longer courtship to females before mounting (Figs. 15 and 17).

In practice, it is difficult to differentiate between the internal aspects of behavioural ontogeny, the external aspects imposed by the social environment, and the coaction of the two. Some segregation of causation seems possible in the inverse relationship between male horn-size and their tendency to mount females with little prior courtship. An ontological parameter may be the late development of courtship behaviour observed in kids. From the onset of the study, kids spontaneously mounted one another very frequently, however, the first courtship pattern by a kid was not observed until September 6 and only 16 times thereafter. It seems likely, then, that this aspect of the development of courtship behaviour continues long after a male reaches sexual maturity. This tendency has been noted in mountain sheep (Geist, 1968b), who showed it not only in the courtship behaviour of males, but also in the interactions of equal sized males

of different horn size classes.

At the present state of knowledge, it might be argued that immature sexual behaviour would be very adaptive to individuals of low dominance since it involves many attempts at a rapid copulation. Confirmation of this hypothesis would, however, require further research involving certain differentiation between mounts and successful copulations.

e. Female response to male courtship

The most obvious negative response of a female to sexual behaviour by the male is the exhibition of agonistic patterns. The ratio of total sexual interactions to those in which the female responded agonistically is shown in Fig. 18 separated into the size-sex class of the male receiver. Smalls received by far the most agonistic responses and Larges by far the fewest. The values for Mediums and Hornlesses are intermediate and approximately equal.

The studies of Lindsay and Robinson (1961b) have shown that in domestic sheep, active mate-seeking and courtship by the female is very important in breeding behaviour. This is probably also true in goats as female courtship plays an important role in determining which males will breed. Female courtship consists of mounting the male and rubbing on his neck, chest and throat. Only two instances of a female mounting a male were observed and in both occurrences the receiver was a Large. Females also prefer larger males as recipients of rubbing (Table IV). Table V represents the correlation coefficients of all female to male behaviour calculated as described earlier. These

values indicate that, in general, females treat Hornless, Small and Medium males almost identically and Large males quite differently. This difference appears to be due to the inextricable qualities of the Large's high dominance and sexual acceptability. Female mountain sheep also preferentially court larger males (Geist, 1968b, 1971).

f. Adaptive value of the sexual system

Sexual interaction occurs in two very different contexts as described earlier. The first is the formalized courtship behaviour entailing a rigid maintenance of all the conventions of goat society. The second is the gang-bang in which all conventions are discarded.

Formalized courtship is a tightly controlled system based on the intermeshing conventions of male competition and female selection. Dominant males guard their females and attempt to prevent subdominants from courting and mounting. The result is that only individuals of relatively large body and horn size display extensive courtship. Females take an active role in selecting mates by displaying agonistic patterns to smaller suitors and courting larger ones. Formalized courtship is, then, an integrated and consistent system that appears, at least, to allow males of larger size to copulate in disproportion to their presence in the population.

Associated with such a precise and predictable system, it is surprising to find gang-bangs where dominance breaks down. All males behave agonistically like dominants and sexually like subordinates. Larges are often butted by subordinate males while mounting the female. Few courtship patterns are delivered. The female herself accepts all males. There is no indication that any class is more suc-

cessful in breeding than any other.

That two such antithetical systems should coexist is puzzling. If one is adaptive, it is difficult to see how the other could also be. One explanation is that gang-bangs are simply a behavioural change associated with high density such as has been studied extensively in many animals (reviewed in Watson and Moss, 1969).

4. Agonistic Behaviour

Agonistic behaviour was described in a previous section in terms of two behavioural associations, the rush and clash associations. This section deals with quantitative differences between these two syndromes in terms of the class of the initiator and his selection of the receiver. Figure 19 shows that, among males, most rush association patterns were directed to males of size-sex classes smaller than the initiator, while the majority of clash association patterns were intra-class in nature. This difference in social directionality is observable in greater detail in the sociograms for the rush and clash associations (Figs. 19 and 20).

The sociogram of rush association behaviour (Fig. 19) shows a number of interesting and predictable relationships. Smalls receive by far the most rush patterns. Smalls are making the transition from the safe and relatively socially inactive life of a kid to the active and unprotected life of an adult male. They possess a low dominance status and lack refinement in their social activity which may result in their apparent persecution.

Females, on the other hand, receive very few rush patterns. This is necessary in the sexual context since aggressive behaviour

would result in female withdrawal rather than the desired approach. This tendency is quite evident in species in which the male breeds in a small territory, such as the Uganda kob (Buechner and Schloeth, 1965) and other herd-living bovids such as the mountain sheep (Geist, 1971). Males are also quite tolerant of kids since kids were seen frolicking on and around resting males. Females, however, tend to rush and mercilessly butt kids other than their own. No immediate objective appeared to be derived from this behaviour.

Larges deliver by far the most rush patterns as a result of their high dominance status and extensive sexual guarding. Hornlesses and kids deliver the fewest due to their low dominance and reticence to interact socially.

The sociogram of the clash association is treated as bidirectional in nature since definite initiators and receivers could not be determined for the "head wrestle" and "normal clash" patterns. Figure 20, then, does not imply initiation or reception but simply interaction. The inverse relationship between male horn-size and propensity to clash is apparent as in the general restriction to intra-class interaction. The departure from this rule in Large with Medium interaction index results from interactions involving a known individual. He was a highly aggressive Medium with horns almost of sufficient size to warrant calling him a Large. The high value of Medium with Hornless interaction results from behavioural similarities between the two classes which will be discussed later.

The tendency for formalized fighting to occur primarily between individuals of equal size and/or social rank has been reported in

several bovid species; e.g., dairy cows (Schein and Fohrman, 1955), wild cattle (Schloeth, 1961); ibex (Nievergelt, 1967), mountain sheep (Geist, 1966, 1971) and Grant's and Thompson's gazelles (Estes, 1967).

Rush association patterns are initiated for the purpose of socially altering the environment so as to realize a concrete and immediate gain external to the interaction itself. Such a gain may take the form of acquisition of a desirable feeding or resting spot, a cessation of bothersome social contact, or the prevention of breeding by another group member. The behaviour type characterized as rush association behaviour is the prerogative almost solely of the dominant in goats as it probably is in all ruminants (Geist, 1971). In goats this results in the observed social direction of rush association patterns since dominance in males appears to be correlated with large body and horn size.

In contrast, interpretation of clash association behaviour never revealed the obtainment of such an immediate and concrete advantage. Exhibition of male sexual behaviour as an expression of dominance and of female sexual behaviour as a signal of subordination occurred only near the end of dominance fights which indicates the dominant-subordinate differentiation occurs during the dominance fight itself. Dominance fights certainly function in generating the dominant-subordinate relationship.

Sparring matches are less intense, involve little sexual activity and have often a playful aspect to them. This correlates with the greater propensity for smaller, younger males to clash fight than larger ones (Fig. 20). Goats also seem to have a drive to hit their heads against something. Wodin, in the absence of social partners, was seen

to butt inanimate objects. Similar behaviour has been described in desert bighorns and termed "clonking" (Welles and Welles, 1961). Frequent sparring would function in developing fighting ability, in reaffirming the existing rank order and in providing a relatively safe mechanism whereby an individual might correlate the behavioural and morphological characteristics of his opponent with the punishment received in the fight (Schaller, 1968).

Agonistic differentiation, then, results in a highly specialized system of agonistic control that creates and maintains a rigid and highly efficient unidirectional hierarchy. In males, the position in the hierarchy is correlated with horn size. Between individuals of decidedly different horn size, the rank order would exist by inspection alone based on experience gained in sparring matches. Between individuals of equal horn size, dominance appears to be determined by a dominance fight and maintained through individual recognition or the exhibition of very subtle social signals presumably emergent from the dominance fight.

5. Flehmen

It was observed that 94.5% of female induced Flehmens were followed by a complete cessation of further sexual patterns by the male. This would indicate that, in goats, Flehmen itself, or the stimulus invoking it, is a very efficient means of causing a cessation of sexual activity and, presumably, of establishing the non-estrous condition.

Little is known of the physiology or function of the Flehmen. All species exhibiting Flehmen have a well developed vomeronasal organ (Ewer, 1968). This is a tubular sac which opens into the oral cavity

by way of the nasopalatine canal. The sac itself is lined with epithelial tissue resembling olfactory epithelium which, by analogy, has the same function. The vomeronasal organ connects with the accessory olfactory bulb and the hypothalamus by nervous connections separate but parallel to the main olfactory apparatus (Winans and Scalia, 1970). Presumably, Flehmen opens the nasopalatine canal allowing chemical substances to enter the vomeronasal sac which sends impulses to the hypothalamus. These impulses are olfactory in nature but separate from conventional olfactory signals (Winans and Scalia, 1970). In a variety of artiodactyls, Flehmen occurs as a response to not only urine but any volatile substance such as ether or valerian (Schneider, 1930; Banks, 1964).

In the goat, Flehmen probably is not a conscious act of opening the nasopalatine canal but more likely a reflex resulting directly from some property of the chemical substance. This is indicated by the manner that the head is snapped into position and by the maintenance of the Flehmen even when the animal is alarmed during the course of the pattern.

Flehmen undoubtedly serves to aid in the analysis of urine in all species in which it is observed. However, interspecific comparisons show little uniformity. For example, in antelope, as in the goat, Flehmen is usually followed by a cessation in male courtship (Walther, 1958), however, in the Defassa waterbuck, Flehmen is almost always followed by a mount (Spinage, 1969). In mountain sheep, the course of courtship is not altered significantly by the occurrence of Flehmen if the female urination is performed during the courtship itself. If,

however, the urination is performed prior to the exhibition of the first courtship pattern, the subsequent courtship is curtailed (Geist, 1971).

In the goat, it appears likely that Flehmen is a consummatory act in itself and not a component of a chain of behaviour that leads to copulation. I would hypothesize that much courtship behaviour of the goat is in actuality urine-soliciting behaviour which Schenkel (1966) terms "Harnforden". Such behaviour would be of considerable importance in a seasonally polyestrous animal such as the goat since it would provide rewards for male sexual attention throughout the extended breeding season and yet would reduce harassment of the female.

6. Urine-marking

Figure 21 shows the larger males spray themselves with urine more often than do smaller ones. This relationship between size and/or rank and marking behaviour has been noted in many mammals (reviewed in Ralls, 1971). In goats, this probably results in a stronger urine scent being associated with larger and more dominant individuals.

There is no direct observational evidence as to the motivation, significance, or effects of urine-marking in goats since this pattern did not appear in close temporal association with any particular pattern type. In many other mammals, however, the relationship of androgen level to scent marking and the association of marking behaviour with aggressive activities indicate that scent marking has primarily agonistic significance. This is also undoubtedly the case in goats where differential urine-marking would result in an olfactory rank symbol with concomitant implications of threat and sexual acceptability.

Urine-marking may partially explain the retention of the beard in the male goat. While the beard evolved as an organ of broadside threat enhancement in the goat's ancestors, this display has been much reduced in the goat. The beard's continued existence may, in part, be due to its use as a receptacle for the urine smell.

7. Social Position of Hornless Males

It is obvious from previous discussion that the behaviour of Hornlesses differs significantly from that of other classes. The data are too limited to determine exactly what role Hornlesses play in goat society. In general, Hornlesses are retiring from social interaction; initiating as well as receiving few patterns (Fig. 14). In terms of mode of interaction, correlation analysis (Table VI) shows Hornlesses to resemble Mediums very closely.

Agonistically, Hornlesses hold a dominance rank somewhere in between that of Smalls and Mediums, but the level of agonistic activity is lower than that of any other male class.

Sexually, Hornlesses exhibit quite abnormal behaviour. The total amount of sexual activity is the lowest of all male classes. Kids are preferred as sexual objects over females. Females appear to prefer Hornlesses over Smalls as sexual partners. The low level of sexual activity may be coupled with impaired fertility and/or hormonal upsets associated with the polled condition. The preference for kids as sexual partners may be a result of apparent avoidance of agonistic encounters by Hornlesses. Since females are often guarded by other males, Hornlesses vent sexual urges on unguarded objects,

that is, kids. Geist (1971) interprets this as the motivation behind the "raping parties" of mountain sheep where subordinate males, frustrated in their attempts to copulate with the female, mount young males.

In general, Hornlesses are inactive socially and appear to be the least successful breeding component of the adult population.

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TABLE I. Number of individuals in each size-sex class present in the population per 100 adult females. Determined as the average of the proportions observed in 178 groups.

K = Kid, H = Hornless, S = Small, M = Medium, L = Large

K	H	S	M	L	Adult Males
54	11	13	58	32	114

TABLE II. Matrix of interaction constants ($C_{i,j}$), interaction indices ($P_{i,j}$), action indices, and reception indices for total behaviour. Upper figure in each cell is the interaction constant while the parenthetical figure is the interaction index.

INITIATOR	RECIPIENT						Action Index
	Kid	Female	Hornless	Small	Medium	Large	
	Kid	.061 (.030)	.014 (.007)	.000 (.000)	.000 (.000)	.000 (.000)	.036
	Female	.018 (.009)	.009 (.004)	.007 (.003)	.019 (.009)	.009 (.004)	.012 (.006)
	Hornless	.051 (.025)	.041 (.020)	.003 (.002)	.000 (.000)	.003 (.002)	.000 (.000)
	Small	.032 (.016)	.073 (.035)	.010 (.005)	.559 (.271)	.003 (.002)	.002 (.001)
	Medium	.060 (.029)	.130 (.063)	.021 (.010)	.042 (.020)	.078 (.038)	.007 (.003)
	Large	.096 (.046)	.240 (.116)	.033 (.016)	.234 (.113)	.111 (.054)	.087 (.042)
Reception Index	.154	.245	.036	.414	.099	.052	

TABLE III. Correlation coefficients showing qualitative similarities in the sexual behaviour directed by each male class to adult females. Calculated from the number of sexual patterns directed by each male class to adult females.
♀ = adult female, H = Hornless, S = Small, M = Medium, L = Large.

[illegible]

TABLE IV. Interaction indices and number of occurrences of adult females rubbing on males. H = Hornless, S = Small, M = Medium, L = Large

	H	S	M	L
Interaction index	.000	.000	.042	.266
Number of Patterns	0	0	4	15

TABLE V. Correlation coefficients showing qualitative similarities in the behaviour directed by adult females to each male class. Calculated from all pattern types. ♀ = adult females, H = Hornless, S = Small, M = Medium, L = Large.

	$\begin{array}{c} H \\ \uparrow \\ \sigma \end{array}$	$\begin{array}{c} S \\ \uparrow \\ \sigma \end{array}$	$\begin{array}{c} M \\ \uparrow \\ \sigma \end{array}$	$\begin{array}{c} L \\ \uparrow \\ \sigma \end{array}$
$\begin{array}{c} \sigma \\ \rightarrow H \end{array}$	1.0000	.9577	.9239	.6306
$\begin{array}{c} \sigma \\ \rightarrow S \end{array}$		1.0000	.9731	.6425
$\begin{array}{c} \sigma \\ \rightarrow M \end{array}$			1.0000	.6369
$\begin{array}{c} \sigma \\ \rightarrow L \end{array}$				1.0000

TABLE VI. Correlation coefficients showing qualitative similarities in the behaviour of each male class to all size-sex classes. Calculated from all pattern types. H = Hornless, S = Small, M = Medium, L = Large.

	H	S	M	L
H	1.0000	.8713	.9953	.9239
S		1.0000	.8082	.6656
M			1.0000	.9431
L				1.0000

Fig. 1 Saturna Island goat habitat. Looking from the south side of prominent ridge to sea-bench. Note the goat trails on the open slope.

Fig. 2 Saturna Island goat habitat. Looking from sea-bench pastures to slopes of prominent ridge. Domestic sheep and horses grazing in foreground. Goats spend most of their time on the open slopes.

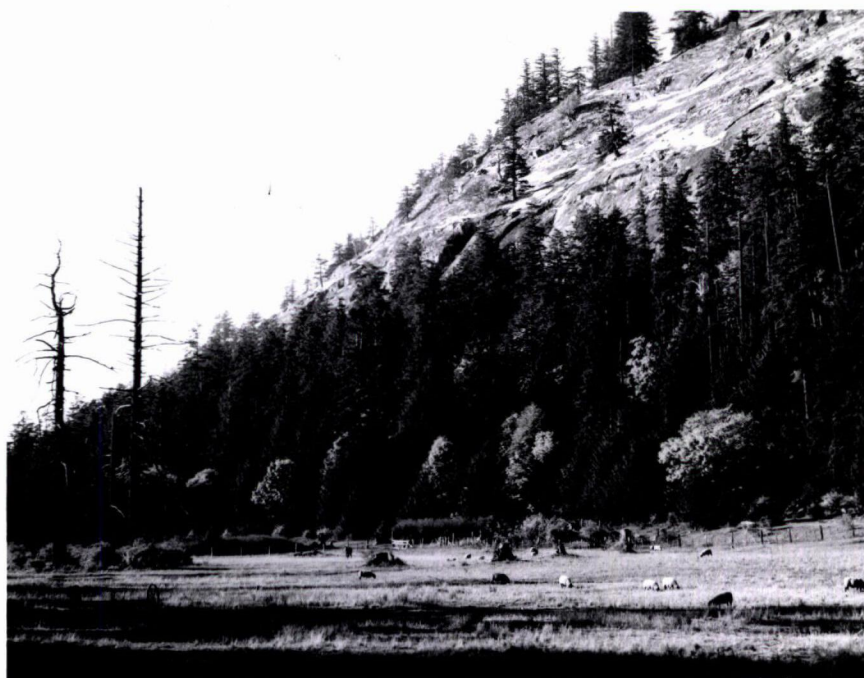


Fig. 3 Average size of groups observed during 2 week periods. Thin vertical lines represent standard deviation. Broken line following October 31 indicates the large groups of unknown size observed in early November.

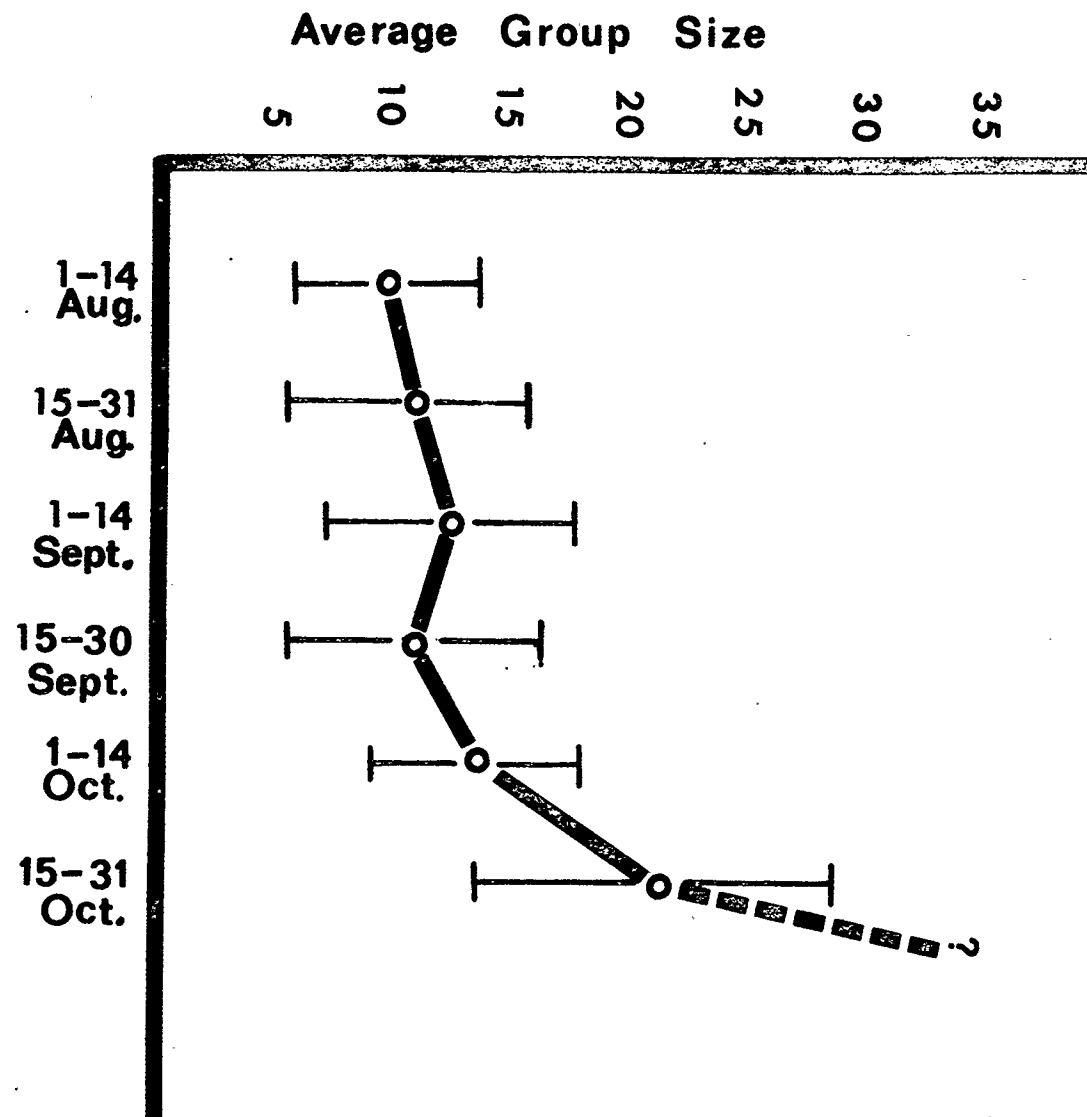


Fig. 4 Frequency of group sizes observed.

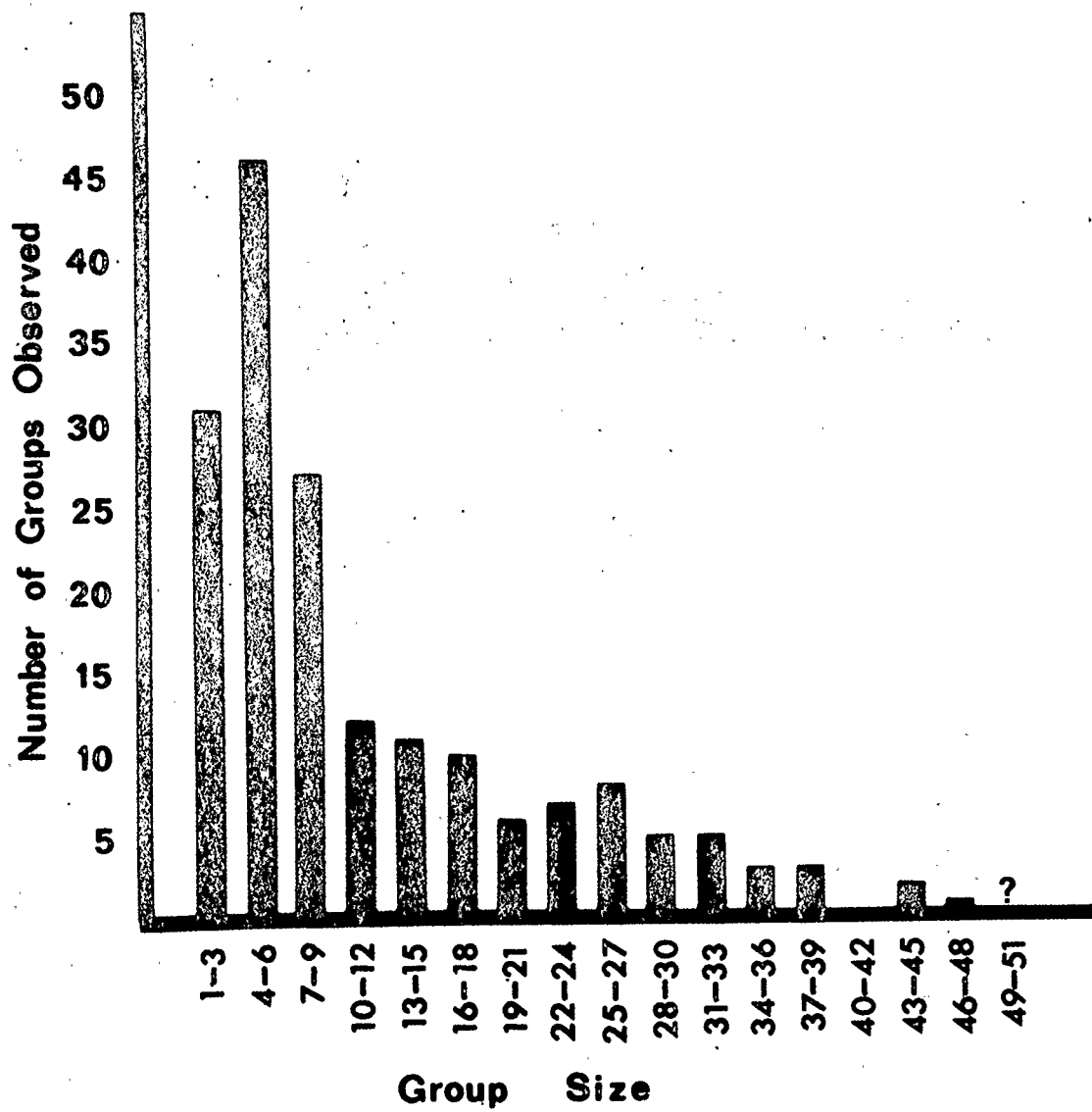


Fig. 5 Alarm posture of a female and her kid.



Fig. 6

Flehmen. The upper lip is curled and the head is slightly elevated. From a photograph.

Fig. 7

Female urinating while male allows the stream of urine to enter the side of his mouth. From a photograph.

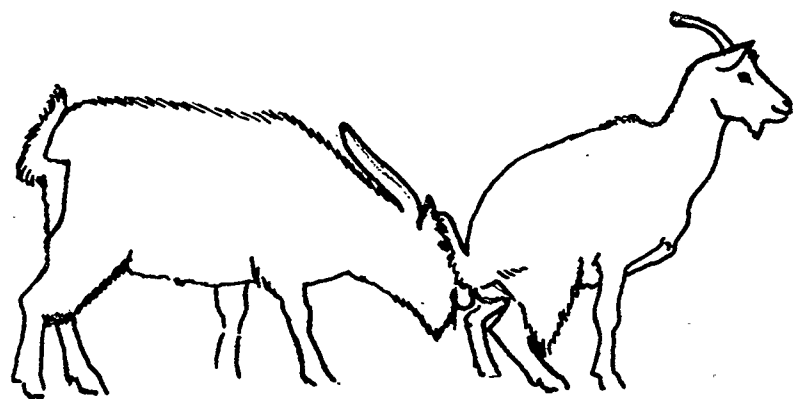


Fig. 8 The gobble directed by a Medium to a retreating female. Note front-kick and the extended tongue. Slight mutilation of the male's ear is evident.

Fig. 9 The butt delivered by a Medium to a Hornless.



Fig. 10 Aspects of the clash. Traced from photographs.
Each picture is from a separate clash.

- A. Individual on the right rears while the one on the left prepares to take the blow.
- B. Same as A. Note the ears of the rearer are laid back behind the horns.
- C. The rearer twisting his head directly before contact. The receiver braces himself to receive the blow between his horns.
- D. Head to head contact is made. Note the straightened legs of the rearer and lateral twisting of the receiver's head. In this instance, horn to horn contact was not made.
- E. Reorientation of bodies after contact.
- F. Individual on right shows reduced broad-side display.

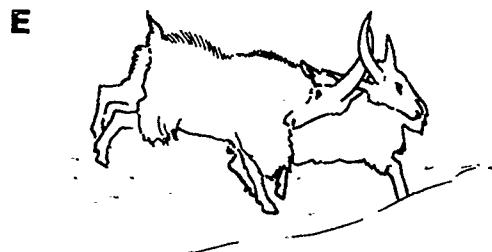
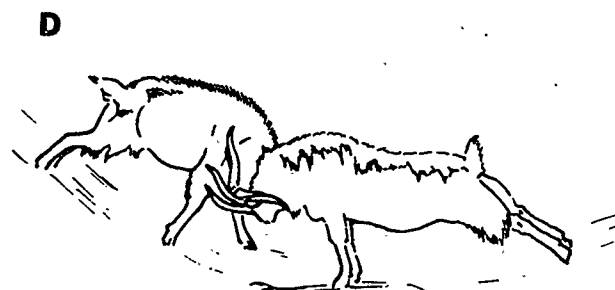
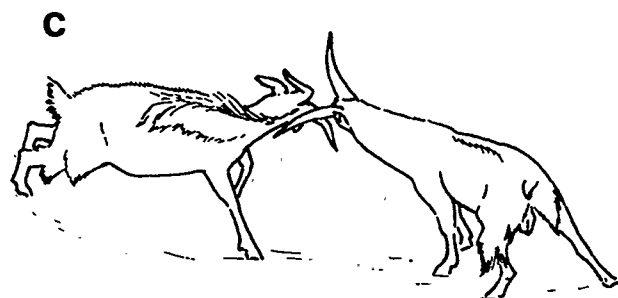
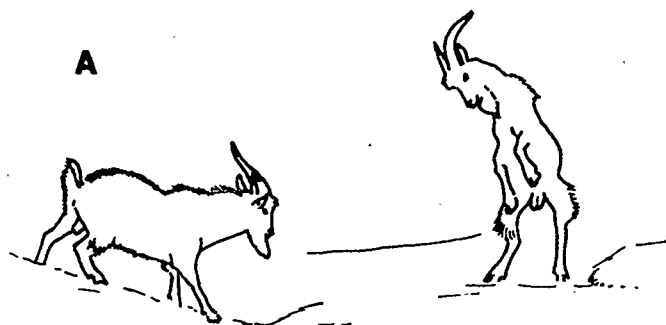


Fig. 11

Relative deviations from the number of patterns expected to be delivered by any size-sex class and received by any other size-sex class. See text for explanation. Based on a matrix with 25 degrees of freedom; therefore, independent statements may be made about 25 of the 36 values. The areas above the upper dotted line and below the lower dotted line indicate the 25 most deviant values.

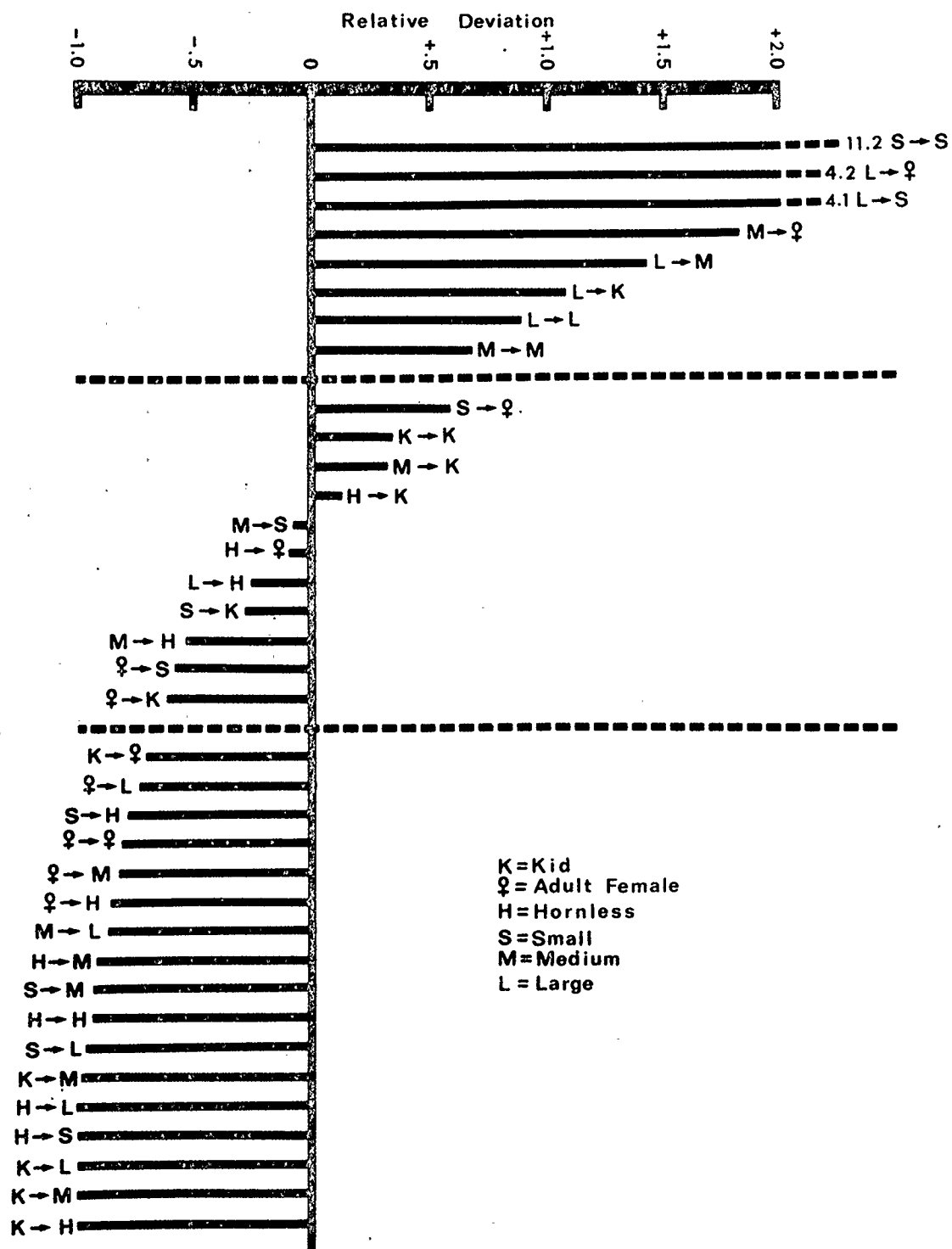


Fig. 12 Sociogram of total social behaviour. Each solid line represents .05 of the interaction index. Each dotted line represents less than .05 of the interaction index. The upper figure on the line is the interaction index for that behavioural dyad while the lower parenthetical figure is the actual number of patterns observed. Within the circles, the upper figure is the action index while the lower (parenthetical) one is the reception index.

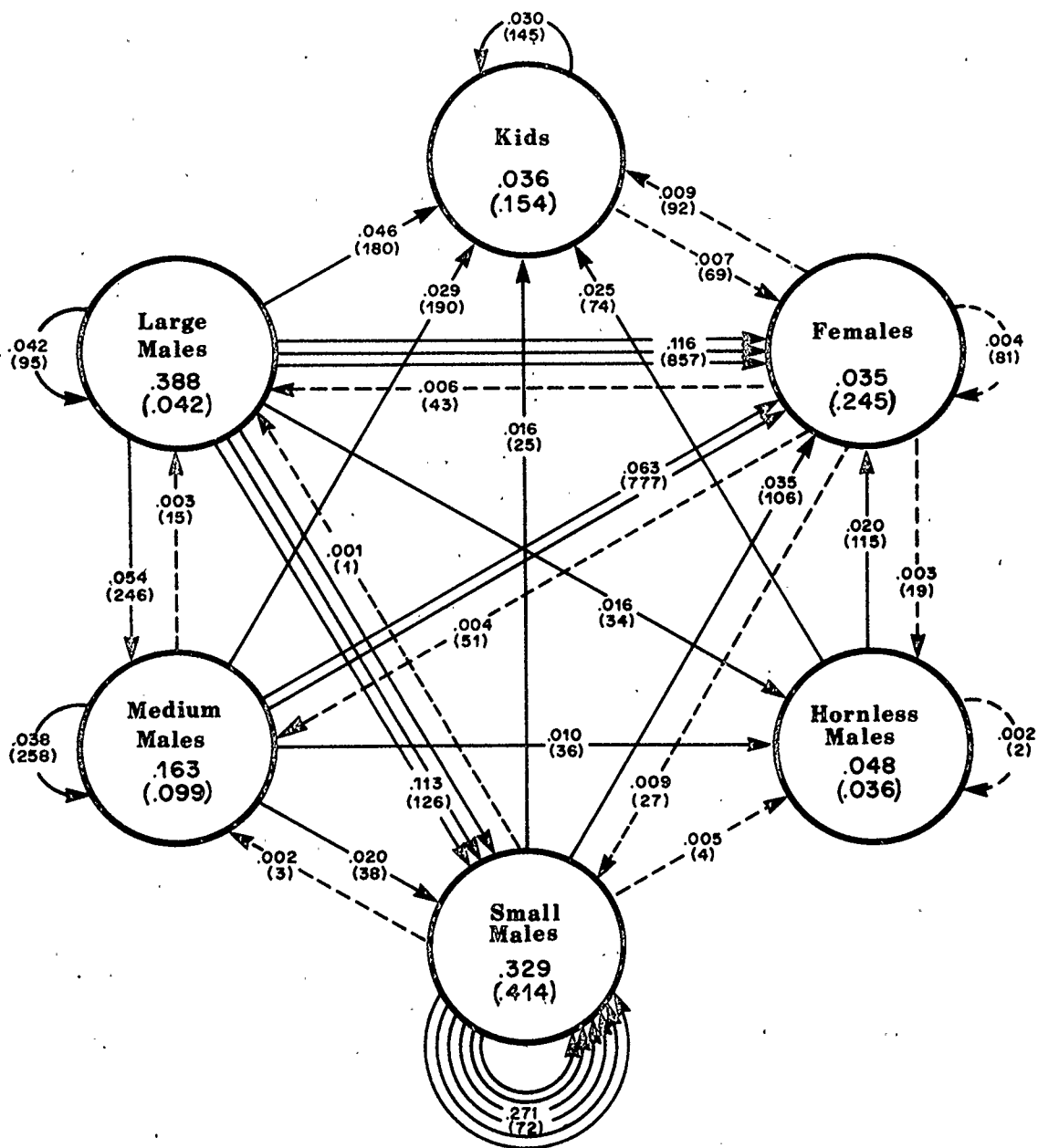


Fig. 13

Sociogram of sexual behaviour. Each solid line represents .05 of the interaction index while each dotted line represents less than .05 of the interaction index. The upper figure on the lines is the interaction index for that behavioural dyad while the lower parenthetical figure is the number of patterns actually observed. Within the circles, the upper value is the action index while the lower parenthetical figure is the reception index.

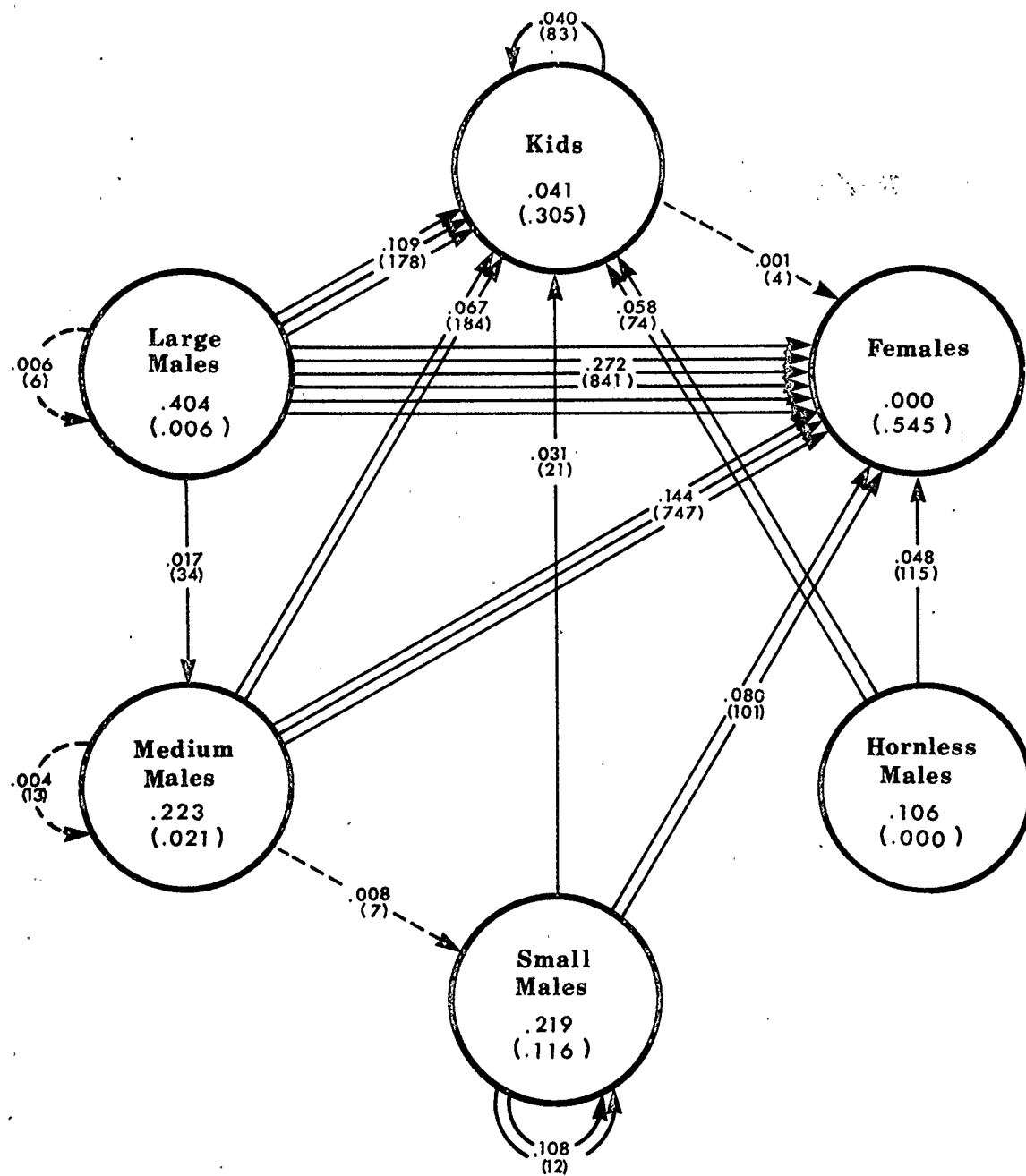


Fig. 14 Ratio of the observed to the expected number
of sexual interactions performed by each male
class with adult females and with kids.

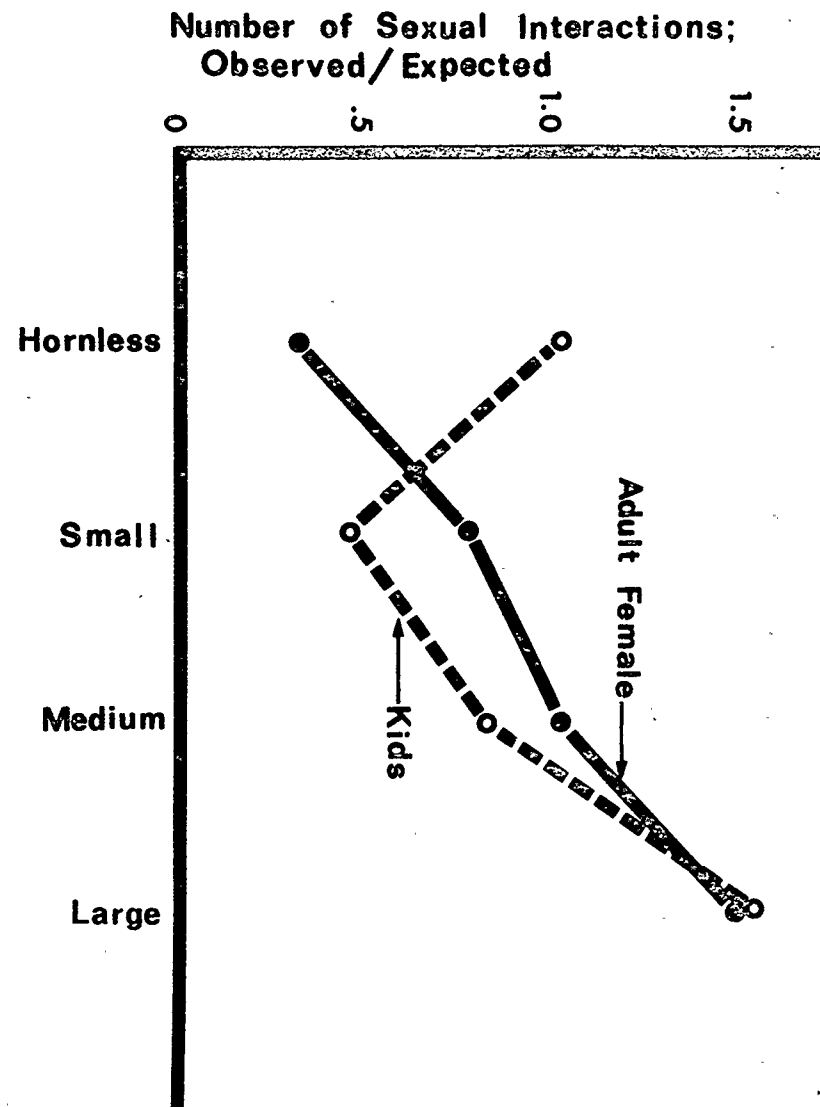


Fig. 15 Average number of sexual patterns per sexual
interaction delivered by each male class to
adult females and to kids.

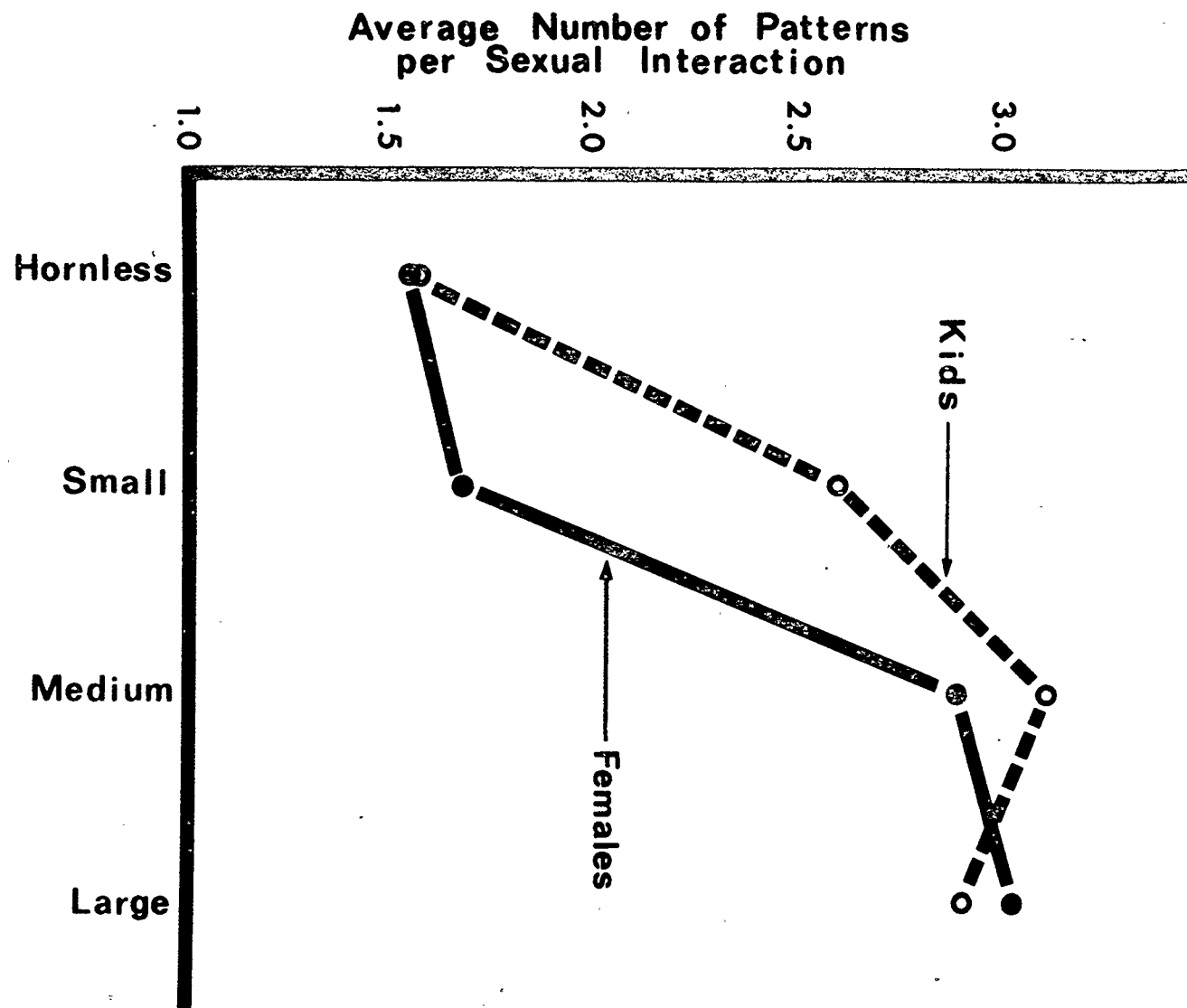


Fig. 16 The ratio of the interaction index for sexual behaviour directed by males of each class to adult females to the interaction index for sexual behaviour directed by males of each class to female kids. Horned males appear to prefer adult females by a factor of about 1.5X over female kids.

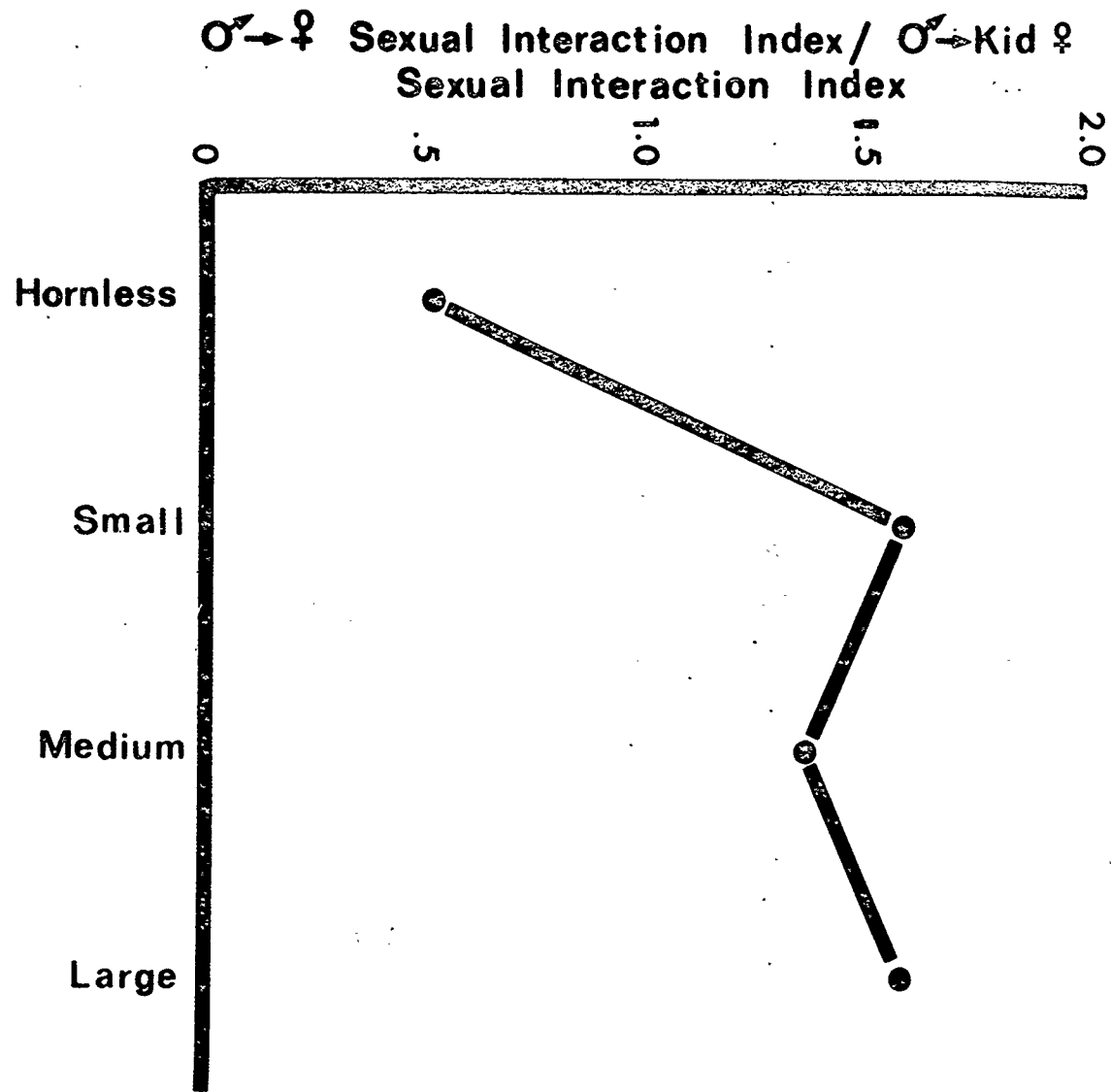


Fig. 17 Ratio of the number of mounts to the number
of courtship patterns displayed by each male
size-sex class to adult females (solid line)
and to kids (dotted line).

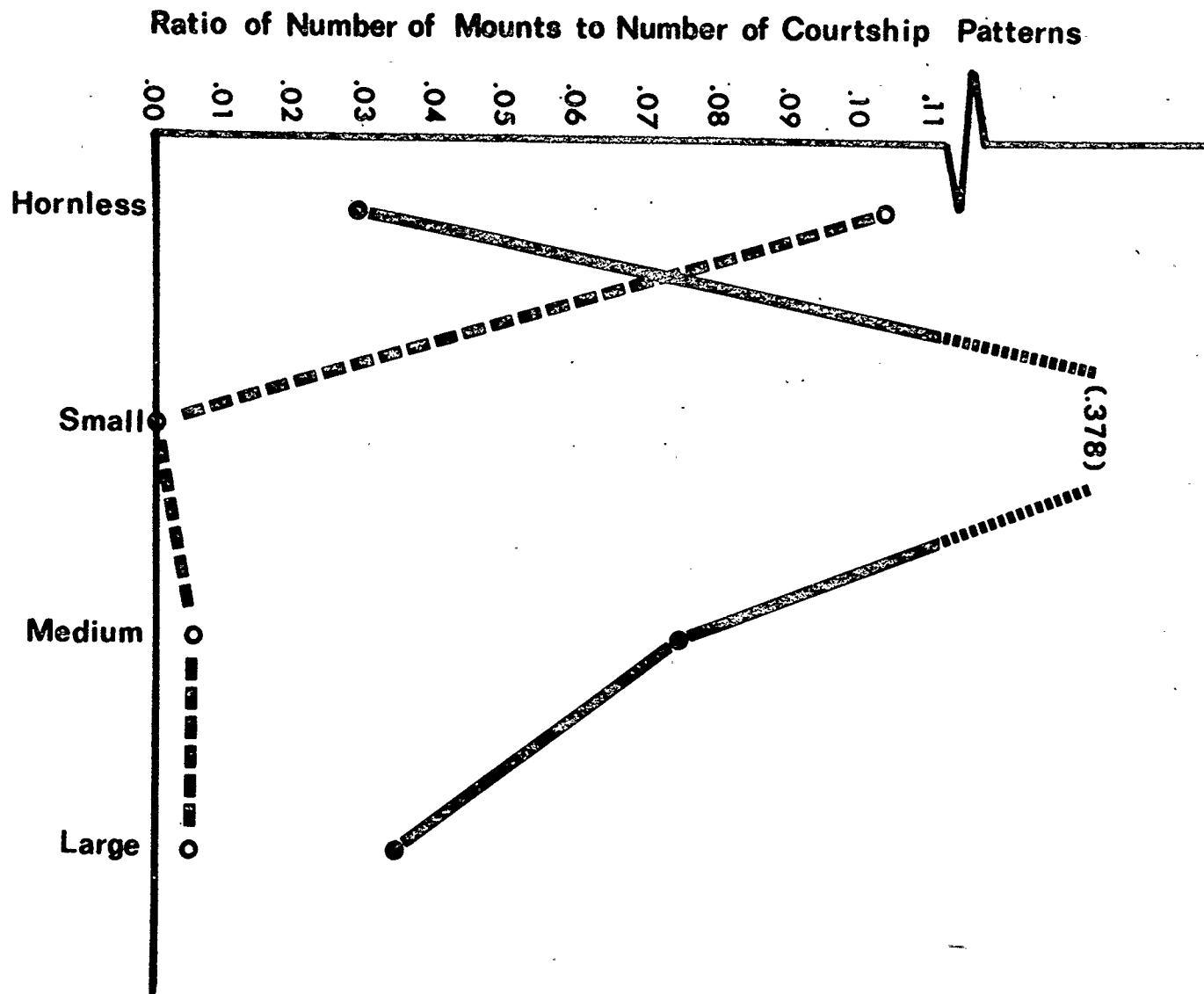


Fig. 18 Percentage of male sexual patterns directed
by each male class to an adult female that
resulted in an agonistic response by that
female.

Percentage of Male Sexual Patterns
Evoking Agonistic Response by Female

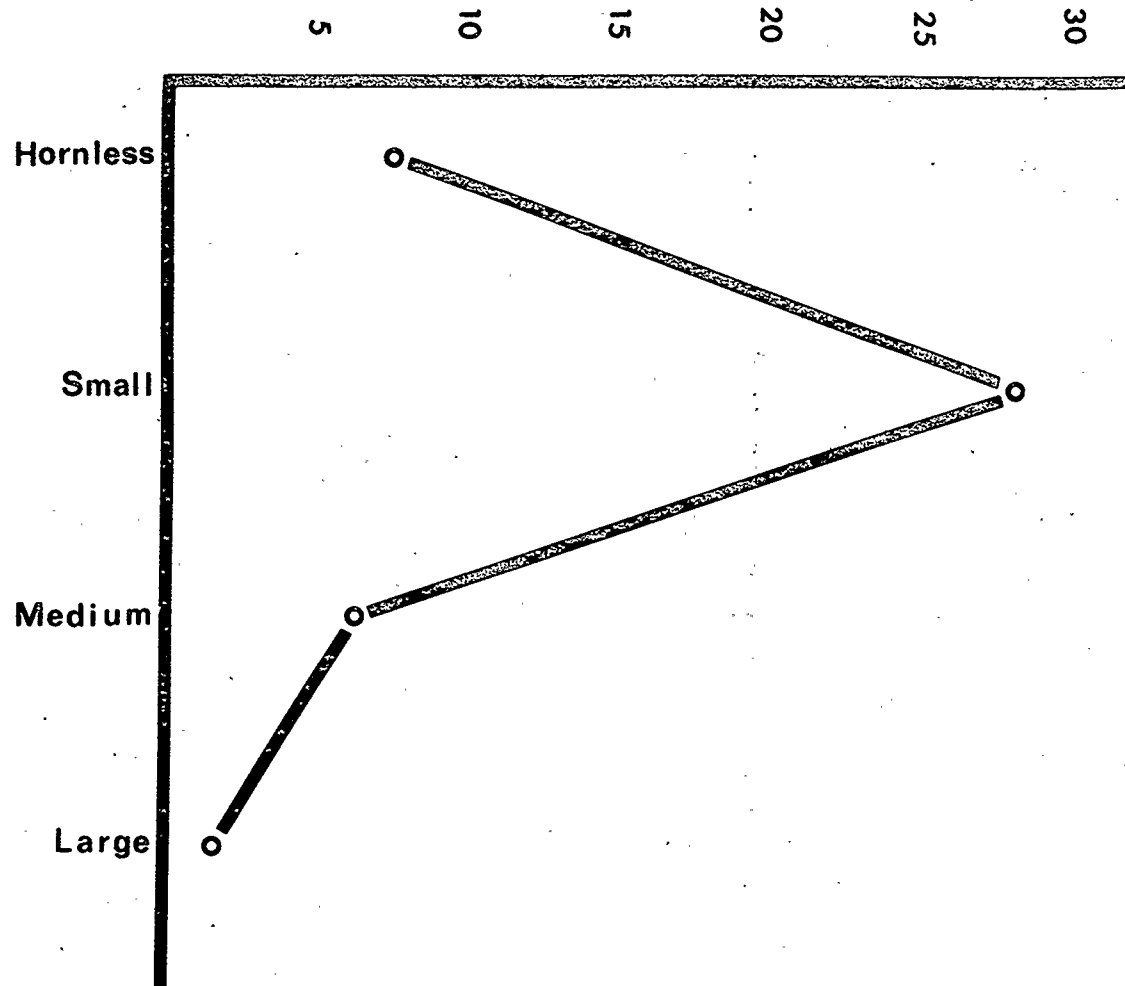


Fig. 19

Sociogram of rush association behaviour. Each solid line represents .05 of the interaction index while each dotted line represents an interaction index value of less than .05. The upper figure on the lines is the interaction index for that behavioural dyad while the lower parenthetical figure is the number of patterns actually observed. Within the circles, the upper value is the action index while the lower parenthetical figure is the reception index.

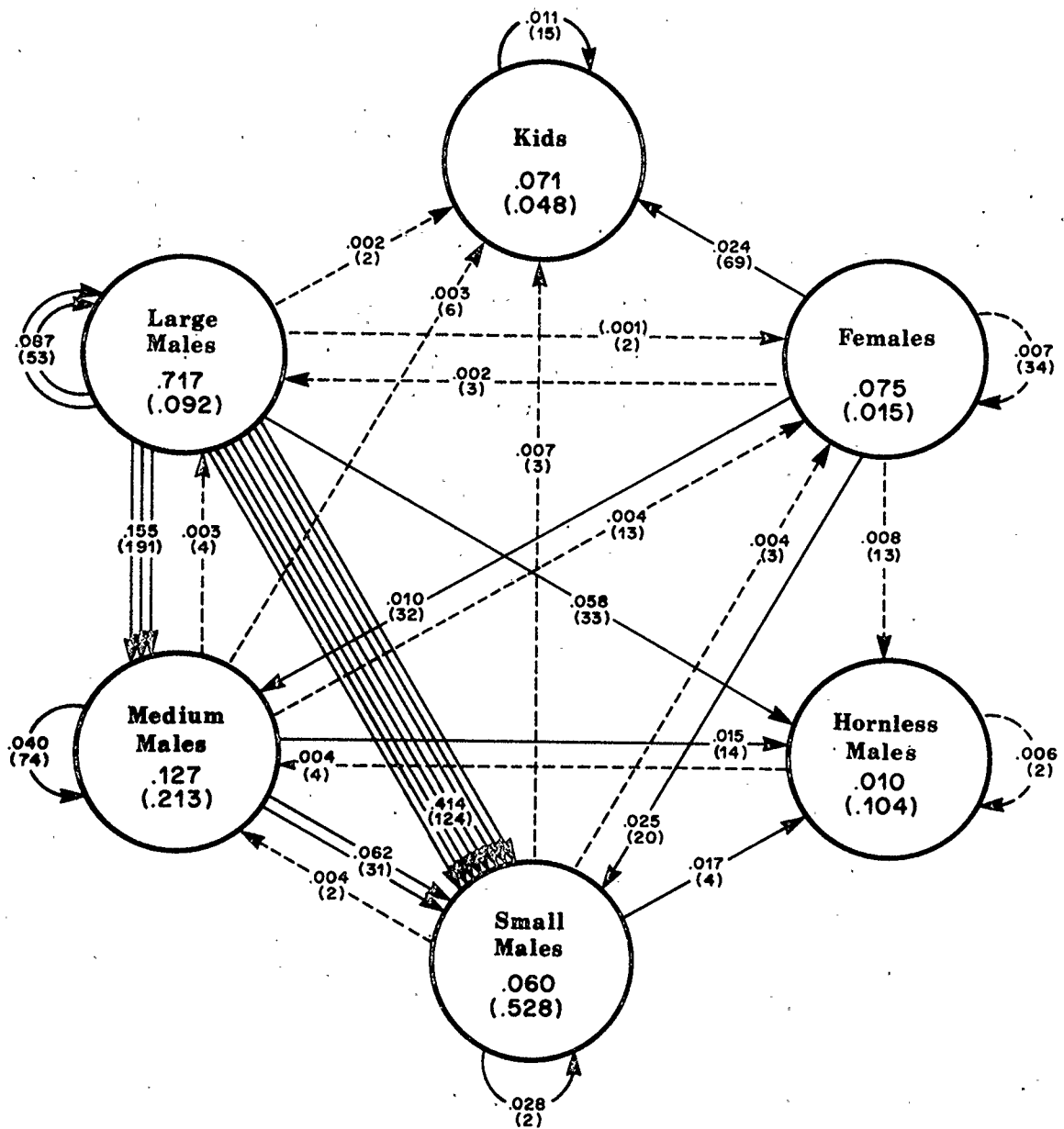


Fig. 20. Sociogram of clash association behaviour. Treated as bidirectional in nature. See text for explanation. Each solid line represents .05 of the interaction index while each dotted line represents an interaction index value of less than .05. The upper figure on the lines is the interaction index for that behavioural dyad while the lower parenthetical figure is the number of patterns observed. The figure within the circle is action-reception index.

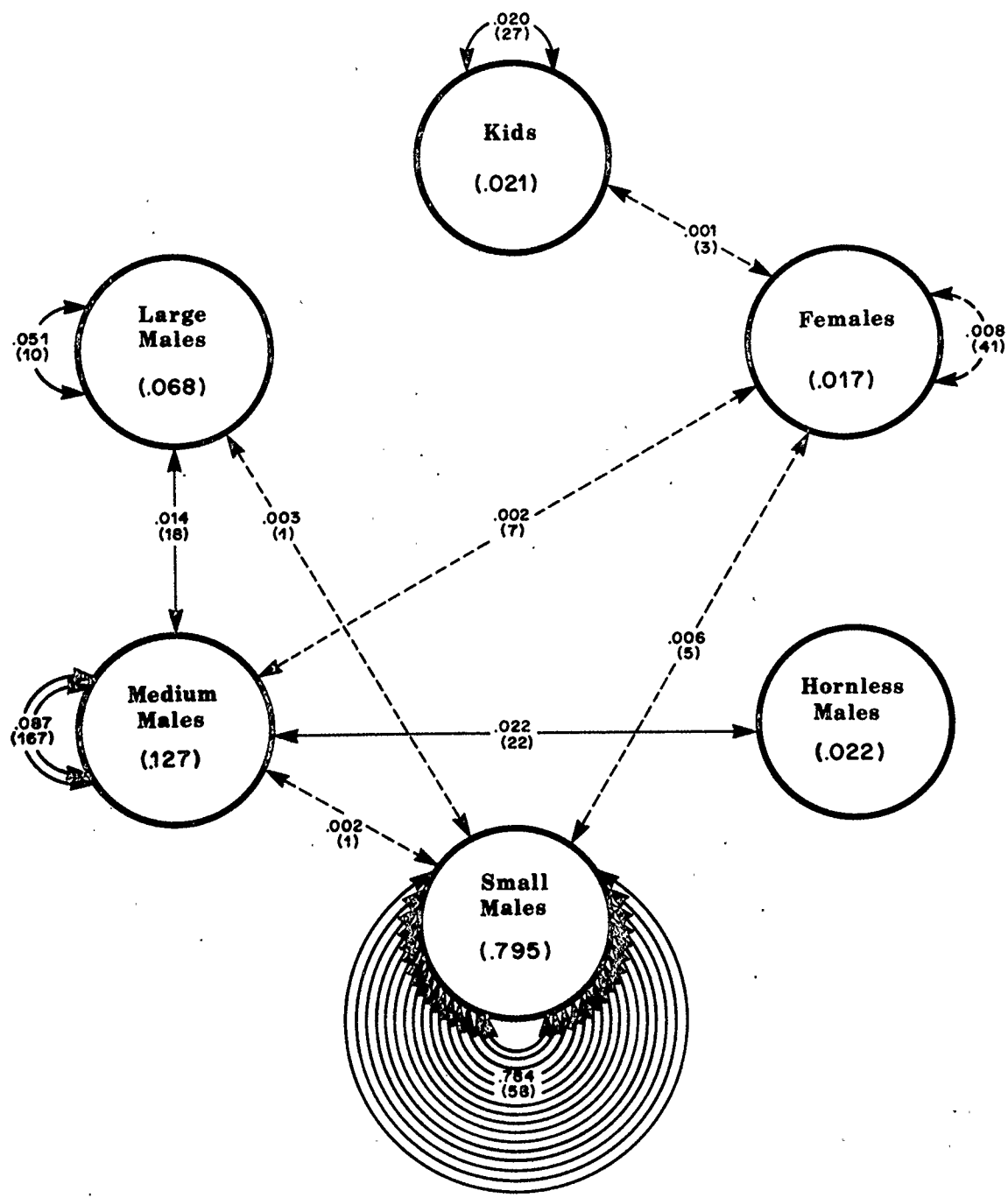


Fig. 21 Ratio of the number of observed to the
 number of expected urine-markings per-
 formed by each male class.

Observed / Expected Number
of Urine-Markings

