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VALERIUS GEIST

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ON THE BEHAVIOUR AND EVOLUTION
OF AMERICAN MOUNTAIN SHEEP

## ABSTRACT

The aim of this study was to discover the rules of social behaviour of sheep and to explain the selection forces responsible for their evolution. Three populations of freeliving sheep (Ovis dalli stonei, o.d. dalli, & o. canadensis canadensis) were studied during all seasons. Their behaviour was described. Each social interaction was transferred to a computor card; 3800 interactions were analysed and form the basis of the quantitative data reported. The evolution of mountain sheep is conceived as follows:

Sheep evolved from a rupicaprid ancestor who innovated a new defense mechanism against hornblows of conspesifies. The blows were caught with the horned head which led to the evolution of pneumated skulls, thick facial skin and heavier horn basis. The generalised, damaging combat form of the rupicaprids was replaced by a ritualised fight, in which opponents clash head on with little damage to each other. This is one prerequisite to the formation of a dominance hierarchy. Horns became not only weapons, but also shields and ultimately display organs and rank symbols.

The mechanism which is responsible for the development of large horns, appears to be neoteny. The ram remains "juvenile" in character for 5-6 years past sexual maturation. This concept explains their prolonged behavioural and bodily maturation, the increased sexual dimorphism, the intense gregariousness of rams prior to ultimate maturity, the independence and leadership of matured rams, the disappearance of neck ruffs in advanced sheep and the differences in aggressive behaviour between bighorn and thin horn sheep. Females are paedogenic in that they can only reach a developmental stage in appearance and behaviour similar to yearling rams. Hence, there is no distinct female "form" in sheep. In correlation we find that rams have no distinct behaviour shown only to females, rather they treat females and subordinate rams in almost identical manner. Conversely, subordinate males may behave like females,

towards dominants. The social behaviour of adult rams falls into two categories, that of the dominant and that of the subordinate; the non-estrous ewe acts like a sexually immature juvenile. When in estrus the ewe changes behaviourally into a young, subordinate male. This explains why ewes in the non-estrous state form unisexual bands and also why they are more gregarious than rams.

The neotenic characters of sheep appear to be a by-product of selection for large horns. Sheep evolved rapidly whenever they colonised new habitat in the wake of retreating glaciers. They increased in horn and body size, sexual dimorphism, rumppatch size and legmarking, and reduced or lost the neckruffs; concurrently they specialised in clashing and replaced the broadside with a horn display. Large horns and specialised clashing were adaptive in the colonizing, expanding populations, in which rams had a relative short life expectancy. Selection for these characteristics came to a half in the stable populations when life expectancy of rams increased while horn and body size decreased. This concept explains the clines of Asiatic and American sheep.

In their evolution, sheep changed apparently primarily in social adaptations. Habitat - body care - and social behaviour evolve largely independently of each other.

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PUBLICATIONS

Geist, V. 1959. Diurnal activity of moose. Memo. Soc. Fauna & Flora Fennica. 35: 95-100.

1960. Feral goats in British Columbia. Murrelet 41 (3): 1-7.

1963. On the behaviour of the North American moose (Alces alces andersoni Peterson 1950) in British Columbia. Behaviour 20 (3-4): 377-416.

1965. On the rutting behaviour of the mountain goat. Mammalogy. 45(4): 551-568.

1966. Validity of hornsegment counts in aging bighorn sheep. J.Wild. Mgmt. 30 (3): 634-635.

1966. Ethological observations on some North American Cervids. Zool. Beitrage 12: 219-250.

1966. The evolution of horn-like organs. Behaviour (in press)

1966. The evolutionary significance of mountain sheep horns. Evolution (in press)

1966. On fighting injuries and dermal shields in mountain goats. J. Wildl. Mgmt. (in press)

I. McT. Cowan and V. Geist. 1961. Aggressive behaviour in deer of the genus Odocoileus. J. Mammal. 42(4): 522-526.

# ON THE BEHAVIOUR AND EVOLUTION OF AMERICAN MOUNTAIN SHEEP

by

VALERIUS GEIST

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A THESIS SUBMITTED IN PARTIAL FULFILMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in the Department
of

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We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

OCTOBER, 1966

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# ABSTRACT

Behaviour studies were undertaken on three populations of free living American sheep, one being a Stone's sheep (Ovis dalli stonei), one a Dall's sheep (O. d. dalli) and one a bighorn sheep population (O. canadensis canadensis). The habitat-, body care- and social behaviour patterns - except those of mother and young - were described in detail. Each social interaction recorded was transferred to a computer card. 3800 interactions were analysed and form the basis of the quantitative data reported. American sheep show only minor quantitative differences in their social behaviour. However, behavioural differences within populations of the same species occur and appear to reflect population quality. Sheep evolution is conceived as follows:

Sheep evolved from rupicaprid ancestors. They evolved large horns, pneumated skulls, lost or reduced display hairs, increased the size of the rump patch and increased sexual dimorphism. The damaging fighting forms of the rupicaprids were replaced by a ritualised form of combat. Sheep lost the thick hide as a defence mechanism, and defend themselves by catching the horn blow with their horned head. Skulls evolved to absorb concussion. The broadside display was replaced by horn displays. Ram horns function not only as weapons, but also as guards, display

organs and rank symbols. Sheep appear to have evolved rapidly whenever they colonized new habitat in the wake of retreating glaciers. The expanding populations would experience intense selection for forceful clashing and larger horn size. Large horn size is a function of neoteny in rams. Rams mature sexually at 1.5 - 2.5 years of age, but do not mature behaviourally or reach ultimate growth form until they are 7 - 8 years old. Females are paedogenic forms which remain similar in appearance and behaviour to sexually mature yearling rams. Neoteny also explains the long body growth of rams, the reduction and loss of the neck ruff, increased sexual dimorphism, the intense gregariousness of females and of juvenile rams, the increasing independence and leadership of rams as they grow older, and the more frequent use of aggressive patterns by bighorn as compared to thin horn sheep. Rams prefer to interact with rams of their own horn size and with females. They treat subordinates, irrespective of sex, much the same as they treat females. Rams change their behaviour not with the sex of the companion but with its dominance rank. The more that subordinate rams resemble females in appearance, the more they are treated sexually by dominant rams. Subordinate rams may act like females to the extent of urinating, or, assuming lordosis when mounted. Non-estrous ewes withdraw from rams, but estrous ewes remain and act like subordinate rams. Ewes are guarded and defended singly as they come into heat. They are followed by a group of rams. The largest horned rams guard and mount estrous ewes. Rams fight throughout the years, not for females, but for dominance. Despite intense competition, the dominant ram takes the estrous ewe away from the subordinate uncontested.

Sheep changed primarily in social adaptations, which evolved quite independently of habitat - or body care adaptations.

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# TABLES OF CONTENTS

# LIST OF FIGURES

FIGURE PAGE

FIGURE PAGE

# LIST OF TABLES

# INTRODUCTION

The life of a large, social mammal is intrinsically interesting since a knowledge of the rules it lives by stimulates comparisons and ultimately contributes to man's knowledge about himself. To live socially means to live by rules, whether or not these rules are largely conceptual though not arbitrary - as would appear true for man - or are largely fixed in the still mysterious central nervous system and acted out in intellectual blindness. Our outlook on living socially is linked with the notion of progress. This notion appears to be an unspoken theme in Allee's concept of animal cooperation (Allee, 1951). It may well have arisen from the "romantic fallacy", as Ardrey (1963) so aptly names it, which regards man as the epitome of progress, a notion which our social institutions continuously project and reinforce. Stated bluntly, since man is social, living socially is progressive, living otherwise is not! Some will recoil from this statement, yet how many of these would unhesitatingly tick off the advantages of living socially versus solitarily? Yet, here is the crux of the matter. If the animals' way of life are adaptations, solutions to larger and minor problems posed by an environment, then living socially or solitarily are adaptations and cannot be inherently progressive. There cannot be advantages in living socially over living solitarily, not if both are products of evolution. Clearly, the question of what advantages social species A has over solitary species B is unanswerable in principle.

The facts remain that a variety of mammalian societies do exist, that they do have order and rules of behaviour (see Eisenberg, 1966), and that we still know little about why, how and when they arose. I hope to answer this in part for one group of closely related ruminants, the sheep. The approach has been not to search for advantages of social living, but to explore the evolution of social behaviour and external appearance of American mountain sheep. What selective forces are responsible for the characteristics, structures and actions of these animals? A study of this nature does not deal with one, but with many problems and is held together only by one common theme. The findings can be read in the Abstract and Conclusions.

Since, in this thesis, behaviour was used as a key to the understanding of an animal's evolution, it was my first concern to produce a detailed documentation of mountain sheep behaviour and its variables. This appears to be essential before valid inferences can be made about the function of sheep adaptations and the selective forces shaping these. Secondly, a detailed documentation is essential to allow the reader to check the reported findings himself. Unlike the results of a laboratory study, the findings of a field study can only rarely be readily checked, hence the data must be exact, detailed, organized so that the reader can see how each conclusion was formed, and voluminous enough to allow him some exploration of his own.

These thoughts are reflected in the organization of the thesis. The first three parts deal mainly with a description and analysis of social behaviour, while the fourth part deals with interpretation of it in the light of sheep morphology and zoogeography. However, the division is not so clearcut. Although the first part deals mainly with descriptions of behaviour patterns, I have added essential information to each description and interpreted these, to make each behaviour pattern as completely comprehensible as possible. Furthermore, two essays on the habitat and body care behaviour are added to clarify their position in the evolution of sheep.

In the second part, the rules which sheep follow when interacting with one another are traced out. Here the behaviour patterns have been analysed quantitatively, and it is shown which sheep interacts, how it treats the chosen companion and how it is treated in return, and how such interactions vary. The third part of the thesis is again descriptive. The social behaviour patterns described and analysed previously are shown in their natural context. The behaviour of sheep during fall and early winter is described with a special emphasis on rams. The first three parts familiarize the reader with those characteristics of sheep which are important to the fourth part.

In the fourth part of the thesis I have attempted to answer how sheep evolved, why they evolved and, to some extent, when they evolved. There are no complete answers here; such answers are probably impossible to give. The concepts proposed may be valid for northern ruminants other than sheep. And what about sociality? It appears as a by-product of the sheep's evolution, which is not directly but indirectly selected.

## DESCRIPTIONS OF THE SPECIES STUDIED

Stone's sheep (*Ovis dalli stonei* Allen 1897) (Fig. 1):

Stone's sheep are dark coloured Dall's sheep which characteristically have large variations in colour and shade patterns. They may be black, ash-grey, silver, brown, yellowish or almost white in colour. In the black sheep there is a brownish tinge in the hair. Individuals of various colours may be found in one band; on my study area the black and dark grey forms predominated.

The individuals are not uniformly coloured. The head, the nape or even the whole neck is lighter than the body. The white belly, rump patch and leg markings differ somewhat from those of bighorn sheep (p.127 and Fig. 101); the latter lack the belly-band which is often seen in Stone's rams (Fig. 4), while old rams usually lack the clearly defined, white belly of Stone's rams. The tail is larger than in bighorns and is virtually always continuous with the dark dorsal streak. The horns are dark amber or brown in colour and vary in shape, size and spread between individuals. On my study area the rams usually had close curled horns; broomed horn-tips, characteristic of bighorn sheep, were not uncommon.

On the study area, large rams in early fall would probably have a weight of between 180 and 220 lbs. In Table I some vital statistics are given for a ram and a ewe. The ram was shot during the rut and appeared emaciated. He had little fat and a small rumen fill, hence the low weight. The ewe, an unusually large and old individual, was also shot in early December. A $2\frac{1}{2}$ year old ram, collected with the ewe, had a live weight of 117 lbs. The percent weight of the dressed out carcass was 55 for the ram, 50 for the ewe and 50 for the $2\frac{1}{2}$ year old ram. These sheep were cut into pieces and weighed with a pocket spring scale (50 lbs.) shortly after their death. Live weight was calculated by multiplying carcass weight plus vicera by 1.08 to compensate for blood loss. (The factor 1.08 is based on 70 ml. of blood per kg. of body weight as is found in domestic goat.)

The Stone's sheep study area lies in northern British Columbia, on the southern fringe of the Eagle Nest Range, north of the Spatzisi river. I stayed on the study area from June 19, 1961 to January 27, 1963, and again from November 26 to December 11, 1965.

Even a passing acquaintance with sheep in northern British Columbia makes it apparent that Stone's sheep now live in widely dispersed, isolated relic populations, which appear to differ from one another. The Stone's sheep I studied lived thinly dispersed at the edge of one of the larger relic populations. On the study area sheep appeared to be heading slowly towards extinction.

Sheep are grazers which depend a great deal in winter on grasses growing on exposed slopes or in rock terrain. In the Stone's sheep study area, good habitat was localized and not abundant. The mountains were largely overgrown by dwarf birch scrub (*Betula glandulosa*) and timber which left precious little living space for the sheep. This was a wet country with large snowfalls. Sheep appeared to survive the deep snows by the accident of frequent warm, humid winter storms which swept in from the Pacific and removed the snow from a few, small areas. This is where sheep spend much of the winter.

There were few sheep on the study area. The bands were quite small but the individuals appeared to be large and were lively and reproduction was high. I observed vigorous dominance fights in this population only, although I watched many more bighorn and Dall's sheep. The small number of sheep on this study area was an advantage since it allowed me to get to know the individuals better. These sheep contributed more to the study than the other populations.

Dall's sheep (Ovis dalli dalli Nelson 1884) (Fig. 2):

Dall's sheep are pure white, although some individuals with dark hairs on the tail do occur. They are similar in size to Stone's sheep. A $5\frac{1}{2}$ year old ram shot close to my study area in October weighed 226 lbs., live weight. The rams on this study area carried distinctly more flaring horns than did the Stone's sheep, which can be seen in the photographs.

The study area was located on Sheep Mountain, Mile 1066 Alaska Highway, at Kluane Lake in the Yukon Territory. I stayed with the sheep from September 15 - November 24, 1965.

The Dall's sheep in the St. Ellias range lived in a much more favourable habitat than did the Stone's sheep in the Eagle Nest Range. Glaciation had been relatively recent and the glaciers were still large. The mountains were bare of timber except for a broken fringe at their bases and north slopes. The climate was dry; winds were frequent and strong. The mountain slopes were sparsely covered with grasses and forbs, while a few patches of willow followed the creek beds. The slopes carried a considerable cover of dust, which was probably deposited by the frequent dust storms created by winds descending along the river valley from the glaciers.

There was a huge expanse of sheep habitat, the best that I have seen to date. Sheep were the dominant ruminants here; mountain goats (Oreamnos) and moose (Alces) were rare and caribou absent from the study area. Although the sheep on the study area appeared to be large, they were less lively than my Stone's sheep; the rams interacted surprisingly infrequently with butts or clashes. There were very many sheep; I learned to recognize during my short stay only a few individuals. These sheep contributed primarily film documentation and qualitative observations.

Bighorn sheep (Ovis canadensis canadensis Shaw 1804) (Fig. 3):

Bighorns are considered larger in body size than Stone's or Dall's sheep, and they have heavier, usually close curled, broomed horns. No description need be given here, since, unlike Stone's sheep, the physical features of bighorns are well known (Cowan 1940, Moser 1962, Cowan and Guiguet 1965).

The bighorn study area was the Palliser Range and Bare Mountains in Banff National Park, Alberta. I stayed here from May 6 - September 10, 1963, and from May 1964 - June 1965.

These bighorns lived in larger populations than did the Stone's sheep I observed. Their habitat was primarily open, grassy slopes which were once forested, and which were again being slowly invaded by forest (Flook, 1964). The sheep were in my opinion not large for bighorns; unfortunately weights are not available for the study animals. The yearlings were small, they matured late, reproduction in the years I was there was poor, and I do not hesitate to classify these sheep as of low quality. Furthermore, the young lambs were listless compared to the Stone's lambs I observed, and the older rams tended to get exhausted quickly in the rutting seasons. These bighorns contributed the bulk of the documentary film, photographs, and the mortality data plus some quantitative behaviour data.

## METHODS

### Classification of sheep into sex-age classes

Sheep were classified on the basis of horn-, body-size and sex into distinct classes, of which I recognized seven in the Stone's and Dall's sheep study, and eight during the bighorn study. These classes were - lambs, female yearlings, adult females, male yearlings, adult rams of horn-size I, II, III and IV. For Stone's and Dall's sheep, classes I and II were combined into class II. Such a classification is essential if variation in behaviour due to sex or age is to be discovered. The individual classes were characterised as follows:

Lambs: The smallest sheep in horn and body size, age 1 day to 1 year (Figs. 5 & 6). The lambs of Stone's and bighorn sheep are born mouse-grey, with Stone's lambs having a black tail. This juvenile coat is shed between August and October and is replaced by a coat similar to that of adults. At six months of age, Dall and bighorn lambs (Figs. 5 & 6) have rather small horns compared with equal age desert bighorn lambs (Hansen, 1965). With the term "yearling-lamb", I denote subadults 11-14 months of age. This class was not further differentiated by sex, since male and female are exceedingly similar in appearance as lambs.

Yearling female: This class includes females 14-24 months of age. They are somewhat larger than lambs in horn and body size but not as large as females or yearling males. They have short "lamb-like" faces and short horns usually with perfect tips (Fig. 7b). There is some danger of confusing well developed yearling females with exceptionally poorly developed yearling rams. Yearling females occasionally become sexually mature at 18 months of age (Woodgerd, 1964).

Adult female: This is the most common class of sheep. They reach definitive appearance and proportions shortly after 24 months of age and vary only little thereafter. Their horn growth is negligible and these organs remain small. Adult females are the standard of comparison for other sheep classes (Fig. 7c).

Yearling male: This class is difficult to distinguish from adult, or exceptionally well developed yearling females. At 14 months of age the males may be separated from equally aged females by larger body size and slightly longer, wider horns. The male continues to grow throughout summer and fall and, during the rut, has a striking resemblance to adult females in normal populations. They are similar to females in body size, horn length, and (in bighorns) in possessing a white belly. They differ in having slightly wider horn bases and more divergent horns; their faces have a more lamb-like expression, the hairs on the occiput and neck are longer than in ewes and give yearling rams a slightly more "chunky" head. In exceptionally well developed males the testes may be plainly visible at 18 months of age. They differ somewhat in behaviour from ewes in using the low-stretch more frequently. In some populations they are sexually mature at 18 months of age but participate only little in the rut (Figs. 7d, 8 & 9).

Class I rams: These rams are 26-36 months old. They are conspicuously larger in horn size than yearling rams or adult females, and in normal, healthy populations exceed adult ewes in body size (Figs. 7f, 10). All class I rams which I observed were mature at 30 months of age and participated actively in the rut. Occasionally, a poorly developed ram over 36 months of age was included in this class. In the Stone's sheep study, I included these rams with the next larger class.

Class II rams: Rams 3-5 years of age: rarely 6. The horns have formed about half an arc but not $\frac{3}{4}$ of an arc. The horn tips are intact. These rams are less chunky and heavy in appearance than the next largest ram classes, although body size differences between these and older rams are slight (Fig. 7g).

Class III rams: Rams 5-8 years, rarely 9 years of age, with horns forming $\frac{3}{4}$ of an arc. These are the "$\frac{3}{4}$ curls". Their horn tips are usually still intact among bighorns, but do show the first signs of splintering. When horn tips are intact, the tips are close to eye level. The horn bases have reached nearly ultimate thickness and the ram's facial features are very similar to those of the larger rams. It appears that their skulls have reached almost their final dimensions (Fig. 7h).

Class IV rams: Rams rarely 7, usually 8 years or older. If horn tips are still intact, they protrude well beyond eye level. If horn tips are "broomed" (broken) they must reach almost eye level while the horns must be very heavy throughout most of their length and form a near perfect circle. If the horns were heavily broomed and formed only $\frac{3}{4}$ of an arc, and the broomed horn ends were nearly as large as the diamäter half way between tip and base, I classified such rams into the IV category. In body size class IV rams do not differ consistently from class III rams (Fig. 7i). Rams of class III and IV are usually darker in colour than younger rams, and their belly patch is progressively invaded by brown hair.

<u>Differences between Dall's sheep and bighorn sheep classes</u>:

Generally sheep of the <u>dalli</u> group have less horn growth at each comparable class than bighorns. The Dall lamb (Fig. 6) in fall carries no visible horns but the bighorn lamb of comparable age and development does (Fig. 5). The yearling ram's horns are thinner than those of bighorns, making it even more difficult to distinguish these rams from ewes. Note that the horns of an average $3\frac{1}{2}$ year old Dall ram are only about the size of those from a $2\frac{1}{2}$ year old bighorn (Fig. 32). Among rams I used the same horn size criteria to distinguish the various classes; the ages also coincide between the two species.

## Methods of collecting data

All data was collected in the field, where I lived in sight of the study animals. Most behaviour data was obtained during observations at long distance of sheep apparently unaware of the observer's presence. A locality was selected 600 - 2,000 meters from the sheep which allowed a maximum of terrain to be viewed, so that one could follow visually all movements of sheep. At first a tripod mounted 25 power monocular spotting scope was used. This instrument caused eyestrain and headaches during continuous observations over many hours. Later a binocular spotting scope, 15 x 60 was used and proved to be comfortable during long use. The monocular spotting scope, due to its light weight, was carried on long hikes and continued to give useful service in identifying spotted sheep.

The following was recorded:

(1) The number and sex-age classes of sheep under observation. I attempted to watch no more than six sheep simultaneously.

(2) After every five minutes of observation I noted the number of sheep feeding, standing, moving about, and resting. This maintained a record of the animals' activity.

(3) Every social interaction was recorded. The following was noted:

(a) The sex-age class of the sheep initiating the interaction and the class of sheep it chose to interact with.

(b) The kind and sequence of behaviour patterns (described from p. 39 on) used by the sheep initiating the interaction, and the patterns it received in reply from the other sheep.

(c) The number and classes of sheep which were in the immediate vicinity of the sheep which initiated the interaction.

(d) The special situation - if any - in which the interaction occurred, i.e. whether it took place between two rams in a huddle, or outside a huddle (p. 86), or in the presence of an estrous or non-estrous ewe.

Later each social interaction was transferred to a computer card. These cards, layout and programmes are stored with the Zoology Department, University of British Columbia, Vancouver, B.C., Canada. 3,800 interactions were later analysed.

In recording behaviour, the individual patterns, the class of behaving sheep and their responses were recorded in shorthand as they took place. By breaking down behaviour into patterns and recording these, subjective evaluation was kept to a minimum. Thus, I was not interested whether a ram had "lost" or "won" an engagement, but only which behaviour patterns, when and in what order he used. The decision whether he "lost" or "won" would come from the frequencies and types of behaviour pattern used. A few lines of recorded data would look as follows:

"..... fc. Lauf III (o), Lauf (o), twist III, III horn b. fc. / $10^{15}$ fc. nose III ....." etc.

(fc. = class IV ram, III = class III ram, (o) = no response to the behaviour pattern, Lauf = front-kick (see p.42 ), twist is also a behaviour pattern as is nose (low-stretch). The meaning of this recording is that a class IV ram kicked a III ram who did not respond, the class IV ram kicked again (no response) then twisted to III. The class III ram turned and horned his larger opponent's head. The slash indicates that five minutes of observation are over, and a new five-minute observation period begins at 10.15 hours, etc.)

It was not easy at first to decide when a behaviour pattern had ceased and begun anew, so I used arbitrary cut-off points. For instance, the low-stretch is a long lasting pattern. If a ram walked in low-stretch, stopped and held the display it counted as <u>one</u> low-stretch. If he walked on however anew after the chosen companion, it counted as <u>two</u> low-stretches. If the ram held his display but followed X times, it was counted as X low-stretches. Should the ram interrupt the display even for a moment and then resume it, it was counted as <u>two</u> displays.

Horning, rubbing and nuzzling of large rams by small ones presented a similar problem. If a ram horned his opponent's neck for several minutes but interrupted this activity for a few seconds, should this be recorded as one or two hornings. I recorded it as two hornings. If a ram horned without interruption, it was recorded as one horning irrespective of whether it lasted one minute or one second. In this study I had to ignore the temporal differences between behaviour patterns since the sophisticated recording machines necessary for this kind of recording were absent.

The second method of gathering information was to approach sheep, film and photograph their behaviour, and record the sounds and minor pattern variations which escaped me at a distance. For filming I used a Bolex R.X 16 with 25, 75 and 150 mm lenses, and the light handy tripod of the same make. The still cameras were single lenx reflex, Pentax H2 and SV model with 50, 200 and 400 mm lenses. The 200 mm Takumar lens I used most frequently.

When filming few notes were taken and these were excluded from the quantitative analysis to counter the argument that my presence adversely affected the behaviour of sheep. I detected no such influence despite many hours of observing sheep at long and short range. Such notes were used together with films and photos to describe the various behaviour patterns more accurately.

On the Stone's sheep study area 36 sheep were recognized individually by differences in coat patterning, colour and horn shape (Fig. 4). Since few sheep were present, and the markings were distinct, I could quickly recognize individuals, and recognized them equally quickly after almost three years of absence from the study area. Each known sheep was identified by letter (i.e. D - ram) and a record was kept of where and when it migrated and with whom it interacted.

In Banff Park, a large number of bighorns had been tagged with small aluminium tags by the late warden, Mr. J. E. Stenton. Individuals could be recognized by the presence and number on the tag, a method which was no more reliable to me than identifying sheep by their personal features. At long distance, however, I found bighorns more difficult to identify than Stone's sheep.

The age of rams was determined by counting horn segments (Geist 1966a). The horn segments of Stone's and Dall sheep are much more clearly visible than those of bighorns (Fig. ). On a clear day without mirage, using a 25 power spotting scope on a solid rest, they may be seen as far away as 600 yards. Accurate counts can be made at about 400 yards on rams eight years of age or less. Since horn segments decrease rapidly in size after 7 years of age, some merge with the hairline close to the horn, or are camouflaged by deep grooves on the basal part of the horns. The following four Stone's rams which had been aged prior to their death fell into my hands.

| Ram | Estimated Age | Actual Age (checked on dead animal) |
|---|---|---|
| D - ram | 11 yrs. + | 14 years |
| "fc" | 10 yrs. | 12 years |
| Cliff-ram | 10 yrs. | 10 years |
| Unnamed but known ram | 8 yrs. | 9 years |

It can be seen that even with very old rams a fair estimate of their age may be obtained.

In Banff Park, time was devoted to the search for dead sheep. A record was kept of the age of each sheep, the length and basal circumferences of ram horns, and the lengths of each horn segment. Horn segment length was measured from groove to groove on the outside edge of each horn. Similar measurements were made from all horns collected of all sheep species.

There are a few considerations about working with sheep which should be placed on record. Wild sheep can be tamed easily. I became aware of it first on the Stone's sheep study area when, dressed in white overalls and moving slowly, it was possible to get into good filming distance. Later, some rams were undisturbed by my close presence and even lay down without looking at me. It was in Banff Park that I became fully aware of how tame mountain sheep can become and still live in the wild state. For this I am grateful to the late J. E. Stenton, Park Warden of Bankhead District. He habituated sheep to lick rock salt in his hand and while they licked he clamped on ear tags. The Palliser sheep come into touch with humans only at Lake Minnewanka on a few occasions during the summer. Yet they retained their tameness. Between 1963 to 1965 I climbed to these sheep regularly. While offering salt one could, with caution, free the hairs from the ear tags and after some manipulation of the ear, read most tags. Sheep which were quite wild at the beginning of the bighorn study soon tamed and could also be handled.

During fall, 1965, I observed Dall's sheep which lived close to the Alaska highway and were somewhat habituated to the cars and humans on the road below. They were a little wild at first but after three weeks they were tolerant enough to let me stand within 25 - 30 paces. It would have taken little more effort and time to tame them entirely. Welles and Welles (1961) describe rather similar experiences with desert sheep in Death Valley, California. It can be safely suggested that any unhunted sheep population may be tamed and studied.

# PART I

# DESCRIPTIONS OF BEHAVIOUR PATTERNS OF SHEEP

## Introduction

The behaviour patterns of sheep can be grouped into three major categories. These are habitat behaviour, body care behaviour and social behaviour. Habitat behaviour is directed at the physical environment of the animal - its habitat. Body care behaviour is directed mainly at the animal's own body, while social behaviour is directed at other members of the same species. Social behaviour patterns have meaning to conspecifics, in so far as these may respond predictably, but some patterns are understood beyond the species limit, such as threat behaviour. In this thesis, social behaviour is of major concern.

How does one recognize social patterns? They appear to differ from "normal" stances and actions by very specific deviations. Normal movements are slow and relaxed, never rigid. A rigid stance can be just as conspicuous as its converse and serves as a rather disturbing signal to sheep (Fig. 27). Social behaviour patterns deviate from normal behaviour by unusual conformations of body parts, by faster, jerkier or slower and stiffer movements than normal, by non-random orientations towards conspecifics and by the release of specific sounds and odours. Ultimately, a social behaviour pattern must have some effect on the conspecific it is shown to; it must have some "social meaning". Unfortunately, there is no simple way to determine this "meaning" objectively. It appears though that it could be determined objectively by comparing a normal rank ordering of behaviour with a similar rank order recorded after the occurrence of a social behaviour pattern. The meaning of the social pattern should be inversely proportional to the correlation coefficient of the two rank orders. In this study I determined social behaviour patterns subjectively.

Sheep have somewhat more limited means of social expression than other mammals. Unlike moose or deer, they cannot raise a mane on the neck or erect the body hair. Their ears are very small and although they do assume characteristic positions, they change the appearance of sheep little. A flick of the ear can markedly alter the appearance of a cow moose or deer, but not of sheep. Unlike primates or carnivores, sheep have almost no facial expressions save for slight changes when closing the eyes or dilating the nostrils. However, sheep appear to use their tongue for visual and tactile expression.

All coloured American sheep have large, white rump patches and a white nose. Sexually mature rams, in particular, have a pronounced white muzzle. These shade patterns are most conspicuous in fall and early winter when sheep carry their darkest coat. Since the guard hairs are very brittle (except on the face) the coat becomes worn in winter and becomes progressively lighter. Thus a ram crossing through some thick dwarf birch one December morning, left a shower of broken hairs in his tracks. In spring some bighorn ewes were so light that the rump patch disappeared (Fig. 24). In addition, rams are strikingly differentiated anteriorly by their large horns. Hence, sheep tend to be most conspicuously marked anteriorly and posteriorly during early winter. The primary organs of expression for sheep are its head and neck, and, to an undetermined extent, its coat patterning.

Before concentrating on the social behaviour, it appears important to understand what relationship habitat and body care behaviour have had to the evolution of sheep. Hence a short description of these behavioural adaptations will precede that of social behaviour.

## Habitat behaviour

The habitat adaptations of Dall and bighorn sheep are those of a generalised mountaineer, capable of running at great speed over short distances, who jumps rather than climbs in treacherous terrain, but who is specialized to grazing which in turn restricts him to areas with low winter snow. The habitat, and to a small extent the social behaviour of sheep is influenced by this central theme in its adaptations.

Sheep are normal cross-walkers, which many gazelles are not (Walther, 1958). Unlike mountain goats, sheep quickly begin trotting or bounding, whereas the goat tends to walk even when escaping. American sheep are superb jumpers and traverse cliff terrain often in this manner. The large *Ovis ammon poli* is apparently a poor jumper and climber, who in confinement shuns rocky terrain - unlike ibex or markhor (*Capra ibex* and *C. falconeri*). Sheep travelling on brittle snowcrusts spread their legs and place hooves and dew-claws simultaneously on the surface.

The manner in which Eurasian wild sheep lie down and rise has been described by Lannier-Tanner (1965); American sheep follow the same pattern.

The resting positions of sheep show some variability of leg placing, but are less variable than those of deer (Odocoileus) or moose (Alces). They rarely rest with all four legs stretched from the body; I have never seen sheep lie flat on their sides as moose (Geist, 1963) or deer (Fig. 11) occasionally do. During cold weather sheep draw their legs tightly against their body (Fig. 12), but extend them often in warm weather. Some rest with the muzzle or a horn tip placed on the ground.

Sheep tend to rest together and to use the same beds repeatedly (Fig. 13). Small lambs frequently rest uphill close to their ewe (Fig. 14). The prerequisites of bedding sites are level areas large enough to hold a sheep, and good visibility. Sheep may rest at night high in the cliffs, particularly during spring.

In contrast to sheep, moose rarely use the same bed twice in winter (Des Meules, 1964). Moose slump into deep snow to rest and partially bury themselves (Fig. 15). The deep, fluffy snow apparently serves as insulation and thus in heat conservation. Des Meules noted that moose left an area, once the snow was trampled and searched out areas with fluffy deep snow. I have not seen sheep use snow in this manner. However, they do go into caves to rest during cold winter days, or search out cracks in cliffs.

An important adaptation of sheep is scratching. It is used to paw beds, which due to continuous use, become enlarged by this activity. Scratching removes the rocks and pebbles which have rolled down the slope on to the bed. This is demonstrated by a Dall's ewe in Fig. 10. After the bed had been cleaned to the soft sand, the ewe lay down. Yet, as Walther (1961) correctly pointed out, pawing is not an intelligently performed behaviour, for sheep paw on any sort of substrate prior to resting, be it sheer rock, soft grass, or a concrete plate. I observed that lambs 7 days of age began to paw for the first time. They incorporated it into play. They pawed, jumped, and frolicked, pawed, jumped, etc. I have seen one lamb paw a bed, then step three paces forward and lie down. These animals used pawing, but not with any apparent insight. This is further indicated by adult sheep attempting to remove conspecifics from a salt block by pawing their backs. The same behaviour is used to get a conspecific to vacate a bed (Fig. 17).

Sheep paw craters into the snow blanket (Fig. 18) and feed on the uncovered grasses. Pawing is very stereotyped in sheep and is used frequently in winter as long as the vegetation is covered by soft snow. Other ruminants found in the mountains, such as mountain goat, deer (<u>Odocoileus hemionus</u>), elk (<u>Cervus canadensis</u>) and moose also resort to pawing snow from vegetation; of the four species mentioned moose do it least often. Pawing the snow blanket from forage is, however, by no means universal. Buffalo (Bison), like cattle, do not paw but push the snow away with their snouts (Fuller, 1960).

I shall describe the home range and migration characteristics of sheep, as well as some of their other habitat behaviour elsewhere.

## Body care behaviour

The peculiarities of the coat of mountain sheep appear to be related to certain characteristics of their comfort movements. Sheep have long, brittle guard-hairs underlaid by an abundance of fine wool. Unlike mule deer, mountain sheep appear to have only one moult per year. Ryder (1960) found for mouflon (O. musimon) that there is one conspicuous spring moult when the primaries (guard hairs) and the secondaries (wool) are shed, and that a second peak of primary shedding appears in fall. The same may be true for American sheep, however, only the spring moult is conspicuous.

The moult is a most striking event. The hair comes off in matted bunches and may hang like towels about the animal (Fig. 19). The first sign of moult appears in March but the sheep are not completely shed until July. It is during the moult that sheep show occasionally frantic comfort movements, from which one can infer that the loss of hair is associated with some discomfort.

The most common comfort movement in spring is body rubbing. Sheep move to rock outcroppings, dead trees, small bushes, coarse rubble fields or erosion sites and proceed to rub hard against the rough surfaces. They polish their sides, shoulders and rear ends back and forth against the obstacle. The hair is not always rubbed off but broken off, resulting in strips and spots of old hair bases still firmly embedded in fields of newly growing ones (Fig. 7c). I have never seen elk, moose or mule deer act like sheep do, but neither do these cervids have a moult in which the matted guard hair and wool comes off in strips and decorates the countryside wherever they go. From 650 comfort movements of rams counted in spring 1964, 263 (40.5%) were body rubbing.

The moult is greatly accelerated on the withers of small horned sheep. This appears to be due to the presence of the tick (Dermacentor andersoni). Sheep scratch their withers with their horn tips and remove with it hair and scabs (Fig. 20). The whole upper shoulder region may be laid open and be full of small scabs and round, whitish marks where ticks apparently attached, broken brushes of guard hair, engorged and actively crawling ticks (Fig. 21). The ticks were surprisingly loose in the skin. Those which I plucked out came away with a scab. Wither scratching with a horn was the next most common comfort movement for it occurred in 650 comfort movements 151 (24.0%) times.

A most common method of scratching is with a hind leg. Sheep scratch the chest, upper front legs, neck and head in this manner. It occurred 146 times in 650 comfort movements. Sheep use their tongue and teeth less commonly. Such comfort movement occurred only 79 out of 650 times, while shaking the body - a method of ordering the hair coat - occurred only 11 times. With their mouth, sheep work over front and hind legs, the flanks and occasionally haunches.

There are other comfort movements which have nothing to do with grooming or care of body surface. Sheep yawn, as do deer and moose. They stretch after resting periods (Fig. 22). However, I have not seen sheep hunch their backs in a stretch as moose, elk and mule deer occasionally do (Geist, 1966b, Fig. 1). They do stretch their neck while pulling in the chin sharply.

The urination and defecation postures of sheep are similar to other bovids but deviate from those of telemetecarpalian deer (Geist, 1966b). Defecation occurs from a near normal posture, only that the tail is raised. Sheep do not usually interrupt the activity in which they are engaged when defecating. The urination postures of the two sexes vary greatly. Ewes squat and urinate backwards with a raised tail (Fig. 23). This posture does have some social significance. Rams stand almost normally, their hind legs are only a little farther back and the back is depressed slightly.

The evidence suggests that comfort movements have their own sphere of selection and evolve quite independently of social- or habitat adaptations. For instance, mountain goats and sheep have rather similar habitat adaptations although they emphasize various adaptations within this category differently. Both feed on low herbaceous vegetation, but the sheep is specialized for it and has the longer, sub-hypsodont molars. Both paw to remove snow from vegetation, although the goat is more efficient. Both avoid the cold early mornings by becoming active later in the day. Both frequent precipitous terrain but whereas the goat climbs primarily, the sheep jumps quite frequently. However, in their comfort movements, sheep and mountain goat differ greatly, as in their social adaptations (Geist, 1964).

Mountain goats show comfort movements exceedingly rarely, and whey they do so, they appear clumsy and inept. But goats sand bathe. They dig in dry sandy soil and throw it over their flanks and haunches. Their coat of long guard hairs and wool is impregnated with sand. The fur on the goat's body is very long and dense, which raises the question of whether scratching or nibbling would be an efficient manner of reaching the skin surface. Sand bathing appears to have taken the role played by the movements connected with body surface care (Eisenberg, personal comm.).

As was noted earlier, deer and moose do not rub off their hair coats. However, they possess comfort movements sheep do not have. When the antlers are in velvet, deer and moose rub the antler tips under the raised hind leg. Whereas sheep commonly use the horns to scratch withers or shoulders, I did not observe moose or deer doing so. Generally deer appear to be more nimble and elegant when scratching with the hind leg or nibbling their body than sheep.

The giraffe has evolved comfort movements different from those of sheep, deer or mountain goat. It does some rubbing on tail shrubs or trees; it does not scratch itself with the hind legs or the horns, its main method of cleaning its body surface is nibbling with the incisors and licking or smacking the body surface with its tongue. In addition, the tail is used for swatting, and the skin can be quivered quickly presumably to dislodge insect pests (Backhaus, 1961). To dislodge insect pests, mountain sheep and caribou jerk their hind legs, flip the ears and tail, while caribou may gallop on to large snowpatches or partially submerge themselves in water.

It appears to me that comfort movements are primarily adjusted to the kind of body covering evolved by the animal, using the most accessible means - be it teeth, horns, tongue or hooves - to rub and cleanse the fur; in special cases, such as the long wooly hair of mountain goats common comfort movements atrophied and were replaced by a specialized but more appropriate behaviour. Ruminants evolving in common habitats will probably evolve similar body covers and similar comfort movements, although sheep and mountain goat demonstrate that this need not occur. Furthermore, symbionts like tick-birds of Africa may also do cleansing of the body surface as Backhaus (1961) pointed out, and somehow influence the evolution of comfort movements. This all indicates that a comparison of comfort movements between different species has little merit if the biology of the species is not known.

## Social behaviour

### Attention, alarm, horning and eliminating behaviour

The most common postures assumed by sheep are those of grazing, resting and walking. None of these has social meaning in the sense that no responses to these behaviours are noticeable from other sheep. During normal walking, the sheep's head is held quite low, nose pointing to the ground while the ears are held back and droop down a little. Yet, one deviation from this position, a sharp raising of the head coupled with a tense walk or a rigidly held body at once draws the attention of other sheep. It is the alarm posture (Fig. 25); elk have an almost identical alarm posture (Fig. 26).

An alarmed sheep need not run away, but may move at a stiff, tense walk uphill. It stops periodically, looks at the source of disturbance, and then struts on again. It appears to glance at the disturbance from the corner of one eye. On several occasions single rams carried the alarm behaviour to extremes. They strutted about in tight circles in one place, stopping periodically to look at me, and finally slowly lay down facing me. Murie (1944) described a whole band of Dall's sheep doing this in front of a wolf.

In addition to assuming the characteristic posture, alarmed sheep may stamp the ground with one front leg (but rarely do so), and blow sharply through the nose. This is done by domestic goats (*Capra hircus*), and some Asiatic sheep (Walther, 1961).

A sheep suddenly freezing and staring in one direction, alerts others who then do likewise. This is the attention posture (Fig. 27). The ears are perked forward and the animal may orient its body along the line of sight. A sheep standing and looking steadily in a tense, rigid stance in one direction, has very likely seen something of interest such as a predator, or a distant sheep. A sheep which frequently interrupts feeding and then looks steadily across a gorge, valley or belt of timber, assuming a less rigid posture, indicates that it will soon move in that direction. With its gaze the sheep gives notice of its intent, and the direction it will take. Schaller (1963) and Kühme (1965) described similar behaviour of leaders of gorilla and African hunting dog (Lycaon) groups, respectively.

Neither the defecating nor urinating posture of rams deviates appreciably from the normal stance, and appears to carry no social significance. However, the ewe does urinate in a most conspicuous manner (Fig. 23) and draws the attention of nearby rams. They come and nuzzle the female's vulva and urine, and very frequently perform a lip curl thereafter (Fig. 48). Walther (1958) suggested that in species in which urine or dung played a social role, the urination or defecation posture is conspicuous. The act of defecating or urinating is signalled thereby to conspecifics. There seems to be merit to Walther's suggestion; the defecation posture of cattle is accentuated and defecation is a consistent part of pre-combat behaviour (Schloeth, 1961); the conspicuous defecation posture of Oryx bulls is shown by the dominant male after chasing off subordinate ones (Walther, 1958). However, it is not known what selective forces favour conspicuous elimination behaviour.

Horning of shrubs, grass bunches or small trees may have some social meaning (Fig. 28). It occurs frequently during dominance fights of rams, and is performed equally often by the partners (p.78 Fig. 73). Some of the horning may simply be done to remove an uncomfortable clump or hair or other irritant from between the horns. Occasionally, rams butted heavily against elastic conifer stems and let the backlash carry them back to the original stance. Other rams horned and nibbled juniper branches (Juniperus) alternatively and appeared to grow more excited by doing it. It appeared that rams preferred lodgepole pine (Pinus contorta) for horning, and the twisted, damaged stems of small pines at timberline (Fig. 29) gave ample evidence of this. White-tail deer (Odocoileus virginianus) also prefer conifers for horning (deVos, personal comm.). It may be that essential oils found in conifers stimulate sheep, deer and also elk to damage these trees. I observed one cow-elk tear off bark from pines in sap, then rub her head and neck liberally in the tree's wound. Experiments by Gundlach (1961) on red deer (Cervus elaphus) showed the excitatory effects of pine oils on these deer.

Generally sheep horn during intense social interactions, or prior to long movements through timbered valley floors. Mountain goats were also observed to horn shrubs and grass bushes in agonistic interactions. This behaviour is occasionally contagious, for several rams may start horning after one begins. Horning may be initiated with a butt, after which the horns are rotated or scrubbed under pressure over the grass bunch, shrub or small tree. The horning posture is often tense and the tail may be raised. There is an aggressive overtone in this behaviour.

Orientation towards the conspecific:

When the ewe calls her lamb, she orients herself towards the lamb and looks directly at it. I emphasize this, because for sheep a direct stare appears to be an aggressive pattern and is not tolerated. The evidence for this is indirect. Subordinates look away from dominants when the latter approach (Figs. 30 & 32a) and often turn their rear to them. Even lambs do this (Fig. 31). In this figure note their orientation when the yearling female was present and when she departed. During the post-clash horn display the subordinate ram may close his eyes rather than look at the dominant's face (Fig. 34). Sheep tend to rest in such a manner as not to face each other directly (Fig. 32b). It appears to me that looking at a conspecific directly at short range is the prerogative of the larger sheep (Fig. 32a), and that the smaller sheep which happened to do it were frequently butted in return. Generally, when sheep are close together, they face in the same direction, probably because this minimizes staring.

When sheep are on the move, they discourage others from passing them by displaying, butting, cutting off the one attempting to pass, or running quickly ahead thereby restoring the original position. It can be occasionally observed how a smaller sheep, attempting to walk past a dominant at close range, is butted as soon as it reaches the shoulder level of the latter. It appears that dominants try to keep others behind them. This results in a remarkably stable march order when sheep are on the move, but also gives rise to the illusion that the dominant, leading the sheep attempts to defend its "lead" position.

Behaviour patterns exchanged between conspecifics:

Such patterns can be divided into those which are shown by the ewe and her lamb, and those which adults perform towards one another. Only the latter kind of behaviour patterns will be considered here.

The horn displays. These are the most common social behaviour patterns of sheep, performed usually by dominant towards subordinate individuals. Dominant here always means the animal acts in a manner characteristic of a larger bodied sheep towards a smaller one. The horn displays are indirect - or present - threats (Geist, 1964), comparable to the broadside displays of many mammals. Horns are displayed from two postures, the low-stretch and the present (Figs. 33 & 34). The former is the more conspicuous, and the only horn display I quantified.

From both postures the horns are shown fronto-laterally (Fig. 35). It appears that with this orientation more "horn" is visible to the opponent than from a frontal or lateral position. During the approach in low-stretch sheep may flicker their tongue. The ears are deflected sideways, or the ear on the off-side to the opponent is held straight out (also mule deer bucks, Geist 1966; for black buck (*Antilope*) Walter, 1960, described the opposite): during some low-stretch approaches the ears are pointed towards the opponent.

The low-stretch occurs during the following social interactions:

(1) Between rams in their frequent engagements (Fig. 37). Rams of equal horn size tend to display to each other (whereas normally only the larger horned ram displays).

(2) By rams (and occasionally ewes) when entering a band, leaving a band, passing a smaller individual - or a larger one at longer distance - and occasionally by the ram leading a band.

(3) By ewes and rams attempting to displace a subordinate from his resting place (Fig. 32g) and by ewes towards smaller ewes or subadults.

(4) By rams towards ewes when initiating courtship. Here the ram may crouch slightly and in some instances go very low in front (Fig. 38).

(5) When passing another species, i.e. deer. This I have seen, however, on one occasion only.

The low-stretch is shown more frequently by rams than ewes, more by older rams than younger animals; the earliest age at which sheep perform the low-stretch appears to be 5-6 months. This behaviour is almost absent from the behaviour of lambs.

The "<u>present</u>" is performed with the head held high and the nose pulled slightly away from the opponent, so that displaying rams appear to look past each other (Fig. 34). The ears are usually folded back, the eyes of the subordinate ram may be shut. The present usually follows a clash. The rams recoil back and freeze into the present. It occurs primarily after clashes or threat jumps performed in dominance fights and is usually missing after clashes during vicious battles. The present is commonly seen during huddles of rams, and occurs also during courtship of the estrus ewe (Fig. 94).

The twist: The twist can be interpreted as an intensified horn display from the low-stretch position. The display is intensified by the addition of a rapid rotation of the head about its median axis, intensified tongue flickering, a loud growl, and occasionally a nudge into the opponent's side with the muzzle. A twist may terminate a low-stretch approach and the ram freezes into a horn display; twists may alternate with low-stretch horn displays as the ram stands behind and displays to a smaller subordinate. During courtship of ewes about to enter estrus, young rams may pounce forward towards the ewe, quickly lower the head and twist while flickering the tongue and uttering a growl, then return to a near normal stance. This repeats itself with the ram twisting once left, once right (Fig. 40). The ram remains constantly some distance from the ewe. During ram engagements the dominant may not only nudge the subordinate during the twist and flicker the tongue in his fur, but simultaneously push him with the chest.

<u>The front kick</u> (Laufeinschlag, Walther, 1958): The kick with the front leg is very frequently performed right after the initiating low-stretch or twist. It is a behaviour used mainly by dominant rams. The ram raises a front leg and hits the opponent ventrally on belly, chest or haunches, rarely on neck or chin (Figs. 41 & 42). Occasionally he may take the opponent's body in a front leg - chin pincer. The twist and front kick are frequently combined (Fig. 41). Rams may growl loudly when kicking estrus ewes or other rams during intense ram-ram interactions. Occasionally they bump their chest into the opponent's side during each kick and - rarely - dig a horn tip into his back. Latter behaviour I saw not infrequently among bighorns but only during one dominance flight among Stone's sheep. I have also seen large rams combine the kick with such a strong push with the chest, that they moved the opponent several steps downhill. In extreme situations, i.e. by rams about an estrus ewe, rams may kick so high up on an opponent's haunch that it appears the ram attempts to mount.

The front kick is less a kick than tapping. I have experienced it about a dozen times when getting between two interacting sheep. This is almost completely a behaviour pattern of rams, for ewes perform it very rarely but in the same context as rams (Fig. 71). Old rams perform it more frequently than young (Fig. 103). Very rarely, pawing will replace the front kick if the opponent happens to be resting (Fig. 17).

The front kick is a characteristic behaviour pattern of many, though not all ruminants. It is absent in deer, but does occur in both living species of the Giraffidae (Walther, 1960) and many, but not all, tribes of the Bovidae (Walther, 1960). In all species for which this behaviour pattern was described, it is performed during courtship by the male on the female, often it is highly ritualised as, for instance, in the geenruk (Lithocranius) (Walther, 1958). Mountain sheep appear to differ from this rule as males perform front kicks on other males during agonistic interactions. I shall demonstrate later that rams really do not deviate from the rule, and that the front kick among sheep is still a courtship pattern. Sheep differ from other known bovids insofar as they do not differentiate behaviourally between male and female. A big ram treats everything smaller than he is with courtship patterns irrespective of sex. I cannot completely agree with Walther (1964) that because the front kick appears in agonistic situations between sheep, it must be looked upon as derived from aggressive behaviour. In American sheep the front kick is now part of the males present-threat complex.

The neck fight (Fig. 43): This is a very rare behaviour pattern of rams which, in the few instances observed, was performed on rams as well as ewes. The ram puts his chin and throat over the withers of his opponent, however, no wrestling or pushing follows. This behaviour pattern, common and functional in the barbary sheep or aoudad (*Ammotragus*) (Haas, 1958) must be considered vestigial for mountain sheep.

The mount: Mounting is performed by dominants on subordinates of both sexes. Ewes mount each other rarely. Exceptionally a young ram may mount a larger, older ram when both are part of a huddle group. The mounting posture of sheep is quite erect, with the nose frequently pointing at the back of the partner. Pelvic strokes are performed, irrespective of the sex of the mounted. Prior to mounting, the penis may be partially extruded. It was noted earlier that dominant rams treat subordinates as if they were females. In addition, subordinates may react like females to the actions of the dominant. Thus the small ram in Fig. 44 mounted by the larger one, performs lordosis.

Mounting is part of the dominant - subordinate behaviour complex, and hence occurs throughout the year. It is more commonly performed by young rams than old ones when courting non-estrus ewes (Fig. 116). Lambs during play commonly mount each other.

Ejaculation: Rams may ejaculate throughout the year, during interactions with other rams, while courting estrus or non-estrus ewes; they may ejaculate spontaneously without any visible cause when alone. This happens occasionally in the morning after the ram rises from his bed. Ejaculation is not frequently seen. During the act the ram suddenly crouches in the rear, protrudes the penis sideways past the front legs (Fig. 45) then staggers stiff-leggedly forward or steps around in a narrow circle. When he withdraws the penis, the ram returns from the stiff, tense ejaculation posture to the relaxed normal stance. I saw a Dall ram lick what was probably the ejaculate and perform a lip curl thereafter. Unlike the barbary sheep (Haas, 1958) or ibex (Krumbiegel, 1952) mountain sheep only exceptionally nuzzle their penis during ejaculation. (I saw only one small Dall ram do such.)

Courtship: Courtship is part of the dominant - subordinate behaviour of sheep and contains most of its behaviour patterns. I shall deal with it in more detail later, but shall describe here some of the behaviour patterns more unique to courtship than to other interactions.

In the most probable sequence, the ram approaches the ewe in a low-stretch (Fig. 46), sniffs and licks her vulva (Fig. 47), upon which the ewe urinates and the ram - after nuzzling the urine - performs a lip curl (Fig. 48). Then the ram usually leaves the ewe. This sequence is commonly performed on non-estrus ewes. However, courtship is much more varied than indicated above.

Several rams may court one ewe (Fig. 46). The non-estrus ewe may be courted by smaller rams without the larger ones interfering (Fig. 49). Larger rams do not prevent smaller ones from testing a female's urine and one commonly sees several rams lip curl where one ewe urinated (Fig. 48).

Subordinate rams may urinate to dominants and occasionally a yearling female may urinate to a dominant ewe approaching her in low-stretch. Rams will hence lip curl not only over the urine of ewes, but also over the urine of other rams including their own. Lip curling is commonly observable when rams interact.

It is probable that lip curling indicates sexual maturity in yearling rams. Those yearling rams which lip curled did show some rutting behaviour but not those that did not lip curl. Lamb and ewes lip curl so rarely that I saw only one bighorn ewe do so.

The behaviour patterns described so far are characteristic of large, dominant sheep. The social behaviour patterns following are more commonly initiated by subordinates, while some are equally frequent in the behavioural repertoire of both.

The horn threat: The horn threat is an indication movement to butt and as such belongs to the category of weapon threats (Geist, 1964). It is frequently shown by subordinates towards approaching dominants, or by dominants chasing away or charging at a subordinate. The behaviour consists of lowering the head and inclining the horns towards the opponent (Fig. 33).

Horning, rubbing, nuzzling (contact patterns): These are the most commonly used behaviour patterns of small rams on larger ones. After a small ram initiates an approach he begins to lick and nuzzle the head of the dominant, to horn his face, neck, chest or shoulders, or to rub his face on the face of the dominant (Fig. 50).

Older Dall's rams carried distinct grey and black markings around their preorbital glands and eyes, whereas small horned young rams showed little evidence of this (Fig. 2). I believe these dirt markings are caused by the horning of young rams. During the frequent daily hornings, dirt and the secretion from the preorbital gland would be spread about the eyes of large rams. It is most likely, furthermore, that subordinate rams would impregnate their own horns and faces with the gland's secretion. Therefore, a band of rams would quite likely acquire a group-scent from this horning. At present the function of the preorbital gland is unknown.

I noted earlier that mountain sheep hair is very brittle. This does not apply to the facial hair of rams which is quite tough. It appears to me that this may be related to the facial hornings rams receive almost daily throughout the year. If the facial hair were brittle it would be quickly broken off and removed by the activity of the smaller rams. Removal of facial hair would expose the skin and leave it unprotected during clashes and directly exposed to snow and cold temperatures in winter. Apparently a small air space is advantageous between snow and skin, for caribou, among the cold climate grazers, have completely furred muzzles. I suggest that rams with soft, brittle facial hair would be selected against.

While a subordinate is licking, horning or rubbing the head or neck of a dominant, the latter stands and displays in present, and occasionally kicks and growls at the subordinate.

These behaviour patterns, horning, licking and rubbing are also used by the courting estrus ewe (Fig. 94).

The butt: Horning by the subordinate may occasionally lead directly to butting. This behaviour pattern is used by dominants and subordinates about equally frequently and is the mildest, overt aggressive pattern of sheep (Fig. 51).

It occurs in the horn threat-rush-butt sequence (Fig. 52), with which dominants chase away subordinates, a sequence used relatively more frequently by ewes and subadults than rams. Dominant rams tend to butt subordinates which pass too closely in a low-stretch, and subordinates may butt dominants which come to them in a horn display. Bighorn rams occasionally combine the front kick with a butt on smaller rams.

The butt is an attempt to hit the opponent with the horns. It is a hammer-like downward blow with the head during which the chin is drawn in and the horns tilted out. After contact is made with the opponent, the chin is drawn in even tighter and the horns pushed into his body. The most exaggerated form of the butt is the clash.

The clash: The clash differs from the butt mainly in the force of execution and the means of achieving this. Whereas the butt is performed by one opponent only, both opponents participate in the clash. The clash may be delivered from a four legged stance or a bipedal run. Movie film revealed that the clash is not simply two rams running head long into each other. It can be divided into several stages.

The preparatory stage: The ram initiating the clash faces his opponent, simultaneously lifts one front leg off the ground, crouches in the rear and tilts his head sideways. If the head is tilted left, it will be the left horn which will first make contact with the opponent. The eyes are wide open and the ears are laid back flat. The ram may further get up on his hind legs and lift the front legs off the ground (see threat-jump) (Fig. 53).

The forward propulsion: The hind legs propel the body up and forward, the eyes are fixed on the opponent. Now several changes take place:

(a) The body straightens out and begins to descend,

(b) Neck and head are moved down at a greater rate than the body,

(c) The chin is pulled in sharply propelling the heavy horns forward and downward.

Hence, there are four forces which increase the forward and downward momentum, (1) the body propulsion, (2) the fall of the body due to gravity, (3) the downward propulsion of the neck and head, and (4) the forward and downward propulsion of the horns. It appears that these forces would summate, producing a far harsher blow than if the ram clashed rigidly into the opponent (Fig. 54).

Contact: Just prior to contact the eyes of the ram close. On contact with one horn edge, the head of the ram begins to rotate so that the nose points down. This brings the second horn into contact with the opponent. It appears that the clash is hence a double blow with the horns (Fig. 55). Now the clash may continue in one of two fashions:

(a) The sheep kicks up in the rear and pivots its body weight about the front legs, thereby "riding home" the clash. The upward throw of the rear - in combination with a rigid body - would increase the downward force of the head (Fig. 65b & 56).

(b) The animal on contact collapses its front legs, letting the rigid body pivot in the acetabulum, and then quickly crouches in the rear. Both these actions would continue the downward force behind the blow after contact (Fig. 67).

The catch-phase: After contact the ram begins to prepare his body for landing (Fig. 55b). This consists mainly of bringing the legs into line with his descent; it is best illustrated when a clash misses (Fig. 58).

There are many variations to the clash. It may occur when the ram's front legs are off the ground (Fig. 59), or the hind legs are off the ground (Fig. 3, Geist, 1966c). The ram may not catch himself with his front legs and thus crash head first into the ground (Fig. 60). The clash is followed during dominance fights by a present (Fig. 34).

Primary effects of the clash: Both the great force and the rough, grooved horns leave their mark on the opponent.

The ridges and grooves of the horns permit a grip on the opponent's body, but tear out hairs in the process. The horn surfaces of fighting rams are usually covered with bits of broken hair. The following effects are noticeable:

(1) Smaller rams may get literally telescoped by the force (Fig. 61). However, I have not seen rams thrown back by a clash, probably because most clashes are initiated by the smaller, subordinate animal.

(2) The nose and orbital regions get badly cut (Fig. 62).

(3) The horn tips get broken and splintered, while chunks get knocked out of the horn edges (Fig. 62). Occasionally, a large part of the horn is lost (Fig. 63).

(4) Gashes are opened on the body with broken horn tips; one ram apparently received a broken shoulder through a fight; one dead ram found had the left horn core snapped off. Considerable amount of blood had accumulated subcutaneously, as was indicated by the dark red connective tissue on the left side of the skull. This ram was probably a fighting casualty.

(5) Hair is torn out, occasionally in great clumps (Fig. 62).

(6) Blood may be found on the horns of rams after they fight. When horns are growing in spring and summer,

blood oozes in large drops from the contact line between horns and facial skin.

I do not know what internal damages, if any, rams redeive during fighting. I have not been fortunate enough to autopsy a ram that had fought. The damage which was observable centered about the head primarily, which is not surprising if the defensive mechanisms of sheep are considered.

A secondary effect of the clash: In an earlier paper I reported that rams can judge by the horn size of a stranger whether he is dominant or subordinate. Large horned strangers are accepted as dominant and small horned strangers as subordinate. Dominance fights occur between strange rams of equal horn size (Geist 1966c). It appears therefore that rams know not only the horn size of other rams, but also their own. How is this possible?

Rams usually display their horns in a present immediately after a clash. They hence experience both the force of the clash and the sight of the opponent's horns. It was noted that the clash had four force components, of which the last one is the downward blow with the horns. This blow should vary in severity with horn mass. A large horned ram should hence deal out a more severe head blow than a small horned ram. This blow is followed at once by the horn display. Hence each opponent experiences a given blow force and sees the horns of the opponent immediately after this. The rams should then connect the strength of blows with the horn size of opponents. Therefore rams should be able to estimate what blows their opponents are capable of purely by looking at their horns. Since clashing occurs quite frequently, rams are constantly reminded of the relationship between horn size and the force of blows. Hence rams should be able to estimate the clash potential of strangers purely from their horn size.

The defense mechanisms: The simplest way to escape the effect of a clash or a butt is to jump aside (Fig. 58), a behaviour commonly resorted to by subadults and females but rarely by rams. Observations in the field and of slowed down motion picture film of fighting sheep, showed that they constantly attempted to face the opponent and catch his blows with their horns. In Fig. 64 a 2 year old ram is in the process of butting a ewe. Note that the ewe is swinging her body around to line up with the direction of the butt. Her head is lowered and the horns are pointed forward to receive the blow. The downward blow would be caught by the horns against the tension of the neck and would force the head of the ewe down, but would hardly do any damage. One function of the horns is hence to shield the animal and neutralize the opponent's blows. This proposed function explains much of the sheep's head morphology.

The first line of defense against blows on the face, is a thick tough hide. In fact, the skin on the nose and front is thicker than on any other part of the body. Unfortunately I had only one specimen, a 6½ year old Stone's ram, to examine. Therefore, I made skin measurements on males of domestic goats. The domestic goat is a close relative of the sheep and possesses similar fighting behaviour. Therefore, they should have similar defensive mechanisms, which is borne out by both skin measurements and skull structure. For comparison purposes, the skin measurements of a mountain goat male are compared with that of domestic goat and Stone's sheep (Fig. 65). The mountain goat does not fight like the sheep or domestic goat with frontal butts, but strikes ventrally at the opponent's belly and haunches. Most blows exchanged by mountain goats land on rump and belly, since the antagonists are positioned anti-parallel to each other (Geist, in press). Note that the goat has a "rump shield" of thick dermis, which in a 9 year old male reached 22 mm in thickness. On the other hand the facial skin of goats is thin, which correlates with the absence of head-to-head fighting in this species. It appears hence, that species develop thick skin where most blows tend to land during fighting.

The skull structure of mountain sheep, rams in particular, appears to be adapted to withstand heavy concussion. Like other ruminants, or swine, which collide head on in fighting, the skull of sheep is heavily pneumated. There are two layers of bone, up to 5 cm apart, overlying the brain. In the space between these bones are numerous cross connections of bone, acting like struts. The double roof extends from about 5-6 cm before the brain to the occiput. Here it fuses into one 2 cm thick spongy textured bone. The bony horn cores, about 10-11 cm in diameter at the base, are formed from the upper skull roof. They are hollow and filled with a maze of cross connections. Some of these bony struts radiate out from the lower bony case encapsuling the brain, and run almost half of the length of the horn core. The bone forming the horn core is very dense and up to 6 mm thick. The nasals are solidly fused to the frontals and are of dense, strong bone. By contrast, the skull of mountain goat is light. The brain is encapsuled in one layer of light, spongy textured bone. The nasals and frontals are both thin. The whole skull is fragile and fractures now and again on goats shot and who subsequently fall down mountain sides.

The space surrounding the lower braincase of sheep, appears to be derived from the frontal sinuses. In mountain goats these sinuses are very small and located just anterior to the brain over the cribriform plate. Domestic goat occupy a position intermediate between mountain goats and sheep. The sinuses are greatly enlarged, but do not reach past the horn cores. Hence the parietals are one spongy textured bone over the brain; in mountain sheep the parietals are split into an upper and lower layer connected by cross struts. The skull of male domestic goats is much heavier and sturdier than that of mountain goats but is not as heavy, complex and probably sturdy, as that of bighorn sheep.

It is most likely that there are other alterations in the skull and the placement and attachment of the brain, or the junction of occiput to the cervical vertebrae. For the present they escaped detection. There is, however, little doubt that the hair, skin and skull structure of sheep has evolved under severe social selection. Besides showing adaptations to the habitat, such as subhypsodont dentition or wide interoccular distance (useful for judging distance when jumping), they are also adapted to the social environment of sheep.

The threat-jump: This pattern is an intention movement to clash and is hence a weapon-threat (Fig. 66). Like the clash it is primarily a pattern initiated by smaller sheep and shown to larger ones. It is shown by both sexes and by lambs (Fig. 53). It occurs commonly in the play of sheep (Figs. 82 & 81). During dominance fights, some threat jumps are followed at once by the present (horn display).

The head shake: This is a behaviour shown almost only by smaller sheep, particularly subadults and females after having been disturbed by a larger sheep. Occasionally, following the head shake the animal bounces forward, frolics, threat jumps and runs on. The head shake may also initiate a threat jump, leading occasionally to a clash. Young rams perform this during play. Typically, the chin is pulled in, the head and neck are raised and the horns hence inclined forward, during the shake. On all occasions observed the sheep shaking the head had its rump toward the dominant. The head shake is not a very common behaviour pattern.

Qualitative differences in the behaviour of Stone's, Dall's and bighorn sheep:

Although the races of sheep which I studied differed greatly in coat colour and patterning as well as in horn and growth characteristics (Cowan, 1940), I could not detect any consistent qualitative difference in their behaviour. The behaviour patterns which Stone's sheep performed were so very similar to those of bighorns and Dall's, that if any difference exists, I did not detect it. Dall's sheep tend to assume a slightly more exaggerated low-stretch in which they hold up their noses a little higher than bighorns usually do. However, the latter occasionally perform this behaviour pattern as do Dall's also, and the difference is more quantitative than qualitative. Quantitative differences will be discussed later.

# PART II

## AN ANALYSIS OF THE RULES OF SOCIAL BEHAVIOUR

### Introduction

The aim of this chapter is to describe some of the rules which sheep follow when interacting with one another. To this end, quantitative data have been gathered about the frequency of social behaviour patterns, their sequence and the situation in which they occur.

The unit of comparison used here, is the interaction. It denotes the happenings between two animals from the time they engage, to the time they move apart and ignore each other. An interaction is hence very variable in time - it may last seconds, or rarely, several hours. On occasions there is, in addition, the difficulty of deciding when an interaction ended and a new one began. For instance, when several rams in a group interact one may move temporarily from his partner and engage with another only to return again. Were these two interactions on the same ram or had the ram merely interrupted the initial interaction? Or, in an interaction between two rams one moves off a little, feeds then returns again to his opponent. One or two interactions? In both examples, I treated it as one interaction. Both partners had to return to feed and separate from each other before the interaction was declared finished. In group interactions (huddles) each ram had only <u>one</u> interaction with each of the others regardless how often it was interrupted, how long the interruption lasted, or how long the huddle wore on. The frequency of various behaviour patterns is indicated in the graphs as <u>patterns per 100 interactions</u>, or as <u>patterns per interaction</u>.

The following behaviour patterns were quantified (abbreviations as used in the graphs follow in brackets):

| | |
|---|---|
| Low-stretch (Lo.) | horning the opponent's body (HB) |
| Front-kick or Laufeinschlag (L) | mounting (M) |
| Twist (T) | threat-jump (TH.) |
| Butting (B) | sniffing and nuzzling of rear (S) |
| Horn-threat (H) | charging or rushing at opponent (Ru.) |
| Rubbing (R) | lipcurl or flehmen (F) |

Behaviour patterns which were rare such as ejaculation, or the head-shake were left out. Licking and nuzzling the opponent's head were quantified under "rubbing". I recorded the response of sheep to being kicked or mounted with the symbols (o) or (-), the first meaning that no response at all occurred and the second, that the kicked or mounted sheep withdrew at once. The behaviour patterns quantified are hence those which sheep perform towards one another; I ignored patterns which were not specifically directed at companions.

The sex-age classes of sheep (Fig. 7) can be arranged in order of resemblance. When this is done, the lamb - which is smallest in body - and horn size - will be found at one end of the series, and the large full curled rams (class IV) at the other. The other classes form a smooth connecting series, each class differing only slightly in appearance from the following and preceding one. This can be seen in Fig. 7. The classes increase in body size throughout the series, quickly between lamb and female and more slowly from yearling to class IV ram. The same is true for horn size, only that horn size increases most between classes yearling ram to class IV ram. The differences in appearance are differences in degree only and the whole series class L. to IV represents one visual gradient, in which the ewe appears only as a "small horned male." In the figures in this section, I have treated this arrangement of sheep classes as such a gradient. That is, each class represents a certain degree of horn-body size development, or "male" appearance.

A number of different "social situations" could be recognized. In the normal situation an interaction between two sheep took place without others taking any notice of it, or being in any way connected with that interaction. When rams interacted in a huddle (Fig. 80), I marked such interactions and evaluated such interactions separately. Other situations were the actions of large, estrous ewe-guarding rams on subordinate ones, the interactions of subordinate rams among themselves in the presence of an estrous ewe, the interactions of rams with estrous as opposed to non-estrous ewes, and the dominance fights of rams.

Whenever the number of specific behaviour patterns is compared from one situation to the next, the patterns appear always in the order - Lo., L, T, B, H, R, HB, M, Th., C, S, Ru., F. This happens to be the order of frequency with which the patterns appear in the interactions of bighorn rams in the normal situation. The patterns have been ranked, and this is the rank order against which all other pattern frequencies from different social situations, species or sexes are compared. The rank order of behaviour patterns for bighorn rams in the normal situation, when larger rams initiate interactions on smaller, is shown in Fig. 71. The graph has been heavily outlined from pattern low-stretch (Lo.) to class(C). Beyond this I added S. Ru., and F. These patterns, sniffing of rear, rushing and lipcurling are not entirely comparable to the preceding ones. The rush is not part of an interaction, it is one interaction. It begins and ends one interaction almost every time it occurs. Sniffing and lipcurling are behaviour patterns which have no social meaning but do occur in social interactions. Hence, I placed them into each interaction but outside the rank order of socially meaningful patterns. Graphs of pattern frequencies within interactions should be read as rank order distortions (using the bighorn ram rank order graph as comparison).

There is no particular reason why the interactions of large bighorn rams on smaller ones during the normal situation should be used to compare others to, except that such interactions were rather common and did contain all the behaviour patterns quantified. This cannot be stated for instance, of interactions between lambs. I used bighorn ram interactions simply because I had to have some basis for comparison, and these struck me as convenient interactions.

## Results and Discussion

### Social preference

The first question about the social interactions of sheep is:

With whom does each class of sheep interact voluntarily? Fig. 67 gives an answer to this. Each of the seven graphs represents the percent distributions of interactions initiated by one class of Stone's sheep on others.

The total number of interactions on which each graph is based, and the symbol of the class in question (IV to L.), is indicated above each graph. For instance, class IV rams were observed in 654 interactions; they interacted most frequently with ewes (36%), next frequently with class II rams (19%), and least frequently with lambs (L.) (4%).

The graphs for rams class IV - II can be directly compared with each other since rams of these classes live in the same social environment. The same is true for graphs O yearling to lamb, since these classes live in the female bands. However, these two groups of graphs may, with some caution, be compared with each other since rams and ewes do come together from early November till late December and it is during this period that most of the interactions were observed. It is evident, that whenever rams initiate interaction with ewes, ewes could do the same. However, they do not. The graphs in Fig. 67 show the following:

(1) Rams interact with all sex-age classes of sheep, whereas ewes interact almost exclusively with sheep of equal or smaller size.

(2) Large rams interact more with rams than do smaller ones (IV = 53%, III = 50%, II = 34% of all observed interactions on rams).

(3) Large rams interact less with subadult females (♀y) and lambs (L.) than do smaller ones.

(4) Ewes and subadults as well as yearling males interact voluntarily primarily with sheep of equal or smaller body size.

It is apparent that the larger rams distribute their interactions over all sexes and ages of sheep.

The number of interactions which a class of sheep performs with another class, depends to some extent on how frequently that class was encountered. For instance, rams made most interactions with ewes (Fig. 67). However, ewes were the most common class of sheep in the vicinity of the acting rams, i.e., the 654 interactions of class IV Stone's rams were performed in the close presence of 196 IV rams, 393 III rams, 649 II rams, 251 ♂y., 947 ewes, 400 ♀y., and 509 lambs. This raises the second question:

Do sheep interact randomly with individuals of all sex-age classes, or do they prefer to interact with particular classes?

Fig. 67 has already demonstrated that small bodied sex-age classes tend to prefer sheep of equal or smaller size. However, the posed question can be answered more precisely.

One can compare the percent frequency with which a class was chosen for an interaction, and the frequency with which it was present in the social environment. Thus class IV Stone's rams performed 9.6% of their interactions on other class IV rams. However, other class IV rams made up only 5.8% of all sheep in their proximity. Therefore, class IV rams acted 9.6 / 5.8, or 1.6 times as often on class IV rams than anticipated, if class IV rams had no preference whatsoever. The ratio of percent frequency of interactions on class x over percent frequency of presence of class x, is called a preference index.

A preference index value of 1 means that the class of sheep in question was chosen as often as it was present in the social environment of the acting class; no choice has been demonstrated where the index value is 1. However, if the index value is larger (or smaller) than 1, then the class has been chosen more frequently (or less frequently) than present. A preference index value of 0.35 of III rams for lambs, shows that III rams ignored the lambs most of the time.

The preference index method is a crude manner of assessing the social preferences of each sheep class; however, it does give repeatable results, and conclusions based on it are supported by different data. We can estimate the social preference of a sheep class in a second manner. If one class of sheep prefers another class, it is likely that it will interact longer, and show more behaviour patterns towards a member of the preferred class than towards a less preferred category. This we do find. In Fig. 68 the solid circles (●)

stand for Stone's sheep preference index data; the open circle (O) for Stone's sheep, for the number of behaviour patterns performed per interaction on each class interacted with; the solid line stands for bighorn sheep preference index data. Fig. 68 shows the following:

(1) Rams prefer to interact with rams of their own size class or of a size class close to their own. Secondly, rams prefer ewes.

(2) Despite a certain amount of preference, rams interact with all sex-age classes of sheep.

(3) Rams are least interested in sub-adults.

(4) Preference index data and the frequency with which rams performed behaviour patterns per interaction on all classes, lead to the same conclusion: III rams not only choose other class III rams more frequently than others, but perform more behaviour patterns on them than on other rams.

(5) The data are not completely consistent, but are consistent enough to establish the conclusions outlined above.

The index of choice data for yearling rams of both species does not follow entirely that of larger rams. The yearlings choose their own class relatively most frequently. Their preference for ewes, however, does not appear too great. There is a good reason for this. Yearling rams remain subordinate to ewes till they have surpassed them in body size. This may occur at 16 - 18 months of age, but for some rams it does not happen till 27 - 30 months of age. As long as the yearling rams are not totally dominant over ewes, it appears to be reasonable that they choose ewes less frequently to interact with than other yearling rams.

## Interaction initiation

The next question is:

How are the social interactions of sheep initiated?

The interactions are initiated either in a low-stretch or with a weak horn-threat; occasionally no particular pattern is used. If we plot the percent frequency with which rams initiate interactions in low-stretch on larger and smaller companions, we find that the low-stretch is used predominantly towards smaller rams (Fig. 69). This is true for Stone's and bighorn sheep. The larger rams use mainly the low-stretch and the smaller mainly the horn-threat when approaching a companion just prior to the interaction.

Ewes and sub-adults initiate very few interactions in low-stretch. Adult Stone's ewes did so in only 14% of the interactions (n = 157), and yearling ewes in only 10% (n = 58). The manner in which sheep initiate an interaction depends on their sex and size relative to the companions they interact with. It should be noted that the data in Fig. 69 demonstrate that sheep are aware of the dominance position of their companion before they interact with him.

## Behaviour pattern sequence

The next question is:

Is there a definite predictable order which behaviour patterns follow after an initiation?

This question was investigated as follows: I recorded the behaviour pattern which immediately followed the approach. For instance, if a ram approached in low-stretch then delivered a front kick, I recorded (a) the manner of approach (low-stretch) and (b) the following pattern (front kick). Next I ranked the behaviour patterns which followed the approach pattern in their order of frequency. I used the interactions of large Stone's rams on smaller ones, when the larger approached in low-stretch as a basis for comparison (Fig. 70 A●, larger on smaller). It can be seen that almost any behaviour pattern could follow the initiating low-stretch. Hence no definite order in which behaviour patterns follow each other could be established, however, this does not mean that one could not predict what would follow once an interaction was initiated.

Fig. 70 shows six groups of graphs, separated into A and B subgroups. A represents interactions initiated in low-stretch and B, interactions not initiated in low-stretch. The numbers above each graph indicate the number of interactions each graph is based on. The circles represent Stone's sheep data, the solid line bighorn data, the -.-.- line without circles represents comboned bighorn and Stone's sheep data. The open circle (O) represents data from Stone's yearling ewes. All contact behaviour (nuzzling, horning, rubbing) has been brought together under rubbing (R). The abscissa represents the behaviour patterns other than low-stretch which may follow the initial approach pattern, ranked in the order of frequency as they occur in interactions of large Stone's rams on smaller ones. It can be seen for instance that any interactions of small rams on larger ones, when the smaller did not use a low-stretch to initiate the interaction (B), small Stone's (O) or bighorn rams (-), used rubbing (R) as the first behaviour pattern after initiation.

A study of the graphs under the situations indicated shows the following:

(1) There is no definite sequence in which behaviour patterns follow in the social interactions. Any social behaviour pattern may follow after initiation, be this in low-stretch or not, however, each pattern does have a situation depending probably on appearance.

(2) The probability with which a given behaviour pattern appears after initiation depends on: (a) whether the initiation was in low-stretch or not. Thus, when larger sheep interacted with small ones, display patterns (front-kick,

twist) usually followed the low-stretch, while contact (rubbing, horning, nuzzling) and aggressive patterns (Butt, clash, threat-jump) followed if no low-stretch was used, (b) whether a larger initiated an engagement on a smaller one or vice versa. In the former, display patterns predominated, and in the latter, contact patterns, (c) whether a male or a female were initiated on by rams. In the former case, display patterns predominated, in the latter, sniffing and nuzzling of the rear, (d) whether a male or a female initiated an engagement. Ewes, unlike rams, use predominantly aggressive patterns and few displays, (e) whether a young ram or an older one initiated an engagement (i.e. ♂ yearling on ♀, versus ♂ on ♀). Young rams use more aggressive patterns and fewer display patterns than older ones.

(3) Stone's and bighorn sheep behave very similarly under similar circumstances for all situations compared.

The most important point, in addition to the lack of a fixed pattern sequence, displayed by the data in Fig. 81, is that the behaviour of sheep towards one another is quite predictable. Assuming that I saw a smaller ram move in a weak horn threat towards a larger one, then I would predict that the larger would be horned, rubbed or nuzzled, and in better than 75 out of 100 times this would be correct.

Next to be examined is the behaviour of sheep which have initiated interactions. What kind of behaviour patterns and how many are exchanged between the interacting companions?

## The "normal" interactions

After rejecting the hypothesis that social behaviour patterns are organized in predictable sequence, I shall present the social patterns which occur within interactions ranked in order of frequency. The standard rank order, against which the frequency of behaviour patterns in various interactions will be compared, is that of patterns performed by large bighorn rams on small ones in the "normal" situation.

The data in Fig. 71 are laid out in the following manner: In each figure, the upper graph shows the action of the larger sheep, and the lower of the smaller one. The bighorn data are represented by a solid line connecting data points; Stone's yearling ewes are represented by a broken line; the Stone's sheep data are represented as solid bars. The numbers above each graph represent the number of interactions on which each graph is based, thus, each figure represents one social situation (i.e. interaction initiated by larger ram on smaller one) and the frequency with which the various patterns were dealt out by the larger and the smaller partner. An examination of the sub-figures in Fig. 71 shows the following:

(1) Any social behaviour pattern, including those of courtship (sniffing rear, mounting), can occur in the social interactions of rams, and of ewes.

(2) The behaviour patterns used most frequently by the large ram are used less frequently by the small ram. One can hence divide behaviour patterns into two groups; those used primarily by the larger ram, and those primarily by the smaller ram. In the normal interactions of Stone's rams, the following behaviour patterns are used primarily by the dominant: Rush (100%), twist (100%), front-kick (94%), low-stretch (81%), mounting (80%); these patterns are used somewhat less frequently by the dominant - horn-threat (47%), butt (43%); these behaviour patterns are used least frequently - threat-jump (22%), clash (21%), rubbing (4%), horning the opponent's body (2%) (n = 1880 interactions). Display, sexual behaviour patterns and chasing away are virtually the prerogative of the dominant, the contact patterns are used almost entirely by the subordinate. The aggressive patterns are used by both, but are initiated mainly by the subordinate.

If we compare the normal interactions of rams initiated by the larger (Fig. 71A) versus those initiated by the smaller (Fig. 71B), then the following will be found:

(1) In interactions initiated by the smaller ram, the smaller performs more patterns than in the converse situation, and he performs more patterns than the larger ram.

(2) The subordinate uses the same patterns, and with the same relative frequency on the dominant, regardless of whether the latter initiated the interaction or not. The only exception is that the subordinate uses more low-stretches (10.) and front-kicks (L) when he initiates an interaction.

The normal female interactions (Fig. 71C) differ from those of males in the following ways:

(1) Females use very few display and almost no contact patterns. They use primarily aggressive patterns.

(2) The large females receive few responses from the smaller ones.

As in the ram interactions, Stone's and bighorn ewes behave rather similarly, while yearling females behave very similarly to adult ones (Fig. 71C).

The nature of interactions between rams, that is, their behaviour pattern contents and frequencies, varies with the social situation. Fig. 71 illustrated the normal interactions. Let us now examine the "huddle".

## The huddle

In this situation most rams of one group get together on a ridge and while standing or moving as a tight knot (Fig. 80), interact on each other. Fig. 72A shows the pattern frequency distribution in "normal" interactions of large bighorn rams on smaller ones, as compared to interactions of the same kind in "huddles". It can be seen that:

(1) Huddle interactions last longer and contain more patterns,

(2) Subordinate rams perform more patterns in the "huddle" situation than in the normal one, but that the proportions of behaviour patterns commonly used by subordinate rams remains similar,

(3) Subordinate rams perform more display patterns in the "huddle" than in the "normal" interaction.

(4) Dominant and subordinate rams threat-jump, clash and butt considerably more in the "huddle" interactions.

I interpret the huddle as a gathering of playing rams in which the subordinate, smaller rams, are least inhibited. This is indicated by the occasional mounting of a larger by a smaller ram, the frequent threat-jumps which are accompanied by head-shaking (which does not occur in dominance fights) and the occasional disintegration of the huddle into a group of frolicking, clashing rams. However, play or not, in huddles the larger and smaller rams act strictly in accordance with their rank and the break-down of behaviour into that typical of the smaller or subordinate and that of the larger or dominant is entirely recognizable.

## Behaviour of the dominant class IV ram guarding an estrous ewe

In Fig. 72B the "normal" interactions of large Stone's rams on smaller ones, are compared to two other kinds of interactions. One is the interaction of the ewe-guarding dominant ram with subordinate rams. Such interactions show the following:

(1) They are brief. The defending dominant displays much less than in "normal" interactions.

(2) They are highly aggressive. In about half of the interactions the large defending ram charges with lowered head at the smaller subordinates.

(3) Small rams show few patterns in reply.

In this very tense social situation the subordinates avoid the dominant which would be highly unusual for the "normal" or "huddle" situations. The second kind of interaction among rams about the estrous ewe, is that of subordinates among each other.

## Behaviour of subordinate rams about estrous ewe

Fig. 72B (-.-.-) shows the pattern frequency of subordinate rams interacting on each other, as compared to the "normal" interaction of larger on smaller Stone's rams. It can be seen that:

(1) The "normal" interactions and those about the estrous ewe are very similar except that mountings by the larger take place with great frequency.

(2) The smaller subordinate ram does not "reply" as frequently to the larger one interacting with him as in the "normal" situation.

In all previous situations, the behaviour of the smaller, subordinate ram differed appreciably from that of the larger or dominant one. This is not true for the next situation.

## Dominance fights

These are interactions between two sheep of equal body and horn size which have met for the first time and are establishing their respective dominance ranks. Fig. 73 shows the frequency with which two rams engaged in a long dominance fight in March, 1962. This fight between two class III Stone's rams is discussed in a later section in detail (p.90 ). Note that each ram acted as if he were the dominant. Both used mainly display patterns on each other, interrupted by severe clashes. They used the same patterns with similar frequencies. Contact patterns (horning, rubbing, nuzzling) are almost absent. The ram which used most butts, and initiated most clashes - G-ram - was also the one who used fewer display patterns. He lost the dominance fight. A dominance fight lasts till one of the opponents begins to use contact patterns and hence stops acting as if he were the larger.

In Fig. 73 I replaced pattern S with "horning of ground" (HG). Both rams used it reasonably frequently during the dominance fight.

<u>Interactions between rams and ewes</u>

Fig. 74A shows the frequency of behaviour patterns used when rams older than 3 years interact with non-estrous ewes. Again the behaviour of Stone's and bighorn sheep is very similar. Fig. 74B shows the behaviour of yearling Stone's rams interacting with ewes. Figures 74A & B show the following:

(1) Rams use the same patterns towards non-estrous ewes as towards smaller rams, but with somewhat different frequencies.

(2) Interactions with non-estrous ewes differ in that rams use more twists (T), do more rear end sniffing and perform more lip curls, than in interactions with smaller males. Furthermore, they use fewer aggressive patterns.

(3) Unlike subordinate rams in the "normal" situation, non-estrous ewes reply with very few behaviour patterns to large rams.

(4) Yearling rams differ from larger rams in that they use fewer display patterns towards the estrous ewe, they butt (B) and mount (M) the ewe more and perform fewer lip curls. Ewes reply to yearling rams more often than larger rams.

The interactions of rams with non-estrous ewes appear somewhat altered interactions of large rams with smaller ones. The differences in the ram-ram and ram-ewe interactions almost disappear if these interactions occur about and on the estrous ewe (Fig. 75). In Fig. 86 it shows that the kind and frequency of patterns shown by the ram on the ewe in heat (-), and subordinate males towards each other (-.-.-), as well as the reply of the smaller sheep are very similar in each case. The estrous ewe is not only treated as if she were a small ram, but she also replies as if she were a small ram. There are minor differences; the ewe horn-threats more frequently, she rubs her body occasionally along the chest of the large ram breeding her, she performs a few coquet jumps (p. 117 Fig. 94), however, on the whole her behaviour resembles that of the smaller ram. The data in Fig. 75 give rise to a major hypothesis: Rams do not differentiate conspecifics on the basis of sex but on the basis of relative size. All "smaller" sheep - irrespective of sex - are treated by rams in the same manner. Thus a class IV ram treats subordinate class IV rams as if they were ewes, and the differences in the interactions with non-estrous ewes, arise from the ewes' reaction to the rams behaviour.

I contend that in sheep society there is no "female" in the usual sense, rather the female appears to rams as a highly desirable subordinate. Rams use more courtship patterns towards smaller rams, the more these rams resemble a female. Fig. 76A shows the frequency per 100 interactions with which Stone's and bighorn rams examined the rear of the various sex-age classes of sheep and Fig. 76B shows how frequently the rams mounted them. It is evident that the more rams looked like ewes, the more they were examined about the rear and mounted.

It was noted earlier that the interactions of rams on non-estrous ewes differed quantitatively from those on smaller rams, but the interactions on estrous ewes were quite similar to those of rams on each other in the presence of estrous ewes. Furthermore, note in Fig. 76B that male and female yearlings were mounted by rams more frequently than adult, non-estrous ewes. These differences appear to be caused by several responses of the non-estrous ewes which break up interactions.

The ewe does two things which subordinate rams usually do not:(a) she withdraws when kicked, (b) she urinates to the male and he promptly lip curls. (Occasionally rams also urinate to a dominant one, however, this is not an easy behaviour to note since the urination posture of rams is not conspicuous). Lip curling in the interactions of rams does, however, occur less frequently than in courtships. Both of these differences disappear when the ewe is in estrous. Thus during 144 courtships on estrous ewes, rams lip curled only 7 times, but in courtships on non-estrous ewes, the rams lip curled 30 - 40 times per 100 courtships (Fig. 74). Fig. 77 shows the percent frequency with which the various sex-age classes withdrew from the kicks and mounts by rams. It can be seen that the ewe in estrous withdrew about as frequently when kicked as rams did. When not in heat, ewes withdrew more than three times as frequently when kicked and twice as frequently when mounted. Therefore, when the ram kicks and the ewe remains standing the "normal" behaviour performed by a ram towards a subordinate can proceed and the ewe gets mounted after a series of kicks.

As indicated above, the second way to interrupt a ram's courtship is for the ewe to urinate. November and December (pre-rut and rut) excepted, ewes urinated to courting rams in about 43% of the courtships, however, this figure is based on a small sample (n = 38). In November, when intensely courted, Stone's ewes urinated during 20% of the courtships (n = 445). During December rams shifted their attention to estrous ewes and courted non-estrous ewes less frequently. Now the percentage of courtships in which ewes urinated rose to 36 (n = 27). Apparently the frequency of urinations in courtships is inversely related to the frequency with which ewes are courted.

If ewes urinate on the approach of the ram, that is, before he reaches the ewe, the courtshkp tends to be very short. Thus, for 122 courtships on Stone's ewes in which urination occurred before the ram reached the ewe, the average number of patterns performed by the ram on or towards the ewe was 2.59. However, in 147 courtships where the ewe urinated after the ram got there, the number of patterns per interaction was 4.7. Bighorn rams behaved similarly to ewes. If ewes urinated before the ram got there, the latter performed 2.2 patterns on the average (n = 14); if the ewe urinated after he got there, the ram performed 4.9 patterns on the average. Therefore, urination by the ewe and lip curling by the ram does appear to reduce the behavioural sequences in courtships. However, it does not appear to matter if the ram lip curls or not after the ewe urinates for such courtships in which rams lip curled are just as long as those in which rams did not. This was true both for Stone's and for bighorn ewes. The function of lip curling and the adaptive significance of the ewe's urination response remain unknown. Lindsay (1955) showed that rams deprived of their sense of smell could not distinguish estrous from non-estrous ewes.

In general, rams treat ewes as if these were subordinate males. They are, however, not able to perform as many patterns on non-estrous ewes because they interrupt the interaction by running away when kicked, and/or urinating which causes the ram to lip curl and end the courtship. When the ewe enters estrous, her hormonal changes probably are responsible for eliminating her withdrawal response to the kick as well as her urination. Now the behaviour of the excited ram towards the ewe is almost identical to that of excited rams to one another when they perceive but are barred from the estrous ewe. Furthermore, the ewe acts not only like a ram by accepting front-kicks without responding, but she also behaves very similarly to a subordinate ram - something she does only when in heat. Conversely, small rams may behave like ewes by urinating to dominant rams or performing lordosis when mounted (Fig. 44).

# PART III

## DESCRIPTION OF SHEEP BEHAVIOUR DURING EARLY WINTER

### Normal daily behaviour of rams

Before some of the unique features of ram society can be appreciated, one needs to know something of their normal daily behaviour. Rams spend most of the day feeding and resting. Stone's rams were active during 65% of the daylight hours in October (n = 93 hours) and 58% in February (n = 114 hours). Rams feed about 75 - 80% of the time they are active and only a small fraction of the day is devoted to social interactions.

During feeding rams tend to be dispersed (Fig. 78). Feeding periods are interspersed with resting period, during which rams tend to rest together. Before a resting or feeding period, rams frequently engage in minor interactions. Particularly rams of nearly the same dominance rank interact quite regularly at this time. Occasionally a large ram displaces a smaller one from a bedding site. During the resting period a ram periodically gets up, urinates and defecates and then turns and lies down again. A lot of urine and feces are deposited on the regular bedding sites and in spring the grass is usually greener and grows longer at the edge of, and below, sheep beds.

When during a minor move rams stop temporarily as a group, small rams tend to nibble and rub their noses on the horns of larger rams. During long marches sheep usually move in single file, with a large horned ram leading ram bands and an adult ewe leading ewe bands. The rule that the largest horned ram leads, was broken only twice from 73 instances. In both cases the band was following a large class III ram while a IV ram was present (Table III).

Ram bands mix with a minimum of strife; sheep live in an open society. A group of three rams which is moving to another group in single file, is shown in Fig. 79. Note that the leading class IV ram is entering the new group in a horn display, a behaviour frequently shown by sheep entering a group or passing an individual. Only when rams of equal size meet, and have not seen each other for months, is there a good chance of observing a lengthy interaction between them. This is not a common occurrence, however,

## Group interactions

Mountain sheep differ from other North American ruminants in that males perform group interactions. The simplest form I termed a "huddle". All, or most, rams from a group gather into a tight bunch on a level spot on top of a ridge or on some level area on a slope. They face the centre of the gathering, their white rumps facing out (Fig. 80).

The larger rams display while the younger ones rub and horn the larger ones. Periodically the huddle may erupt into threat-jumping, clashing rams which freeze into rigid present after the last clash, and then close in for more display and contact behaviour. The front-kick is rarely seen in huddles; mounting occurs occasionally. It is only in huddles that I observed smaller rams mount larger ones.

Huddles were observed throughout the year, but primarily in fall, spring and early summer. They are most frequently seen in the morning and late afternoon. In the dense populations of bighorns and Dall's sheep which I studied, huddles were common, but among my Stone's sheep they were rare.

A rare form of the huddle is the "raping party". A group of rams focuses its attention on one class I ram and begins mounting him. The little ram is courted until he runs away. I observed only four raping parties and these soon disappeared from sight.

Groups of playing rams are more commonly seen in spring and summer than at other seasons. It may begin when rams huddle after rising in the morning and are still in the cliffs above the slopes. One ram turns from the group, shakes his head and begins to bounce downhill. Others follow and begin to frolic. Suddenly the lead ram whirls, threat-jumps and often clashes on the ram behind him (Fig. 81). Both may freeze in present. Others hurry to them forming another temporary huddle until one ram runs away. During such runs, rams may whirl about, threat-jump repeatedly, bound high into the air, cut other rams off or clash in series with several rams (Fig. 82). I have seen as many as eight rams standing in a circle on their hind legs, facing each other.

I soon found that playing could be artifically provoked as long as I could get rams to run downhill towards me. This was not difficult to do since the rams were eager to lick the salt I always carried for them.

The function of group interactions appears to be stabilization of dominance relationships. When huddling, rams can meet and engage in social interactions which lack the tenseness of dominance fights. They can acquaint themselves with the fighting potential of other members of the band, and are steadily reminded of it during frequent huddles. It may also be that small rams continuously impregnate themselves with the secretion from the preorbital gland of larger rams, and acquire a group scent. The significance of this is not clear except that it would contribute to making the social environment familiar and predictable. Huddles appear to be a less wasteful way of stabilizing dominance rank than dominance fights; on the Stone's sheep study area I saw few huddles and almost all dominance fights while for the bighorn and Dall sheep I observed the converse was true.

Some group interactions result when a third ram enters into a conflict between two rams. I observed only once a larger ram (III), breaking up a dominance fight between two smaller rams (II) by attacking the larger. During a dominance fight between two bighorn rams (class IV), a smaller ram (III) regularly clashed into the side of the larger each time the two larger rams clashed. The smaller ram was pirating social advantage from an animal it would not normally attack. The larger ram could not retaliate since his large opponent would have smashed at once into his side. Every time the large IV ram turned to the III ram, his class IV opponent made intention movements to clash and the IV ram turned away from his smaller opponent. It is not uncommon to see a small ram enter into an interaction between two larger rams and begin to horn and butt the second largest. In one other instance, the subordinate of two interacting rams searched out his next subordinate and assumed position behind him. This resulted in three rams standing one behind the other. When the largest kicked, the second largest passed on the kick to the third and smallest ram. Twice I observed two rams "gang-up" on a third, and filmed one of these interactions. One of these rams was a small four year old who was strange to the area and was confronted by two slightly larger rams. The rams clashed and horned with each other and on one occasion the smaller was pushed simultaneously from the front and rear by the two larger ones.

<u>Dominance fights</u>

I observed dominance fights only between rams of equal or near equal horn and body size. Such fights can occur at any time of the year but seem most frequent during seasonal migrations when strainge rams are most likely to meet. For one of the conditions of dominance fights is that the partners are strangers or have not seen each other for several months. I have argued previously that rams appear to recognize each other's dominance rank by their horn sizes (Geist, 1966). Hence small horned rams largely ignore a larger horned stranger, or act towards them at once as subordinates. When rams of equal horn size meet, there is no criterion whereby dominance could be settled a priori, and only a fight can determine it. However, dominance fights are quite rare.

The longest dominance fight I observed occurred on March 19 and 20, 1962, between two seven year old Stone's rams, G and M, both carrying $\frac{3}{4}$ curl horns. Since these rams showed almost all the possible combat phases, and no other dominance fight I ever witness added much that was new, I shall concentrate on this interaction.

G-ram was a resident of Sanctuary Mountain. M-ram crossed with the larger F-ram (class IV) to Sanctuary on the morning of March 18th. M and F-ram did not meet the Sanctuary rams however, till about 10 a.m. of the 19th. F-ram, who was only seven years old (like M and G) but carried much larger horns interacted shortly with display patterns with two class IV Sanctuary rams of slightly smaller horn size, and emerged as the dominant without any fight. Then G-ram came in low-stretch to F, and kicked at his rear. F-ram whirled and rose into a threat-jump at which G-ram turned and moved off. G-ram continued in low-stretch straight at the slightly larger M-ram and kicked him on the chest. Both rams then stood shoulder to shoulder, displayed in present and kicked at each other's chest and belly. Thus at 10.10 a.m. began an interaction which was to continue for 25 hours.

The behaviour of rams in a dominance fight can be divided into several categories which are illustrated in Fig. 83. One engagement cycle goes approximately as follows: one ram approaches the other in low-stretch, twisting his horns and grunting (Fig. 83A), and delivers a kick at the opponent's chest. This begins the kick phase in which rams start out standing shoulder to shoulder, but while exchanging kicks, slide along each other's side (Fig. 83B ). Both opponents display in present and growl on each kick. Occasionally one digs his horn into his opponent's back or butts sideways at his partner's head. The rams may push with the shoulders or chest at each other, which may lead to some circling or whirling shoulder to shoulder about each other. The kick-phase may last for only one kick but may run to 43 kicks. Rams tend to reply to kicks in a tit-for-tat fashion. Bighorns differed from Stone's rams in that they coupled some kicks with a butt at the opponent. The kick-phase ends when one or both suddenly pull their heads down into a low-stretch and move past the other (Fig. 83C). Sometimes one breaks off the kick phase by turning in low-stretch right around while pressing his rear against his opponent's side. After both walk away several steps, both whirl around and rise on their hind legs into a threat-jump (Fig. 83D). This may lead at once to a clash (Fig. 83E) or both rams drop down and freeze into a present (Fig. 83F). The present also follows the clash. The rams may break off here and feed side by side (Fig. 83G) or again initiate (Fig. 83A) and begin once more.

From the 25 hours which M and G fought, I obtained exactly 8 hours of quantitative data. In that time I recorded 92 kick phases; 36 of these were followed by a threat-jump, present and ended at that point on 20 (from 36) occasions; 17 kick phases were followed by a clash - present and only 3 ended at that point. Therefore, 30 kick phases followed at once after a threat-jump or clash and 62 kick phases were non-cyclic. 39 kick phases ended by both rams moving apart and beginning to feed.

When not engaged both rams usually fed side by side carefully watching each other. Suddenly one or the other would jerk up his head, at which the other also jerked up or rose into a threat-jump. I kept note of how such short feeding periods ended. On 38 occasions both rams jerked their heads up and froze into a present display. In 23 instances the rams suddenly rose and clashed, hence, a little more than half of all clashes observed were these sudden engagements terminating a feeding period. In 15 instances the rams only threat-jumped and froze then in present, and on two occasions one suddenly butted the other and both engaged. From these 78 feeding period endings, 64 led on to full engagements and kick phases, and on 14 the rams returned to feed again.

In the beginning of their engagement M and G-rams horned the ground or small alpine firs extensively. In their first hour they horned 4 times, in the second 20, in the third 16, in the fourth 4, after that horning varied between 1 and 6 per hour. On the morning of the 20th the two tired rams had almost stopped horning. This distribution of horning supports the hypothesis that it is a sign of excitement rather than a socially meaningful pattern. M- and G-ram horned equally frequently.

M and G did not butt each other as frequently during the first few hours of the fight as later. In the first 4½ hours of the engagement the rams exchanged two butts, but in the next 3½ hours they butted each other 27 times. Now one began to notice that the rams were badly strained and they began to look tired. I observed how one or both staggered to regain footing after a heavy clash. In some clashes it appeared as if their horns slipped off each other, for one would literally pile up in front of the legs of the other. Occasionally one climbed up and clashed almost straight down. Neither lost its footing in such clashes. Only once did they hook horns and begin a short but violent struggle.

I ended observations at 18.50 hours at dusk. During the night I heard clashes, indicating that M and G were still engaged. In the early morning I found M and G resting opposite each other, still displaying stiffly in present to each other. At 9.00 a.m., I heard the first clash of the morning and returned to observe them. At 10.20 a.m. the last clash fell. Just prior to it, G-ram had entered into almost violent kick-phases to which M-ram hardly replied. It appeared as if G-ram was desperately acting as a dominant. Both rams fed on steadily. At 12.15 p.m., M-ram whirled towards G, then froze in present, but G did not flinch and fed on. At 12.25 p.m., M-ram came to G in low-stretch and began kicking but G turned his rear on M while feeding. From then on he did not reply to any of M's kicking, displays, or threat-jumps. The fight was over. The dominance had been settled. G-ram had lost for he now accepted being displayed to and behaved like a ewe by not replying.

One behaviour pattern which M and G did not show in their fight, but which some other Stone's rams showed was pawing the ground during the engagement. In some dominance fights, this followed after rams disengaged from the kick-phase. The ram pawed the ground 3 - 4 times before or after turning and facing the opponent in low-stretch. Pawing was, however, rare. I saw only Stone's sheep do it. However, Jones (1950) cited an observation of Griggs, who saw pawing by desert bighorn rams during combat. Walther (1961) reported that a captive Marco Polo ram (O. ammon poli) pawed exuberantly prior to threat-jumps in engagements with an urial (O. ammon cycloceros) or against the observer. In American sheep this behaviour pattern may be vestigial.

The opponents in a dominance fight do not necessarily separate once the fight is over. M-ram followed G about on the 20th but did not search him out later. After a dominance fight one class II ram followed and engaged on another for at least 3 days after the initial engagement. Some dominance fights may result in the formation of "dominance pairs" in which the larger steadily follows the smaller ram and the two remain together for months.

The post fighting phase is characterised by the subordinates acceptance of what amounts to insult. I observed the dominant partner not only display to the subordinate, kick and mount him, but also move directly in front of him, look squarely at him then threat-jump repeatedly. Normally, I would expect that, at this, the subordinate would at once clash heavily into the dominant. However, after a dominance fight, the subordinates kept on feeding and slowly turned their rear to the opponent. Regardless of what the dominant did they fed quietly on, and oriented away from him. It may be that turning the rump patch to the opponent somehow appeased it.

In total I saw six dominance fights among Stone's sheep and part of a seventh one. Three took place in spring, one in late summer, and three in the pre-rut. I saw only one, very short dominance fight between two class II Dall rams which was lacking in vigour and the richness of detail the Stone's sheep showed. Among bighorns I saw not a single intense fight, but did observe several poorly ritualised engagements which were dominance fights of sorts. None lasted long; the same two rams mainly clashed now and again then dropped into a stiff present and soon fed on. These differences between sheep on my Stone's, Dall, and bighorn study areas are almost certainly population and not species differences. The Dall and bighorn populations were both quite dense and the individuals acted much more alike than did the Stone's sheep. I noted earlier that huddles on the Stone's sheep area were rare, but very common among the Dall and bighorn sheep observed. It may be that huddles are a simpler manner of establishing dominance orders where sheep are very common and strange individuals meet frequently. There were few sheep on my Stone's sheep area.

Dominance fights between ewes do occur but must be rare. In 42 months in the field with sheep, I observed only one. It was a short fight between two bighorn ewes on October 31, 1964. Three females stood in a group on a ridge. Two ewes are primarily engaged. The subordinate ewe butted the dominant one 5 times, clashed 4 times on her, and nibbled her head quite extensively twice. She received one clash and a weak horn-threat in return. The third ewe clashed twice on the subordinate ewe and mounted the dominant once. It appeared, as in some ram interactions, that a third animal was taking advantage of one, or both, fighting individuals. As in ram interactions, the dominant is the one who can stand and accept the aggressive behaviour (as distinct from courtship behaviour) of the suborinate with little or no reply. A further report on what appeared to be a dominance fight of ewes is found in Blood (1963).

At present a comparison of dominance fights between different races of North American sheep cannot go very far. Good descriptions of fighting Dall rams are lacking. The careful observations of Welles and Welles (1961) and their excellent photography of dominance fights among desert sheep (O. c. nelsoni) indicate that Stone's and bighorn sheep differ only slightly. Stone's sheep paw a little during dominance fights, bighorns very rarely; bighorns use the horn jab into the opponent's back frequently, Stone's sheep rarely. Bighorns combine the kick and a butt which Stone's sheep do very rarely. In general, it appears that bighorns butt and clash more frequently and are generally rougher than thin-horn sheep (see Table IV)

### Unritualised fighting

Vicious, unritualised fights occur between rams about an estrous ewe, but may be induced by providing only limited access to a piece of salt. I have observed and filmed a number of unritualised brawls in the latter situation, and have found them no less fierce than those about estrous ewes. The vicious fights of rams are slugging and wrestling matches of brute force, lacking all ritual and finesse. Rams whirl about one another, trying to keep their horns pointed at the opponent as a defense measure, and try to crash into the opponent's side whenever possible. Rams hit out sideways with their heads (Fig. 84), push each other around with chest and shoulders (Fig. 85), and butt each other wherever possible whilst trying to avoid the blows of the other. Occasionally, horns get locked (Fig. 86) and rams may tug and wrestle or blindly whirl around each other, apparently in an attempt to free themselves. The fight is ended when one of the opponents flees while the other charges head lowered after him.

In the defense of an estrous ewe, a large Stone's ram slammed a class II ram into the snow with a blow to its side. But the small ram recovered quickly. In another fight about an estrous ewe, the defending large class IV bighorn ram stumbled and fell into a snowbank. At once the next largest, a class III ram pounced on him and, using its horns, held the struggling full curl helpless on its side. I saw Stone's rams trying repeatedly to push smaller rams off a cliff during the defense of a ewe. I saw this only at that time among rams, but did see a 2 year old female trying to push a yearling ram off a cliff face. In all instances the sheep jumped to a lower ledge. The vicious fights of rams have little in common with dominance fights.

<u>Yearling rams gain dominance over ewes</u>

When in October, 1961 and 1962 Stone's sheep were returning to the study area, it was noticeable that yearling rams (17 months old) were frequently entering into dominance interactions with ewes. At first yearling and two year old ewes were the main target, then adult ewes. The same behaviour was strikingly noticeable among Dall sheep at Kluane Lake, but I did not observe it to the same extent in fall, 1964, among bighorns in Banff Park. This is probably due to the poor growth of bighorn yearlings on my study area, which at 18 months of age barely reached female size, had small testes and did not enter into the rut. On the other hand, yearlings on the Stone's sheep and Dall study area reached female size before the rut, and had clearly visible, large testes. The Stone's yearlings were very interested in estrous ewes and lip curled over female urine (this appears to be a sign of sexual maturity). Among the Stone's sheep observed, all yearling males dominated females by 18 months of age, some bighorn rams did not manage to do this until 28-30 months of age for ewes were occasionally successful in driving 2½ year old rams from some salt.

Already at 11 - 12 months of age, rams begin to pester yearling ewes ar even small two year old ewes, by standing behind them, suddenly mounting, butting, nudging or displaying to them (Figs. 87 & 88). The low-stretch is still used very rarely at that age, but becomes more common toward fall, although still not as frequent as used by older rams (Fig. 74). The small ewes usually withdraw, but occasionally urinate to the yearling or butt him. In fall, females are most antagonistic to the yearling rams. In a number of instances it comes to short but fierce fights between them (Fig. 89). Dominance is revealed when the ram can inspect, kick or mount the ewes without precipitating a fight or being chased away. Generally, ewes are considerably more antagonistic to this class than to larger rams. Ewes initiate interactions on yearling rams frequently (Fig. 67) and they reply to their interactions more frequently (Fig. 74B). In late fall, occasionally a yearling ram pursued, herded and repeatedly charged and butted a female as if enjoying the license of hard-won dominance.

## The pre-rut

In late October and early November, rams on all three study areas began to appear on the ewe ranges and associated fairly steadily with ewes. Strange rams meeting each other entered into interactions, only very few of which were dominance fights. Rams became increasingly more active. In October they were active about 65% of the daylight hours (n = 93 hours), in the first half of November 67% (n = 60 hours), in the second half of November 73% (n = 64 hours), in December 83% (n = 68 hours), in January 71% (n = 98 hours), in February 58% (n = 114 hours). Overall activity increased to reach a maximum during the rut and subsided in the following months.

Rams court the non-estrous ewes. Young rams in particular show some behaviour which deviates from the courtships described so far. Young rams tend to mount ewes much more frequently than older rams (Fig. 102). After sniffing the ewe, they suddenly attempt to mount with erected protruding penis. The ewes virtually always attempt to jerk free. The only exceptions observed were several 2½ year old females that had reached sexual maturity. They accepted some mountings when not in estrous.

On the Stone's sheep area, I observed a few young rams guarding non-estrous ewes during each rutting season. The object of such appeared to be to prevent the ewe from going anywhere. The moment she moved, the ram pounced in her way and in horn-threat chased her back. The ram could be positioned below or above the ewe. He did not feed but stood and watched her. A few times guarded ewes attempted to break out and the rams gave chase. In only one instance did the ewe manage to escape and join the ewe group. Usually the ram got in front of her and cut her off. Guarding rams which stood above the ewe descended steadily in elevation while those below a guarded ewe steadily ascended, since in every short chase the former ram chased the ewe down and the latter chased her up. The largest ram I observed guarding a single non-estrous ewe was a class III Stone's ram.

I observed only one 5 year old class II Stone's ram guarding a non-estrous ewe and defending her as if she was in estrous against another 5 year old ram and a 3 year old. On three successive days in December, 1965, I checked on this group and noted that the guarding young ram did not feed, rested very little, and prevented other small rams from reaching the group he guarded - an adult ewe with lamb, plus a 2½ year old ewe reaching sexual maturity. I must stress here that his behaviour is highly exceptional, for rams normally guard only estrous ewes.

During the pre-rut, rams frequently moved alone between groups of females or wandered over the rutting ranges. These searching rams moved to projecting rock outcroppings and frequently stood and scanned the slopes and cliffs about them. Searching rams move normally at a walk along established trails, stopping here and there to scan the countryside or sniff and lip curl over a urine spot. They lick their lips frequently when moving, and now and again call with a deep, loud "baa". Dall rams appear to have a higher voice than bighorns. Wandering rams descend to groups of females or rams in low-stretch and begin social interactions. After I got to know the rutting ranges of Stone's sheep, I noticed that searching rams systematically visited and looked over the localities favoured by sheep.

Periodically a young ram showed an extended interest in one ewe and persistently courted the uncooperative female. In a few instances I observed such a ram stand several paces behind the female and while low-stretching, and twisting, perform a front-kick into the air. The young ram persisted in his efforts but remained at a distance, periodically advancing 2 - 3 steps, twisting, tongue flickering and grunting and then pulling back 2 - 3 steps to assume the previous position (Fig. 40). He kicked rarely. With each twist-growl approach the ewe bounced forward a few steps. A few young rams literally see-sawed behind the ewe. Walther (1961) described a similar see-saw courtship for a Marco Polo ram.

## Estrus in ewes

The end of November brings a slight change in the behaviour of the larger rams. One old ram begins to guard a ewe. He horn-threatens subordinates or blocks their way to the ewe by intercepting them in a present. He may kick the subordinate a few times or push him away with his shoulders or chest. Smaller rams withdraw or keep their distance and move on to court unguarded ewes. Nothing in the female's behaviour indicates the approach of estrous. She still withdraws from the kicks and permits no mounting. Occasionally the guarding ram makes a short horn-rush ahead of the ewe if she begins to walk away, and it invariably makes her turn. In this pre-estrous period the guarding large ram keeps close to her, feeds, rests, discourages other rams from courting the ewe, and displays to her periodically.

A group of rams following one ewe indicates that the ewe will shortly enter into estrous or is already in it (Fig. 90). Right behind the ewe is the largest horned, dominant ram who discourages others from passing by whirling to face or rush at any subordinate who attempts it. If a smaller ram does succeed in getting past the guarding full curl, he gets behind the ewe and a wild chase results. While the female flees, the smaller ram attempts to mount her in full flight. The guarding male is right at his heels, butting his rump and usually succeeds in knocking the smaller ram off the ewe. In most instances the dominant literally crashes into the flanks of the mounting subordinate and sends him sprawling (Fig. 91). At this point a short, sharp, vicious fight between the guarding ram and a near equal may erupt. However, it breaks up quickly for a smaller ram may be pursuing the ewe. Vicious sideways butting develops between the guarding ram and a subordinate if it attempts to pass. For a short stretch the two rams run shoulder to shoulder, butting at each other until the dominant forces the subordinate into another direction and gives him a parting blow on haunches and flank. Usually the dominant soon gets behind the ewe and the chase ends - if the female is in estrous.

Once the rams have been excited by a chase, and the female does not stand, the dominant, followed by the subordinates, pursues her. The ewe attempts to escape the rams by running into steep cliffs or forest, preferably both, and here begin her evasive manoeuvres;

(a) If a ram is right on her tail, she may jump up high, turn by $180^{o}$ and run past the rams.

(b) She runs past a very narrow spot on the trail, turns, steps on to the narrow spot, presses her side against the rock face and faces the rams.

(c) She jumps off the trail on to a narrow foothold on a cliff face where there is only room enough for her.

(d) She stops and presses her side against a cliff face and holds still while rams fruitlessly try to mount her.

(e) She comes to a crack in the cliffs, quickly turns and backs into it.

(f) She throws herself on the ground and for a while resists all attempts by the rams to get her up.

(g) She zig-zags while galloping over an open slope. Every time a ram tries to mount, she dashes sideways.

The most common kind of evasive actions of the ewe appear to be a, b, c and d. None of these will be frequently observed for a number of reasons. When estrous ewes depart into cliffs or timber, they usually escape observation. Sometimes, they run entirely out of the study area or cross through it during pursuit by rams. If deep snow covers the ground, the chases tend to be more localised. This impression I gained while comparing the Stone's rut in 1961, when deep snow covered the ground, with the rut in 1962 and 1965 when almost no snow lay on the mountains.

None of the ewe's escape actions appears to be very successful. The excited rams kick and push her, and almost wedge her away from rock faces or out of crevices till she dashes off. Ewes which threw themselves down were kicked and butted to their feet. The chased ewes gave up rather quickly. They began tolerating kicks and stood for mounting. Stone's rams holding an estrous ewe delivered a series of kicks and then mounted, then delivered another series of kicks, before mounting again.

The frequency with which rams court and mount appears to depend on how much copulating they have done previously. On December 7, 1961, I observed a 12 year old Stone's ram chase down and begin breeding the first estrous ewe of one band. In one hour he not only chased down the ewe but mounted her 11 times. Then the rutting group disappeared from sight. The following morning the 12 year old full curl was markedly less vigorous in his defence of the female and he did not mount. A 4 year old class II ram managed to steal the ewe from the guarding ram and chase her into some broken cliffs. The old ram searched for, but did not find, the couple. In the following three hours the young ram mounted the ewe 39 times. Then the old ram returned and found both. The young ram left the ewe uncontested, but the old ram did not mount again and soon moved away leaving the ewe to smaller rams. A seven year old full curl, mounted an estrous ewe on the second day of her heat only 11 times, and only after extensive courtship by the ewe. After the first excitement estrous ewes appear to be mounted only 2 - 3 times per hour. Despite the presence of the ewe, I have seen two guarding full curled rams ejaculate spontaneously.

Most of the time the estrous ewe feeds, while the large dominant ram stands between her and the subordinates (Fig. 92). He rarely feeds, but mainly stands watchfully beside the ewe and occasionally courts and mounts her. Periodically one of the smaller rams approaches the couple and looks at them. The dominant may react in several ways. He may low-stretch at the subordinate, twist, growl and advance a distance towards the intruder. He may lift a front leg and wave it at the subordinate. This usually suffices and the subordinate reluctantly steps back while inclining the horns at the dominant and glancing backward. Then he suddenly spins around and dashes off, which often triggers the dominant into a short but hot pursuit with lowered head. A dominant discovering a subordinate close by, may charge him at once with a lowered head (Fig. 93). Sometimes the dominant pulls up into a present and slams his chest against the body of the subordinate. At the same time he kicks and pushes the smaller ram downhill. Or, the dominant may block the way to the ewe by assuming a present and turning broadside to the intruder (this may give the false impression that rams have a broadside display).

Usually the guarding ram is a large full curl and his largest competitor is usually a 6 - 7 year old class III ram. Such rams need not be hesitant in their approach to the breeding pair. They can attack and forcefully butt or clash while trying to break through to the estrous ewe. This can lead to short vicious fights in which the class III ram may suddenly discover himself close to the ewe and at once give chase. He will succeed now and again in driving off the ewe, particularly if the dominant ram is exhausted, and will begin to copulate and defend her against smaller rams, just as the larger ram did previously. If the full curls are bad runners due to exhaustion, or perhaps lungworm infection, these 6 - 7 year old rams may do an abnormally large part of the breeding. This situation was present in 1964 on the bighorn study area in Banff Park.

When the guarding ram is large and successfully intercepts the approaches of subordinates so that few chases result, then most mounting is done by the large ram. If, however, the ram guards badly due to small size or exhaustion so that many chases develop, then the subordinates do a considerable amount of mounting. For instance: November 19, 1964, I observed for 88 minutes a group of bighorn rams about a breeding pair. The guarding ram was very large (Fig. 92) and only a few short chases developed. The three class IV rams mounted altogether 25 times, the III ram 3 times, the II ram 7 times, and the two I rams 4 times, and a yearling male none at all. Therefore, 25 of 39 mounts attempted were made by the full curls of which almost all were by the guarding ram. On November 30, 1964, I observed for 25 minutes a rut group in which a lot of chasing took place. The two IV rams mounted 13 times, the III ram 14 times, the three II rams mounted 15 times, and the I ram mounted twice. In this situation, where a vigorous III ram successfully chased off the ewe from an old guarding full curl, the full curls performed only 13 of 45 mounts. Among the Stone's sheep I observed, small rams had little chance to mount estrous ewes due to the vigorous, spirited defence by large, even very old rams. The bighorns I observed appeared listless and very tired by comparison and were noticeably short of breath. This may well be the reason why smaller rams mounted estrous ewes rather often on the Banff study area. Mounting frequencies by various classes of rams on estrous ewes are given in Geist (1966c. Fig. 14).

A ram defends the estrous ewe against smaller rams. Peculiarly enough though, when a larger ram arrives on the scene, the smaller one leaves the ewe without a contest. They walk hesitantly away from the dominant who then begins to court the ewe. They do not attack, nor are they capable apparently of comprehending that they could have easily chased the ewe away to another locality. It appears that when a ram runs after a ewe he is not chasing, but rather following, an escaping female. Herding the ewe out of the way when a larger rival arrives, is not part of his normal behaviour.

Twice I saw guarding full curl rams leave the ewe voluntarily, feed, rest and pay no attention to the next largest ram who took over the ewe, copulated, and defended her against smaller competitors. In both instances the larger rams returned after resting, walked over to the estrous ewe, and the smaller guarding ram left.

Only once did I see two ewes in estrous in the same band. They were periodically exchanged between the two largest rams. When one left his ewe and walked over to the other breeding couple, the smaller ram left and went over to the ewe his larger opponent deserted.

On two occasions a rather unusual interaction was observed. In both instances a class III Stone's ram moved suddenly in present against the slightly larger guarding ram, slammed his chest against the latter's side and proceeded to kick and display. These two subordinates then acted as if they were dominants. In both instances the dominant's response was to whirl around and clash into that subordinate. Once, while the dominant turned, the subordinate quickly mounted him. In both instances the subordinate rams quickly dashed away, followed closely by the charging dominant over a short distance.

Ewes in estrous returned on their own to the largest ram and occasionally courted him as will be described later.

The group of subordinate rams which gathers about a breeding couple, is far from passive. They interact extensively with each other. Larger rams court and mount smaller ones as if these were estrous ewes whose behaviour they resemble (Fig. 75). Larger rams may nuzzle the penis of the smaller and lip curl. Generally the smaller ram stands, except when being mounted excessively. Twice I saw a small Stone's ram being chased by a courting III ram. The chases went over cliff regions and the larger attempting to mount on the smaller. The III rams pursuing and raping a smaller ram ignored non-estrous ewes they passed. Once during a chase a class III Stone's ram mounted the large defending full curl in front of him. The full curl whirled and heavily clashed into the offender's body.

In the interactions between rams about estrous ewes, the guarding ram tended to deal out more blows and receive less than the other rams. Thus in interactions about 9 estrous ewes on which I recorded quantitatively, 10 class IV rams dealt out 36 blows and received 9, 12 III rams dealt out 17 and received 36, and 7 II rams dealt out 2 and received 9. Though class I rams do deal out some blows and received some in return, they interacted too little to be recorded. As stated earlier, fights about the estrous ewe tend to be unritualised, and vicious. However, once I did see two rams fight in ritualised fashion for a few minutes before dashing off after the ewe.

Unlike the subordinates, the guarding large ram feeds and rests little. The ewe usually feeds. When no estrous ewe is present, the large ram again feeds regularly and does not interfere with the courtships of subordinate rams on non-estrous females. I observed, however, a number of times that excessive interest of one ram toward a ewe quickly excited others. At once the largest began to defend her and attempt copulation even though she was not in estrous. Then, as soon as he was alone with the ewe he showed no more interest and left her. The ewe was interesting only when pursued by other rams.

On the Stone's sheep study area ewes came into heat rather late in the year. I observed the first ewe in estrous on November 25, and the last on December 16. In total I saw 16 Stone's ewes in heat in the complete rutting seasons of 1961 and 1962, plus the greater part of the 1965 rut (November 27 - December 10). One individually known ewe was in estrous in 1961 on December 4, in 1962 on December 2, and in 1965 on November 29. On the bighorn study area in Banff, in 1964, I observed the first ewe in estrous on November 19, and the last on December 4; I saw five estrous bighorn ewes. One adult Stone's ewe remained of interest to rams on three consecutive days, while a $2\frac{1}{2}$ year old ewe of the same population remained of interest for only two days. Since the ewes have definite wintering areas, they tend to be bred on successive years in the same general locality. N-ewe, mentioned above, was bred in 1961, 1962 and 1965 in the same cliffs. She was guarded and bred in 1962 and 1965 by the same ram.

Several points are important. Mountain sheep herd no harems but defend each estrous ewe as she reaches estrus. Non-estrous females, which mountain goat, elk or moose, guard, may be courted with impunity by smaller males in the presence of a larger. Unlike the cervids or the mountain goat, rams feed during the rut except for the guarding ram about an estrous female when potential challengers are present. Unlike some African antelope, i.e. Adenota (Buechner, 1961) or Gazella thompsoni (Walther, 1964), which court and breed females on a mating territory unchallenged by other males, mountain sheep experience intense challenge about the estrous ewe. The breeding success of rams in healthy populations declines sharply with their dominance rank. Probably all estrous females are inseminated by several rams although virtually all the first 20 - 50 copulations are performed by the largest ram. In the presence of the ewe, the subordinates mount smaller companions extensively; it is in this situation that the ram's tendency to treat subordinates alike (irrespective of sex) manifests itself clearly. There are behavioural differences between populations. Thus, the old, large bighorn rams I observed in Banff appeared to suffer from a shortage of breath which may have been caused by lungworm infection. Panting heavily they attempted to follow the departing younger rams with the estrous ewe. Then they gave up and began to feed. They had no difficulty reclaiming the ewe once the chase came to an end, by simply walking over. The smaller guarding ram left. It was apparent, despite insufficient quantitative data, that here the younger rams assumed a larger part of the breeding. The actions of all the rams about the estrous ewe were much more lethargic than those of Stone's rams and the spirited interactions between rams were few. However, the bighorns did not appear terribly exhausted after the rut as were some large, old Stone's rams.

## Courtship by the ewe

This behaviour is very rarely seen. From 21 estrous females which I observed, only three did some courting. It appears that female courtship arises only under rare circumstances: The ewe is courted by one single male and the ram is already exhausted from frequent copulations. In the presence of several rams, the exhausted dominant would be quickly relieved by eager subordinates as I described earlier. There would then be no need for the ewe to stimulate an exhausted ram.

I observed the extensive courtships of a Stone's ewe on December 4, 1961, under above circumstances. A seven year old full curl had associated himself in late November with a 12 year old ewe and her two followers, a yearling female and a ram-lamb. On the morning of December 4 the old ewe was well in heat and the ram already exhausted. During the day I witnessed 26 interactions between the breeding couple, of which 18 were initiated by the ewe. The ram initiated only eight interactions on the old ewe, five on the lamb and three on the yearling female.

The behaviour of the courting ewe is best described from a sample of my notes:

> "N-ewe has been feeding a little. Now she stands facing away from F-ram. Suddenly she bolts, and F-ram almost reflex-like bounds after her a few paces and freezes in a low-stretch. N-ewe whirls and horn-threatens F (Fig. 94). Then she comes and rubs her side along his body while he stands frozen in a low-stretch. Again she bounds away a few paces, turns, butts F-ram on the head, jumps back again, horn-threatens then ducks under his chin and rubs her side and haunches along his chest Fig. 94) and neck, and stops with her haunches pressed against his chest. F-ram assumes a position directly behind her and mounts three times in rapid succession.

N-ewe moves forward a little and F-ram follows. She moves again, but he remains standing. N-ewe turns her head and looks at the ram who has begun to graze. N-ewe turns and moves back to F-ram. She goes close to him and feeds parallel with the ram almost in body contact. This lasts a few minutes. Then N-ewe horn-threats to F-ram, slips under his neck and rubs her side again along his chest. She stops for a moment with her haunches against his chest and then steps forward. F-ram makes a sudden rush at her with lowered head. She avoids him, turns and butts him on the head. Then she moves close beside him and both walk in low-stretch - apparently in body contact - several paces forward. Both stop simultaneously. She turns and trots away, but stops and looks at F-ram. F-ram just stands. Then he paws a bed and lies down. N-ewe does likewise."

The behaviour patterns of the courting ewe include hence, a sudden bounding away, which I termed a "coquette run" (Fig. 94A). This run is short and is terminated by the ewe turning towards the ram. During her approach in horn-threat the ewe may prance a little (Fig. 94B). She often horns and butts the chest and shoulders of the ram (Fig. 94C) before rubbing her body along his chest (Fig. 94D). N-ewe nuzzled the head of F-ram only twice in 26 interactions, however, this behaviour was shown more frequently by a 2½ year old ewe in her first heat period. In the 26 interactions, N-ewe performed the horn-threat approach 17 times, horned the ram's body 10 times, performed the coquette run 10 times and butted F-ram three times. F-ram mounted her 11 times. In one respect the ram behaved unusually. He charged the ewe quite often, seven times in total, and also charged the yearling female twice. Both ewes evaded him easily.

The behaviour of the courting, estrous ewe is similar to that of the young ram towards an older ram. Like the latter, she accepts front-kicks and twists without running away; she approaches the dominant in horn-threat on her own; she butts, horns and nuzzles him; she arches her back when mounted. She differs only in that she performs coquette runs and seeks body contact herself. The latter is achieved in the normal interactions of rams by the dominant pushing his chest at the subordinate's side. The estrous ewe, hence, shows a remarkable behaviour reversal.

<u>Post-rut</u>

After the rutting season, most rams return from the ewe ranges to their own specific wintering areas. On the Stone's sheep study area, which was thinly populated with sheep, rams were much more solitary after the rut than at other seasons. This is shown in Fig. 95. In January, 1962, when deep snow forced rams on to a limited wintering area, the solitary tendency was much less apparent than in January, 1963, when very little snow lay on the ground and the rams dispersed. In 1962, as the winter moved on into spring, rams became increasingly more social and formed bands.

Older rams were more solitary than the younger ones (Fig. 96). It can be noted that only after 7 - 9 years of age was the tendency to go about alone very conspicuous.

# PART IV

## ON THE EVOLUTION OF MOUNTAIN SHEEP

### Introduction

The Caprini are a successful tribe of ruminants. They have spread to virtually all major mountain ranges in the northern hemisphere, and evolved great diversity in external appearance, size and climatic adaptations. Despite this diversity, they appear to be very closely related as is indicated by hybridisation experiments. All wild sheep that have been crossed with domestic sheep have produced viable, fertile hybrids, as do interspecific crosses in the genus Capra (Krumbiegel 1954, Petzsch 1957, Young and Mansville 1960). Hybrids have been obtained from the intergeneric crosses of Ammotragus and Capra (Pletzsch 1957 a) and Hemitragus and Capra (see Krumbiegel 1954). One can obtain hybrids even from such distant genera as Ovis and Capra, but only after some laboratory manipulation of the semen and artificial insemination (see Schmitt 1963). On the whole, the genomes of rather diverse caprids are surprisingly compatible.

Fossil evidence indicates that the caprids are evolutionarily very young. Ovis and Capra appear for the first time in the early Pleistocene. They are preceded by Sivicapra and the late Pliocene genus Tossunnoria from China (Thenius and Hofer 1960). The great diversity of forms found in the Caprini apparently evolved in the short time-span of the Pleistocene.

The caprids are therefore diverse, closely related and appear to be young. This indicates that they apparently evolved very rapidly. The purpose of this chapter is to examine how they evolved morphologically and behaviourally, and to explain the selection forces responsible for the direction and speed of their evolution.

The Primitive Caprids. The fossil evidence indicates that caprids evolved from rupicaprid ancestors (Thenius and Hofer 1960). If this is true, then the most primitive caprid is the one which most closely resembles the rupicaprids. This would be Hemitragus. It is surprising how many features it has in common with the American goat-antelope (Oreamnos).

Typical rupicaprid characteristics of Hemitragus are the hair-pants on front and hindlegs, the well developed hair ridge, the lack of a rump patch, the narrow, pointed ears, the rather short, backward pointing and annulated horns, the small sexual dimorphism in hornsize and shape, as well as the four teats, of which however only the last pair are usually functional (Rammel and Caughley 1964). Like Oreamnos, Hemitragus males pair off during the rut with one female and apparently guard her in the non-estrous state, yet fight so rarely that fights have not yet been witnessed (Anderson and Henderson 1961). Oreamnos males fight primarily by the hooking of their opponents rear and belly and carry as a primary protection a thick hide (p. 55). We do not know how Hemitragus fight, however, they have killed deer in Woburn park by disembowelling them (Anderson and Henderson 1961). They could only achieve that by hooking at the belly of their victim in the manner of Oreamnos. Furthermore, Hemitragus males have a thick, heavy hide. It may weigh as much as 60 pounds from males in wintercoat which weigh 300 - 350 lbs. The hide from a nine year old Oreamnos male shot in early winter weighed 35 lbs; the males live weight was calculated at 246 lbs. It is likely that the thick hide in males of both genera evolved as protection against a similar mode of combat. Males of both genera engage opponents with a broadside threat display. However, Hemitragus uses a stretched posture and does not pull the head from the opponent as does Oreamnos.

Hemitragus is hence similar to rupicaprids except for the broad, sharply keeled horns. The keel, I suggest, is an adaptation which increases the effectiveness of butting by localizing the force over a smaller surface area than would round horns. It is probable that Hemitragus males will attempt to catch some blows of their opponents with the horns. It is also likely that--as in Oreamnos--there will be only one fighting type in Hemitragus, and it will be comparable to the vicious, unritualised brawls of Ovis males (p. 98 ). A distinction between vicious and ritualised fights will probably not be possible.

The rupicaprid ancestry is still apparent in Ammotragus, the next most primitive caprid, but it also has features, reminiscent of sheep. Ammotragus is primitive in that it still uses a horn thrust like Oreamnos (Katz 1949); it is the only caprid beside Hemitragus which can inflict stabwounds with its horns (Haas 1958). On this basis it seems probable that old Ammotragus rams will have a thick hide. Sexual dimorphism is relatively small, while females are aggressive and can keep males at a distance (Ogren 1965, Haas 1958). These are both rupicaprid features. *Ammotragus* has no rump patch, its tail is long, its ears are typically rupicaprid and its males apparently live solitarily except during the rut (see Brehm 1916).

*Ammotragus* is advanced in that males interact frequently and not only butt, but also clash. The clashes are less forceful than those of sheep, but seem to be otherwise similar to those of mouflon (*O. musimon*). *Ammotragus* males also wrestle by hooking horns and neck fight, behaviour patterns which are present in rudimentary form in American sheep (p. 44), These behaviour patterns may be somewhat specialized derivatives of the vicious, generalized fight. As yet we do not know how two large rival males fight. It is unlikely that their combat forms will be as ritualized as those of advanced sheep (p. 90). *Ammotragus* rams will most likely show a mixture of some ritualized clashing and vicious wrestling, neck fighting and occasional hooking at the opponents flank or rear.

As in sheep, the estrous female is guarded by one male against several others (Ogren 1965). Subordinate *Ammotragus* males, unable to reach the female in heat, may mount each other as do sheep but no known rupicaprid. Like *Capra* or *Ovis*, *Ammotragus* males commonly ejaculate spontaneously, but resemble goats by taking the penis into their mouths (Haas 1958). *Ammotragus* rams are not malodorous, they have only a short hair ridge running dorsally along the neck to the withers--just like all urials and argalis, they carry a cheek beard and a ventral throat mane which is similar, but more extensive than that of urials, and they possess relatively large horns with heteronym winding

Although Ammotragus may cross with Capra (Petzsch 1957 b ), it has a blood serum protein picture similar to that of Ovis but not Capra (Schmitt 1963).

A present-threat has not yet been described for Ammotragus. It may well be an inconspicuous fronto-lateral display, shown by antagonistic large males prior to a serious fight. The *low-stretch appears to be absent; the twist appears to be present in courtship (Haas 1958), but also as a threat (Katz 1949). It is however fairly certain that neither display nor contact behaviour are nearly as well developed and frequently used as in sheep.

I shall use Ammotragus as a basis of comparison with advanced caprids.

## Changes in the external appearance of caprids

Let us turn now to the external appearance of caprids and see how it changed. This happens to be better known than other features of caprid biology. But more important, the structure and function of caprid adaptations is interrelated.

Petzsch (1957 b ) pointed out that Ammotragus, stripped of its ventral mane, is strikingly similar to the Caucasian tur (Capra cylindricornis). This form blends into the West Caucasian tur (Capra caucasica) which strongly resembles the true ibex (Capra ibex). If these species are arranged in order of resemblance, we get the series shown in Fig. 97.

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* These forms of postures are described on p. 38 .

Ammotragus, however, resembles even more the western urials (Ovis ammon), particularly the races ophion (Cyprus) and gemelini (Armenia). We can assemble Asiatic sheep in order of resemblance, put Ammotragus out front and obtain the following line up: Ammotragus, Ovis ammon gemelini, orientalis, cycloceros (the "arkal" form from Turkestan), severtzovi, nigrimonta, poli, karelini, ammon and darwini. This series is partially illustrated in Fig. 98. Other forms, such as ophion, musimon, or hodgsoni may be regarded as branches deviating from the proposed line up. (All descriptions based on Clark 1964, Geptner et al, 1961, Lydekker 1898, 1913).

On the basis of external appearance alone, Ammotragus can be regarded equally well as a primitive goat or as a primitive sheep; it also links the most highly evolved goats and sheep into one series.

The above mentioned series of Asiatic sheep and Ammotragus, is also a geographic series. Those forms which resemble each other most, are also neighbours; the greater their diversity, the further they are situated from each other (Fig. 99). The series stretches itself from North Africa in a slightly curved line to Mongolia.

The sheep series runs furthermore from the old Pleistocene refugia of North Africa and southern Asia, deep into the formerly glaciated parts of central Asia. The advanced forms, cycloceros to darwini, could hardly have been present where they are now during the glaciations. These appear to be forms which colonised the vast expanse of living space after the retreat of glaciers. The series appears to be a real evolutionary series in which one form gave rise to the next more advanced one. This is a more reasonable explanation; than the assumption that each form evolved quite independently but--by some unexplained feat of nature--lined themselves up geographically in order of resemblance. Let us see how these sheep changed externally.

(1) The horns changed from a heteronym to a homonym winding (Fig. 98). First they increased in length and later in mass (i.e. _poli_ horns plus upper skull from an old ram weighs 25 lbs., but in _ammon_ 49 lbs. (Clark, 1964). The horns became sharply keeled laterally. This angle became reduced and almost lost in _karelini_ to _darwini_ (Fig. 98).

(2) The haircoat showed the following changes. The cheek-beard and ventral neck-ruff were gradually reduced and then lost. The dorsal hair ridge was lost except for a short ridge on the neck. A rump patch appeared and progressively increased in size. The amount of white hairs increased on the rear aspects of hind and front legs.

(3) The ears became shorter and rounder (Fig. 98).

(4) The sexual dimorphism increased by the female becoming relatively smaller in body and hornsize and by her losing the neck ruff (Fig. 100).

These morphological changes went on simultaneously. Sheep with the largest horns also tend to have the largest rump patches, greatest sexual dimorphism, and the least display hair.

On the basis of these observations about the distribution and differences in external appearance of Asiatic sheep, one can formulate a tentative conclusion. It appears, that sheep evolution is linked with their advance into formerly glaciated terrain. Whenever they invaded new habitat which followed in the wake of glaciation, they changed simultaneously in several external features. If these are valid relationships, then they should apply to other sheep also. With this in mind, let us turn to the next large group of sheep, the American sheep.

These are all rather advanced sheep, compared to the Asiatic forms. They have lost the neck ruff entirely as well as the dorsal ridge of hair on the neck. Their horns are quite long and already massive. In eastern Siberia, we find the <u>nivicola</u> group. Alaska, the Yukon and northern British Columbia are home of the <u>dalli</u> group, while the <u>canadensis</u> races occupy western North America south of the Peace River to the tip of Lower California.

It is generally assumed that sheep crossed to North America via the Bering-Chukchi platform from Siberia and then spread along the mountain ranges of western North America down as far as Mexico. The Wisconsin glaciation separated sheep into two major groups. <u>Ovis dalli</u> survived in the Alaska-Yukon refugium and <u>canadensis</u> in the southern refugium (Cowan 1940).

If the conclusion reached from Asiatic sheep is valid, then <u>nivicola</u> should be the most primitive of the American sheep, and <u>canadensis</u>--which moved furthest--the most advanced form.

Sheep of the dalli group should be intermediate. There is, however, a further consideration. After the Wisconsin glaciation, sheep invaded the formerly glaciated areas. Hence, the most advanced forms should really be found there, and not in the old refugia. Therefore, one should first compare sheep from the old refugia, and then sheep from the old refugia with forms from the glaciated areas.

Indeed, nivicola does seem to be the most primitive. However, relatively little information exists about it. In size, it is similar to dalli and stonei. Cherniavski (1962) lists live weights of 154 - 167 lbs. (70-76 kg.) for rams 6 years of age or older. Geptner et al (1961) state that three rams (6-8 years) weighed 184 - 220 lbs. (86-100 kg.), and five females weighed 101 - 119 lbs. (46.9 - 54 kg.). A very large ram weighed in early fall 281 lbs. (128.4 kg.). Reliable weights are surprisingly rare for either dalli or stonei. Ulmer (1941) reports the weights of four Dall's rams as 173 - 185 lbs. These were old rams weighed shortly after death. A seven year old Stone's ram shot during the rut weighed 170 lbs., but the animal was in poor condition. A six year old Dall's ram shot in early fall weighed 226 lbs. The largest Stone's ram which I shot would have weighed about 250 lbs. live weight.

Although very similar in size to dalli and stonei, sheep of the nivicola group appear to have smaller horns. This is expected. Geptner et al (1961) give as maximum dimensions for nivicola a horn length of 111 cm. (43"), and a basal circumference of 36 c.m. (14-1/4"). Clark (1964) in his patient search uncovered a good number of horn measurements for nivicola. The longest hornlength he reports is 41-1/2"; the largest basal circumference as 14-1/2". These maxima fall well below those of dalli and stonei. The longest hornlength recorded for dalli exceeds 49", and for stonei 51". Although dalli and stonei are better sampled than nivicola in this respect, there does seem to be a real difference here. Certainly basal circumference well beyond 15" has been repeatedly reported for both dalli and stonei. (see Anonymous, Records of North American Big Game).

Nivicola is also primitive in having a small rump patch which does not extend beyond the root of the tail (Lydekker 1898, Clark 1964), and in having only very little white on the rear margins of front and hind legs (Fig. 101). Otherwise, one would be occasionally hard pressed to distinguish between it and Stone's sheep. The colour and shade patterning of both races appear to be similar. Lydekker (1898) reports that nivicola has shorter ears than other American sheep. However, Geptner et al (1961) list the ear length for males as 9 - 9.5 cm (3-1/2 - 3-3/4") and for females as 8 - 9 cm (3-1/4 - 3-1/2"), and this is the same as for Stone's sheep. Two rams had ears 3-3/4" long; one exceptionally large female had ears also 3-3/4" long (measured from the notch).

In North America, the old Alaska refugium is presently occupied by the white Dall's sheep; it is possible that the northernmost Stone's--the patchy, gray "fannin" sheep of the Yukon--are also found in the eastern end of the refugium. In the old southern refugium we find a number of canadensis races, of which the most primitive is Nelson's sheep (nelsoni). Cowan (1940) pointed out that this race had its cranial and horn characteristics in close affinity with those of the northern sheep from Alaska and the Yukon. From the Records of North American Big Game I took the first 30 horn base circumferences of rams shot in Nevada. They had circumferences of 14.2 $\pm$ 0.85 (S.D.) inches (12.0 - 16.0). The first 30 circumferences of dalli measured 13.7 $\pm$ 0.56" (13.0 - 15.7). These figures must be compared with caution since many more dalli are shot and recorded than nelsoni, and the dalli recorded here may be heavier in horns than if samples were truly random. Nevertheless, nelsoni, in agreement with the hypothesis, is a little larger in this parameter than dalli and the difference is significant at the 5% level.

We cannot compare the coat pattern of the white Dall's sheep with that of the Nelson's bighorn. However, stonei and nelsoni appear to have much the same rump patch size and shape. Stone's sheep have more white on their legs than nelsoni. Otherwise there is little similarity in coat colour or patterning between the two forms (Fig. 115).

Nelson's bighorn appears to be more similar in bodysize to dalli than to other bighorn races. Welles and Welles (1961) list the average weight of 37 rams at 156 lbs. (127 - 190 lbs.) and of 15 ewes at 96.5 lbs. (74 - 114 lbs.). They are hence about as large as small Stone's sheep of equal sex and age.

We hence find, as anticipated, sheep with increasingly heavier and thicker horns and larger rump patches as we move from Siberia, via Alaska to the centre of the American southern refugium. Two characters do not change as expected. Ear length does not decrease, rather it appears to follow Bergmann's rule. Sexual dimorphism appears to be similar between nivicola, dalli and Ovis canadensis nelsoni.

As indicated before, if sheep changed when they colonized the once glaciated areas, then those forms which are now found there are more advanced than those in the refugium. We have unfortunately no information about the nivicola races in this respect, however, in North America this is what is found. From the southern refugium, canadensis moved north, deep into formerly glaciated regions. This race has much larger horns, rump patch size and sexual dimorphism than nelsoni. The first 30 canadensis rams from Alberta and British Columbia (the northern part of their distribution) listed in the Records of North American Big Game, have a basal horn circumference of 15.6 $\pm$ 0.61 (S.D.) inches (14.3 - 17.0). This is 1.4" more than for nelsoni, however, this difference is most likely exaggerated due to more canadensis rams being shot than nelsoni; the difference is significant at the 0.1% level. The rump patch of canadensis extends higher up on the rump, the corner has been rounded out and lowered, while the dorsal stripe bisecting the rump patch has been reduced and partially lost. A scrutiny of 95 bighorns from Banff park, showed that in 70 the tail stripe had been lost or partially interrupted. Here I differ from Cowan (1940), who states that the mid-dorsal line for canadensis is usually extended to the tail bisecting the rump patch.

Big rams in what must be very healthy populations can grow very large. Cowan (1940) cites live weights of 285-344 lbs. for four rams older than five years of age shot in British Columbia. These must be considered as maximum weights. Sheep from different populations differ in size and so apparently do sheep from the same population in different decades. When rams grow as large as those mentioned above they weigh 2 - 2-1/2 times as much as females; in nelsoni this ratio is only about 1.5 - 1.6.

At this point let us note the following. If sheep evolved in external appearance in the directions discussed whenever they invaded regions vacated by glaciers, then we should find more advanced sheep not only in latitudes vacated by glaciers, but also in altitudes vacated by glaciers. Vegetation lines are altitude-dependent. The warmer it got after glacial retreat, the higher did vegetation lines spread, and the more habitat became available to sheep. Before leaving the *canadensis* group, it may be pointed out that *nelsoni* is surrounded by advanced sheep. There is virtually a ring of evolved forms about this primitive race. Like the northern *canadensis*, these races have larger rump patches and heavier horns, It appears then that the present *canadensis* races were derived from a small relic population which survived the height of the last glaciation at low elevations somewhere in southern California. During the dry period following the glacial withdrawals, sheep spread into the inhabitable uplands. The race which moved furthest, *canadensis*, evolved the greatest differences from *nelsoni*.

From the Alaska refugium, sheep moved south into the Alaska and St. Ellias range, north into the Brooks range, while Stone's sheep moved southeast deep into formerly glaciated terrain. As expected, the Stone's sheep is larger in hornsize and in the upper parts of the skull than Dall's sheep (Cowan 1940). The first 30 Stone's rams listed in the Records of North American Big Game have a basal horn circumference of 14.5 $\pm$ 0.58 (S.D.) inches (13.8 - 15.8). This is 0.8" more than *dalli* and is significant at the 0.1% level. Since *stonei* and *dalli* are both hunted frequently, these measurements appear to be quite valid. The southernmost Stone's sheep are probably also larger in bodysize than Dall's sheep, however, this remains to be verified.

However, the origin of *stonei* is problematic. It appears most unlikely that the white *dalli* form could have given rise to stonei. Cowan (personal communication) suggested that dalli and canadensis met in an interglacial period, and stonei represents the stabilized outcome of ancient intergradation between the two. Alternatively, stonei may be from a relic dalli population which still retained the nivicola colouration. This relic group survived in the eastern parts of the Alaska refugium and spread southeast in post glacial times. Stone's sheep are more primitive than canadensis by having smaller horn bases and a smaller rump patch. However, they are so unlike bighorns in coat pattern that only an experimental cross between dalli and canadensis will suggest whether the hypothesis expressed by Cowan is tenable. The characteristics which distinguish the darker, southern Stone's sheep from the "fannins" of the Yukon could well have been evolved independently. There is also little doubt that dark and light Dall's sheep met and crossed in early post Wisconsin times (Sheldon 1911, in Cowan 1940). Today, with sheep in the North torn into separate, often relic populations, I consider such contact as unlikely.

In general it therefore appears that Asiatic sheep and American sheep have shown parallels in their evolution. In both instances, the concept that sheep evolution was linked to range extension after glacial retreat, is fruitful. This concept appears to be equally applicable to other caprids.

Thus Pseudois, Ammotragus and Capra cylindricornis share many similarities in appearance. If Ammotragus - like ancestors gave rise to the other forms, these should have evolved similarly to sheep. Pseudois and C. cylindricornis are now found in areas which were either glaciated or relatively barren during the Pleistocene. Indeed, great similarities to sheep evolution do exist. Both forms have larger, heavier horns than Ammotragus; both lost the dorsal hair ridge on the neck, the cheek beards and neck ruff; C. cylindricornis has only a tiny chin beard; both evolved a rump patch. Pseudois has a large rump patch and much white on the legs. C. cylindricornis has less rump-and leg marking but it is there (see Petzsch 1958). Sexual dimorphism has increased in both forms. Pseudois is sheep-like in that males are social, and that it has either vestiges or the beginnings of preorbital and interdigital glands. Pseudois is further removed from an Ammotragus-like ancestor from North Africa than C. cylindricornis, and has also changed more in the same directions as sheep.

In these forms, the horn winding remained heteronym unlike the homonym winding of advanced sheep, and their ears remained long and pointed, not rounded as in sheep. This indicates that increase in hornsize need not be linked to the homonym winding;latter hence evolved in sheep for reasons other than increasing horn mass. The ears--as in American sheep--appear independent of selection for larger horns, loss of display hairs, etc.

The last caprids to be considered are of the genus Capra. It is not my aim to tackle the phylogeny of this group of species of obscure origin. I only want to point out that the species with the largest horns, least display hair and greatest sexual dimorphism are found deep in the regions glaciated during the Pleistocene. These are the large ibexes (*Capra ibex*). The southern ibex from Arabia and Ethiopia, may be living today in regions which were during glaciation well above vegetation line and hence barren and uninhabitable.

## Changes in the behaviour of caprids

The discussion has so far revolved about morphological changes in the evolution of sheep. This served to form a model by which to compare behavioural changes. Presumably, morphologically primitive forms have also primitive behaviour. I hope to show later that it is the behaviour of caprids which explains their changes in external appearance.

Unfortunately, we know little about the behaviour of most caprids and are well informed only on the American sheep. Good observations are available for *Ammotragus* (Katz 1949, Haas 1958, Ogren 1965) and the rupicaprids *Oreamnos* (Brandborg 1955), (Geist 1964) and *Rupicapra* (Zedwitz 1937, Walther 1961). Walther (1961) reported important observations on captive *O. a. poli*, *O. cycloceros*, *Capra ibex* and *C. falconeri*. Incidental behaviour and observations are scattered in the caprid literature. Banks (1964) gave good descriptions of the behaviour patterns of domestic sheep. The best behaviour information is hence available for the highest evolved forms and the quite primitive ones. However, since we do have a model of sheep evolution based on morphological characters, we can form some conclusions about their behavioural evolution.

(1) It appears that sheep evolved from a generalized, damaging combat type of their rupicaprid ancestors, to ritualised, relatively harmless combat form. They specialized increasingly in the clash, in which they initially focused the force of the collision on one horn keel (p.50 ), and reduced other fighting forms to insignificance. The vicious fight characteristic of ancestral primitive forms has not been lost entirely.

(2) The chief defense against the opponents blows changed from a thick hide, avoidance of combat by virtue of withdrawal or display, to catching the blows with the horned head. It is this change which allowed the evolution of the clash, and the frequent occurrence of combat which is relatively harmless with the new defense mechanism. Concurrently with the evolution of ritualised clashing the hide became thinner.

(3) With the evolution of large horns and loss of long body hair, the broadside display disappeared and was replaced by a horn display. The horns, besides acting as weapons and shield, now have the additional functions of display organs and rank symbols (Geist 1966). Different sizes of horns probably produce a different force of impact during the clash (p. 53 ), and, since the clash is usually followed by a horn display, allow combatants to associate clash force

with horn size. It is this which allows horns to function as rank symbols, and probably selects for frequent horn display. It is advantageous to show horns to a subordinate, as this would reinforce the association between horn size and clash force.

In the rush-and horn threat sheep remained conservative; these threats are quite similar to those of Oreamnos (Geist 1964). The threat-jump however, is specialized since it is really the intention movements, or preparatory behaviour of the clash. However, Oreamnos, which does not clash, occasionally also threat-jumps to an opponent by jumping up in front and hitting (throwing) backwards with the head. Rupicaprid males may perform rather exuberant jumping and frollicking in which threat jump-like behaviour does occur (Walther 1961). Hence, the prerequisites for the specialized threat jumps of O. canadensis, dalli, poli and Capra males are already present in the rupicaprid stem.

(4) With increased sexual dimorphism, the courtship of the larger males became more forceful while the female became less aggressive. This devlopment is made possible by the absence of sharp horns and the evolution of butting and clashing. Whereas the Oreamnos female is a very dangerous opponent (Geist, in press), the female mountain sheep poses no threat to the ram. It seems to follow that cautious courtship would be selected for in Oreamnos males since it would reduce the chances of the male being attacked and wounded by the female,

whereas there would be little selection against vigorous courtship by the ram. The courtship behaviour of caprids has otherwise remained conservative (see Walther 1961, Haas 1958).

(5) During caprid evolution, males changed from being solitary to being gregarious and finally social forms. It appears that this was made possible by the evolution of relatively harmless forms of combat which permitted the establishment and maintenance of dominance hierarchies via frequent agonistic interactions. Conspicuous hornsize differences among males allow a priori prediction of dominance relationships, hence individual rams live in a familiar social environment even though they meet strangers. Although such mechanisms probably allowed the males to live gregariously, they were not the cause for the males keeping together. This will be discussed later (see neoteny p.144 ).

These are some of the major behavioural changes which appear to have happened in the evolution of sheep, and probably other caprids. It was noted that several lineages of sheep and goats evolved similar external features convergently. It would therefore not be surprising if such end products of evolution as the argalis or bighorns, _Pseudois_ or _Capra ibex_ have evolved similarities in their behaviour. Thus Walther's (1961) observations on captive _poli_ show that their behaviour is very similar to that of American sheep. The _poli_ ram used the low-stretch often, he clashed after a bipedal run holding his head, legs and body like a bighorn or Stone's ram. His clashes appeared to be similar if not identical with those of bighorns (Walther 1961), and like the latter he carried a prominent lateral edge on the horns. The _poli_ ram pawed exuberantly during social interactions, which is also done--but rarely--by thin horn sheep. The similarity extends itself also into courtship behaviour. It is the more remarkable since the behaviour of _poli_ and _cycloceros_ --both from the _ammon_ cline--is quite different.

The _cycloceros_ ram (probably from Pakistan) which Walther (1961) observed, did not hold the low stretch, but he did perform an exuberant twist and only then momentarily dipped into the low stretch. In this, domestic sheep tend to resemble the urials rather than the advanced sheep (see Banks 1964). When clashing, the _cycloceros_ ram charged on all fours like a mouflon or domestic sheep. Walther (1961) noted that the ram may lift the front legs off the ground an instant before the clash. In this clash type _cycloceros_ appears to be advanced over _Ammotragus_, but more primitive than either the argalis or bighorns. This is more or less what could be expected since _cycloceros_ is intermediate in external characteristics between _Ammotragus_ and _O. a. poli_.

The advanced goats are similar to advanced sheep in that they use a bipedal clash. However, outside the bipedal stance there is little similarity in the clash form. _Pseudois_, _Capra ibex_, _cylindricornis_, _aegagrus_ and _falconeri_ all clash bipedally.

The rupicaprids Oreamnos and Rupicapra have a broadside present-threat as has Hemitragus. American sheep have replaced the broadside display with horn displays. The large horned European and Siberian ibexes observed by Walther (1961) appeared to possess no broadside display. However, the markhor, equally large horned to ibex but covered with long display hairs, has a beautiful broadside display. In this display it erects the long hairs on its dorsal line. The markhor is in this respect somewhat primitive. It has also a more primitive tooth structure than ibex or aegagrus, in retaining relatively large premolars (see Geptner et al 1961. Fig. 179). It appears that in the most advanced, long-horned caprids, which have lost their display hairs, the broadside display is lost and the horns assume display function. Bighorn sheep as well as Walther's (1961) poli ram displayed horns from the low-stretch and head high ("present") positions. The rather hairy cycloceros ram appeared to know neither the low-stretch nor the present. It is quite likely that urials as well as Ammotragus have retained some semblance of a broadside display.

These observations substantiate the concept that behavioural changes have paralleled morphological ones in the evolution of caprids. Thus the increase in hornsize, loss of display hairs, and increase in rump patch size appeared to go hand in hand with the specialization of a bipedal clash, reduction and loss of broadside display, and the evolution of horn displays.

Neoteny as a factor in sheep biology

A number of features in the behaviour and appearance of sheep can be explained by the hypothesis that the male is neotenic but reaches an ultimate adult form, whereas the female is a paedogenic form which remains juvenile in appearance and behaviour throughout life. I am using here the definitions of neotenic and paedogenic as formed by Romer (1956). Amongst mammals we do not find larval forms but we do find juvenile forms, and with this minor modification Garstang's concept becomes applicable to mammals.

Males of American sheep mature sexually at 1-1/2 - 2-1/2 years of age, but they are not mature behaviourally, nor do they reach ultimate body proportions until they are 7 - 8 years old. The changes in horn and body proportions are discussed (p. 10 ). Few weights and measurements are available for rams of various ages, however, it is apparent to the unaided eye that they grow bulkier until they are about 7 years old. Cherniavski's (1962) data for nivicola indicates increases in weight by adult rams until they are 9 - 10 years old. Hence, growth continues long after sexual maturation.

As lambs, rams show no displays nor any rubbing or horning on other lambs, but do clash, butt, horn threat and threat jump or, frequently mount other lambs. Their actions are almost entirely aggressive or sexual. As rams mature, they become increasingly less like lambs, by using fewer aggressive patterns or mountings (Fig. 102) and more and more display patterns like the front-kick (Fig. 103A), twist (Fig. 103B) or low-stretch (Fig. 104B). Rams also undergo a psychological maturation. It is shown in Fig. 104A that rams approach their own size class with increasing frequency in low-stretch as they grow older and larger. Since the low-stretch approach is typical of dominants, the ram acts with increasing frequency as if he were the dominant in the face of equal sized companions. It may be that equal sized opponents appear less formidable to them. In this case we expect interactions to become more frequent and intense as rams grow older. This is borne out in Fig. 104 and 106; the former remains to be tested. It is hence evident that rams not only grow, but also change behaviourally after sexual maturation. They are behaviourally mature about the same time that they reach ultimate body proportions which is at 7 - 9 years of age.

The ewe is paedogenic since she never reaches the ultimate growth form, but remains throughout life the very image of a sexually mature yearling ram. They are so similar in body and horn size, facial features and belly marking (p. 12 Fig. 8) as to be easily confused even by experienced observers. The ewe is similar--though not identical--to young males in her social behaviour. Like these, ewes display little and rarely rub or nuzzle other sheep, at least not until they are in estrus. Ewes use mainly aggressive patterns (Fig. 71 c). When ewes are in estrus, they behave towards the guarding ram as do subordinate rams to dominant ones (p. 115 ), and are treated little differently in return. Non-estrus ewes act much like lambs or subadult ewes in their response to the front-kick or mount (Fig. 77). A characteristic of lambs is that they follow other sheep and are hence rarely seen alone. This is equally true for ewes and juvenile rams. In this, these two classes resemble each other more than either does older rams (Table II).

Like other infants of social ruminants such as elk (Altmann 1963) or cattle (Schloeth 1961), lambs tend to form juvenile groups within female bands. They appear to favour the company of equals, but follow adults once these move on. These two tendencies--to associate with equals and to follow an "adult"--explain the actions of young rams. When rams are three years old, they are large and quite distinct from females. They now begin to associate with other rams of equal or similar size outside the female band. When on the move, these young rams follow the largest horned or one of the largest horned rams in the band (Table III). At that stage, young rams are more "adult" in appearance than ewes; the most "adult" looking sheep for these young rams would be rams which had reached the ultimate growth form (Class IV). Hence, the young rams only continued doing what lambs did--they associated with equals but followed an "adult".

As rams grow older, they begin to lose these juvenile tendencies. This is indicated in that they are seen more frequently without company. Table II shows this trend in a dense bighorn population; Fig. 96 shows it much more clearly for Stone's sheep in a sparse population. These data indicate that rams become more independent of other sheep with age.

Since older rams look more "adult" younger rams follow them; since they act more adult by being independent they lead. After all, a leader is the most independent acting animal in a group.

The great sexual dimorphism of advanced caprids appear to be a function of the long juvenile phase of the male. If the male changes in appearance due to growth via a progressively prolonged juvenile phase, while the female matures at 1-1/2 - 2-1/2 years of age and grows little thereafter, then the female will become progressively smaller and more juvenile compared to the male.

For rams, growth in horn and body size was previously linked to juvenileness. An increase in horn mass can be achieved not only by increasing the number of growth years, or intensifying growth within each year, but also by shifting most horn growth into the latter part of the juvenile stage. Here the horns are growing from a wider base, and hence become thicker and more massive. In this respect dalli and canadensis differ in the growth pattern of the horn (Fig. 105) the result being a larger horn in the latter.

If, however, larger horns grow on rams who progressively become more juvenile, then they should also progressively become more juvenile in other features. Thus the neck ruff becomes increasingly reduced and finally lost in ammon sheep (Fig. 98). The ruff is only found on sexually mature rams and more poorly developed in young than in the old rams (Lydekker 1913 p. 104). Hence, rams which grow more horn mass by becoming progressively more juvenile, should also reduce the neck ruff progressively and finally lose it. No selection forces against the ruff need to be postulated. By the same line of reasoning, sheep which grow heavier horns, should also use the juvenile behaviour of butting, clashing and mounting relatively more frequently. Thus _canadensis_ rams should use the patterns more frequently than _dalli_ rams from comparable populations. This is indeed what occurs. I noted a great difference between the dense _dalli_ population I stayed with in fall 1963, and the somewhat poorer quality bighorn population from Banff Park. Bighorn rams clashed daily, Dall's rams I heard clash very rarely; even butting was uncommon. These bighorns clashed even more frequently than the vigorous Stone's rams I observed. This is shown by the data in Table IV.

Although neoteny explains some of the features of sheep, it does not explain every thing. Why did sheep evolve the homonym winding of their horns? At present there is no plausible explanation as to why they changed initially from heteronym to homonym winding (Fig. 98), primarily because we do not know the behaviour of primitive urials. However, once the change in hornwinding began, it had to go on. Note that the circular horns of the urials point directly at the ram's neck (Fig. 98). If such sheep were subject to selection for longer horns, rams would grow the horn tips into their neck.

If the tips miss the neck, then we get the familiar homonym winding as we see it in the northern cycloceros forms (Fig. 98).

The urials evolved a sharp angle on the lateral side of the horns. This indicates that in clashing rams cock the head slightly and--like American sheep--hit first with one horn, concentrating thereby the clash force on one horn keel.

The trend for long, thin angular horns continued as we move via severtzovi and nigrimonta to poli. Here, in the Pamir argali, it reached its maximum expression for poli grows the longest horns of all sheep (up to 75 inches). However, horns much longer than those of poli are not possible--at least not with the manner in which poli clashes. These rams clash similarly to bighorns by racing bipedally at the opponent, inclining the head slightly away and down, hence bringing one lateral hornedge forward for clashing. If two poli rams with large horns were to clash in this fashion, they almost inevitably would hit their horn ends first. This would lead to breakage of the rather light though long horns. This happens in bighorns. Clark (1964) in his interesting account of poli in the Russian Pamir reported the following: Hornbreakage among large poli rams was frequent. Unlike bighorns, poli rams do not broom their horns but break them off usually at the end of the horncores, but often closer to the skull. Although poli horns tend to be nearly twice as long as those of bighorns, and have similar circumferences at the base (55 - 75" long, 14 - 16" circumference), they weigh no more than the horns of bighorns and often less. Clark (1964) reports the weight of the upper skull and horns of a large poli ram as 25 lbs. I weighed the heads of eight heavily broomed bighorn rams, ages 8 - 16 years and obtained a range of 20 - 32 lbs., average 25.3 lbs. (Skull and horns thoroughly dry). Clark (1964) reported as maximum weight for skull and horns of bighorns 40 lbs. This indicates that poli horns are rather lightly constructed. Horn fractures, appear to me to be serious injuries, irrespective of what consequences the broken horn has on the ram's social success. If the horn cores are injured or frozen during winter, the door is open for bacterial attack of the membranes inside the horn sinuses. It seems to me that selection would act against poli rams with very long horns. Clearly, if horns were to evolve further some change had to appear.

The change came in the next member of the cline to the north-east of the Pamir, in the Littedale's sheep from the Tien-shan (Fig. 98 & 99). The angle of the horn shifts away from the eye towards the median line of the skull. This can be seen partially in Fig. 98. It is best seen comparing in Clark (1964) the poli ram p. 59, with littedalei p. 95 and karelini p. 89. This results in a ridge which appears to run down the centre of the anterior horn face (see Lydekker 1913 Fig. 30). The implication is evident. Rams with a more frontally located edge would probably clash more frontally. This would swing the horn tips away and reduce the chances of horn breakage during the clash. In the Littedale's sheep the horns have also increased in diameter and mass.

As we move further north-east, the horn mass of argalis increases steadily. The skull and horns of a good _poli_ weigh about 25 lbs., but those of a good _ammon_ weighed 49 lbs. (Clark 1964). While the weight of skull and horns almost doubles, the body weight increases only from about 300 - 350 lbs. to 400 - 450 lbs. (after Clark 1964, Geptner et al 1961). Furthermore, the horn angle, so prominent in _nigrimonta_ or _poli_ becomes lost as horns increase in diameter in _ammon_ and _darwini_. A similar relationship exists also in the American sheep. The horns of _stonei_ rams I worked with had prominent lateral horn angles; the upper skull and horns of four rams ages 8 - 16 years, weighed 16 - 22 lbs., average 18 lbs., while live weight of old rams would have been about 200-250 lbs. Northern _canadensis_ rams, weighing about 300 lbs. live weight had horns and skull weights of about 25 lbs., but reaching occasionally more than 30 lbs. Similar to _ammon_, _canadensis_ rams have more rounded horns and though the horn keel is present, it is not as prominent as in thin horn sheep. On the basis of neoteny, it can be expected that Siberian argalis will clash more frequently than the thin horned _poli_--just as it is found in American sheep.

The differences in appearance of the caprids are apparently brought about by acceleration, prolongation or retardation of the growth of different body parts. These seem to be superficial changes rather than fundamental ones, changes in the control of genes rather than changes in the fundamental gene constitution. This may be the reason why genomes of different caprid species are often compatible and viable hybrids may be obtained.

An explanation of the major selection forces in sheep evolution

Although neoteny explains many features of sheep evolution, it fails to answer the most fundamental questions. Why did these changes occur in the first place? What possible advantages did the advanced forms gain? Are not the social adaptations of the most primitive caprids just as functional as those of the most advanced? How do such geographic series as that of the ammon races develop? Why have the more primitive members failed to catch up with the advanced forms? I believe that a tentative answer can be given to these questions.

In an earlier paper (Geist, in press) I pointed out that horn size of rams is directly related to dominance rank and breeding success. Large horned rams did almost all the breeding. This indicates that large horns are adaptive and that rams with vigorous horn growth will breed more ewes within one breeding season, than smaller horned (occasionally older) competitors. However, rams with vigorous horn growth, which reach high dominance and breeding status early in life, also tend to die earlier than rams with poor horn growth. Here is a paradox.

The success of any characteristic is judged by the number of offspring its carriers leave behind. The vigorous, large horned ram is clearly successful within one rutting season. However, a ram with somewhat poorer horns who is reasonably high in dominance, will also leave some offspring from each rutting season. Due to longer life expectancy, however, he may leave more offsprings than the larger horned ram with a shorter life expectancy. Hence, the longer life expectancy of smaller horned rams may very well cancel in the long run the reproductive advantage of long-horned rams. This concept, I believe to be the key to sheep evolution.

We noted earlier, that large horns appeared to be products of neoteny. This is the mechanism. Natural selection for large horns in sheep, would mean a selection for this mechanism. Though neoteny explains how horns can grow large, it is selection for large horns which explains the existence of neoteny.

Selection for large horns will occur whenever there is an abundance of rams which have grown close to their genetic maximum. In such a population, phenotypic size variation will be reduced. Rams with poor horn growth will be selected against not only because they will be less successful each breeding season, but because the presence of many larger rams cancels their advantage of longevity. Evolution for large horns will come to an end when there is an abundance of genotypically or phenotypically small rams of long life expectancy. The former condition should exist in the expanding, the latter in the stagnent or declining populations.

Earlier, it was noted that sheep evolution appears to be associated with glaciation. When the continental glaciers of the Würm (Wisconsin) glaciation retreated, they were followed by a dry steppe with some birch and willow shrub in moist sites (Heusser 1965, Bonatti 1966). This is sheep habitat, much as it is found in the St. Elias range in the Yukon today. Sheep moved into this new living space, and the stage for expanding sheep population was set.

To the colonizing populations forage would have been usually abundant, even during the critical late winter months. The individuals would usually have been in good physical condition. Under such circumstances, there would be high reproduction (see Klein 1965), large, well developed, vigorous lambs (Wallace 1948, Schinkel and Short 1961), low neonatal mortality (Gunn and Robinson 1963, Alexander and Peterson 1961, Purser and Young 1959), abundant milk supply for the lambs (Wallace 1948, Munroe 1962), hence great growth rate of lambs (Slen et al 1963). The survival of lambs would most likely be good (see Klein 1965). The yearlings would be of large body size and would mature earlier as has been shown on sheep (Watson et al 1956) and deer (Cowan et al 1957, Wood et al 1962). These sheep would be expected to become large adults (Schinkel and Short 1961, Klein 1964). In short, the colonizing population would be an expanding one in which sheep reached large body size and phenotypic size variability would be reduced. The behaviour of rams in the colonizing population, would be in principle similar to that of the Stone's sheep I studied. I regard it as a high quality population since reproduction was high (in 1962, 18 from 20 known ewes led a lamb in fall), the lambs suckled longer than bighorn lambs from Banff at comparable age and terminated suckling on their own in about 10% (n=84) of the suckles, which I never saw bighorn lambs do. The Stone's yearling rams were in fall as large as ewes, dominated these, and participated in the rut. No bighorn yearling I observed in Banff reached these conditions.

In the high quality population one can expect more vigorous interactions between rams than in a static or declining one. The interactions of Stone's rams were more intense than those of Banff bighorns. This is indicated by the larger number of patterns dealt out per interaction between Stone's rams (Fig. 103 & 106). If mortality of rams is linked to the degree of exhaustion from fighting and courting during the rut--as is indicated by the inverse relationship between dominance and life expectancy--then rams from a vigorous population should die younger than those from a static or declining one. Thus the life expectancy of the bighorn rams I studied in Banff was 12.2 $\pm$ 2.6 (S.D.) years (n=56 dead rams). Woodgerd (1964) however, found a life expectancy of 6.7 $\pm$ 2.4 years (n=17) for rams from Wildhorse Island, Montana. This somewhat limited data came from an introduced bighorn population which had just stabilized its size. It was still of high quality, as was indicated by the high reproductive success and the early maturation age of males and females.

It appears to be no coincidence, that irrespective of population quality, the most intense interactions are shown by rams at the Class III stage, when they are 6-7 years of age (Fig. 103 & 106). This is the age when most of Woodgerd's rams died, and after which the mortality of rams generally increases (see Murie 1944).

In the expanding population we can therefore expect severe competition among rams. The largest, most vigorous rams would be expected to do the breeding. Their individual short life expectancy would be irrelevant to the evolution of larger horns, since these rams would be annually replaced by similar large but young rams.

When the habitat becomes filled and competition reduces forage quality and quantity, the population begins to change. Reproduction declines, juvenile mortality increases, sheep are later in reaching sexual maturity, the average size of the adult declines, social interactions between rams become less vigorous and their life expectancy increases.

In such a population vigorous large rams become uncommon and though they can be expected to be successful during any one rut they participate in, somewhat less vigorous rams of smaller horn size can be expected to do more breeding due to longer life expectancy. In the static population, selection for large horns will hence be slowed down.

This may explain the existence of such clines as the <u>ammon</u> series (Fig. 98). Selection for large horns takes place intensely in the colonizing, outer fringe of a sheep population. Regions close to the ancestral population are filled quickly. Hence selection for large horns has here only a short time to act. The further sheep move, the longer does the colonizing fringe experience intense selection pressure for large horns. Yet as soon as sheep fill the habitat, selection for horn size stops. Therefore, a horn size gradient will run from the ancestral population (small horns) to the population furthest away (large horns). As soon as populations of sheep are static, they freeze their social adaptations at whatever level they happened to have achieved.

<u>In retrospect</u>. In this paper an attempt was made to reconstruct the major evolutionary features of a social species of large mammals. It appears that sheep arose from a rupicaprid ancestor which innovated a new, effective defense mechanism against horn blows. It caught such blows with a horned head. How this innovation arose, cannot be explained at present, however it had far reaching consequences. It led to a selection for a heavy skull, thick facial skin and loss of thick body skin. Butting became specialized and ultimately evolved into a clash. The damage done in fighting became reduced and little harm could be expected in combat. Horn size increased. At first this was probably only a response

to fractured horn cores, with a steady selection for thicker bases. It was achieved by prolonging and intensifying the males' juvenile period, which led to neoteny. The males, remaining "juvenile", ran with each other in the fashion of juveniles. Selection for neoteny also increases the aggressiveness with the consequent frequent but harmless interactions among males. This in turn creates and maintains a familiar, predictable social environment for the animals via a dominance hierachy. However, graded horn sizes resulted ultimately in a priori predictable dominance ranks, in which large horns were most adaptive. Intense selection for large horns led to further extension of the juvenile growth phase resulting not only in larger horns, but loss of manes, increased sexual dimorphism, slow behavioural maturation, and leadership by largest horned rams, while the females became more juvenile in appearance and behaviour.

In this picture, sociality arises as a by-product of selection, and appears to be an extension into adult life of a juvenile tendency to follow others. The rams are social not so much because living in groups is being selected for, as that their adaptations allow this to occur, just as the social adaptations of <u>Oreamnos</u> would prevent it from occurring. Assuming that a group of mountain goat males came together, how would they establish a dominance order? Cattle can lock horns and push; they engage frequently and form firm dominance without serious injury to each other. Mountain goats could only maim each other since they neither lock horns nor clash but only pierce each other's body. Without a dominance hierarchy no priority could be relegated at rutting time. Without a dominance hierarchy the males would not live in a familiar, predictable social environment. This situation the males attempt to avoid. It is this concept which appears to explain the frequent interactions of rams, the long dominance fights of strange rams irrespective of the rutting season, the persistent pestering by smaller rams of a disabled larger companion, as well as the adult mountain goat male's withdrawal into a solitary life or at best a short, distant association with an equal. If this concept is correct then social behaviour becomes comparable to the exploratory behaviour of animals in a strange habitat. It makes the physical environment familiar and predictable to the animal, while the former makes the social environment familiar and predictable. In both instances the animal continues to act until familiarity is achieved.

Whereas the social adaptations of rams allowed them to be social, the social adaptations of mountain goat males prevented it. Yet both of these species may live not only on the same mountains, but often are found on the same slopes or resting in the same beds. These species live in much the same habitat yet they have very different social adaptations. This indicates that the habitat has little to do with social selection forces, at least for the males of these two bovids.

In the caprids the males vary more from species to species than the females. Even when comparing Oreamnos with American sheep, the females act surprisingly similar. In both species they run in small or large groups, they interact very little with one another so that little evidence exists for a dominance hierarchy among females. The bands are not cohesive but break up and are almost continuously reformed, without strife. The dominance hierarchy, so conspicuous among free living rams, appears to be non existent for females but is quickly established with a few butts when access is limited to a salt lick for instance.

It appears to me that social adaptations cannot be readily judged as superior or inferior, not if caprids and rupicaprids thrive in similar habitats but with different social adaptations. I see change but not progress in the large horns of sheep for instance, or their specialized fighting behaviour. Although large horns etc. are an evolutionary advancement, short horned forms are very much with us today, indicating that their social adaptations are just solutions, no better or worse than those of more specialized forms. These evolved during the short pioneering phase following glaciation, because it was highly advantageous to be large and a fighting specialist. The characteristic remained with each population since they contribute towards reaching high dominance and breeding success by rams. This would appear to make a reversal of these trends almost impossible. Each change towards increased horn size and other neotenic features I see as evidence of the sheep's advance into new living space, while forms in old, stable refugia remained socially primitive but successful. A few implications are in order. It appears that the differences between the races canadensis and nelsoni are no more than about 11,000 years old, since this is the time span since the glaciers of the Wisconsin glaciation withdrew. Sheep would have spread in the dry, warm Altithermal interval following glacial retreat, which lasted about 5,000 years. Additional recessions and advances of sheep should have taken place in the two "little Ice Ages" which followed the Wisconsin. The last of these took place in the 16th and 17th century. These should have intensified selection for the morphological characters differentiating canadensis from nelsoni.

If so short a time span as 10,000 years can produce such great size differences, then the presence of large sheep from Pleistocene deposits, tell only of past habitat--fluctuations during glacial advances and retreats. Big sheep should have occurred a number of times. They have appeared in North America and Asia quite independently for the argalis and bighorns despite convergently obtained similarities, are quite different sheep. The skulls, which taxonomists rely on so greatly, tell only part of the story. Argalis are light boned, long legged steppe sheep with little inclination for climbing. The American sheep as a whole are stocky and dwellers of slopes and steep, broken terrain. They are not quite as specialized as ibex, but they are truly a mountain, not a steppe sheep. It can also be seen that they differ considerably in the position of the rump patch. For the reasons outlined, I cannot at all agree with Stokes and Condie (1961), that large _Ovis_ skulls from American Pleistocene deposits indicate _Ovis ammon_ as a direct ancestor of _Ovis canadensis_. The large _ammon_ forms are a terminal branch of sheep evolution just as much as the northern large _canadensis_. I suggest, that both forms are products of the last glaciation.

In closing, may I point out that the evolutionary changes described for the caprids, have also taken place in other ruminants who invaded the glaciated areas of the continents. Deer of the genus _Cervus_ evolved many features similar to _Ovis_. The most primitive species are also found in Southeast Asia. Species in the formerly glaciated areas have large antlers, they are social, the rump patch is present and largest in the species furthest from southeast Asia (_C. canadensis_), and the sexual dimorphism is great. The species which swarmed over the periodically glaciated regions are often characterized by huge, horn-like organs, not only sheep and goats, but also _Bison_, _Megaloceros_, _Alces_ and its predecessors, and _Rangifer_. Large horned forms are a general Pleistocene phenomenon and _Ovis_ is but a surviving, particular ease of this.

# CONCLUSIONS

Sheep appear to be rupicaprid in origin. They evolved from a form which in combat began neutralizing butts by catching them with the head. This allowed selection for:

(1) Heavy, pneumated skulls to absorb concussion and sturdy horn bases to resist fracture.

(2) A thick skin over the nasal-and frontal bones to reduce damage to the head.

(3) A concurrent reduction of ancestral defense mechanisms, which in part consisted of a thick heavy hide.

Since the new defense mechanisms neutralize horn blows, males can interact without injuring each other severely. This reduced selection pressure against:

(1) Frequent agonistic engagements.

(2) Cautious courtship by the male of the now harmless female.

(3) Males associating with one another and living in groups.

As a consequence, dominance hierarchies could arise and be maintained in male groups. Since hornsize is directly related to dominance rank and thus to access to receptive females, vigorous horn growth is adaptive. Large horns were produced via prolonged, and intensified annual growth. This is postulated to be due to neoteny. Neoteny produced the following effects:

(1) Rams mature in external appearance and social behaviour 5 - 6 years after sexual maturation.

(2) Age dependent horn size gradients appeared in male bands.

(3) Since females mature at 1.5 - 2.5 years of age, but the growth of rams is extended progressively past sexual-to ultimate maturation, the female becomes progressively more juvenile in appearance. She is paedogenic in that she retains not only a juvenile external appearance throughout life, but also characteristically juvenile behaviour.

(4) Sexually mature rams continue two juvenile tendencies.

(a) They follow larger sheep when on the move, and (b) they associate with equals during the normal daily routine.

This explains why

1 - rams disassociate from ewes once they exceed them in horn-and body size,

2 - rams follow the largest horned ram during longer movements (since it is the most "adult" in appearance),

3 - rams prefer other rams of equal horn size in social interactions.

(5) The more rams prolonged the period of growth in response to selection for larger horns, the more

they increased elements of juvenile (aggressive) behaviour, and reduced or lost the neck ruff.

Since neoteny produced horn-and body size gradients in which the adult female is almost identical in external appearance to sexually mature yearling males, no absolute female form exists for sheep. In correlation we find:

(1) Rams treat all smaller sheep as they would females. Rams change their behaviour no so much with the sex of the companion they interact with, as with its dominance rank.

(2) The more that juvenile rams resemble females, the more sexual behaviour patterns they receive from larger rams. Subordinate rams may perform behaviour typical of females in response to dominant rams.

Since rams act towards females no differently than towards young rams (except that females are more preferred), females have means to reduce the length of interactions with rams. These mechanisms are shown by non-estrous ewes. Females can assume two behavioural states which correlate with the presence or absence of estrus. The estrous ewe acts towards the male like a sexually mature, subordinate ram; the non-estrous ewe acts like a sexually immature juvenile. In estrus, the ewe associates with rams, does not respond to kicks and most mounts, she uses contact and aggressive behaviour towards rams and urinates rarely to the rams courtship. The non-estrous ewe associates with equals (other ewes), withdraws from kicks and mounts, and often urinates to approaching rams. These actions reduce her interactions with rams. It appears that specific hormonal changes switch on and off the female's "male" behaviour.

Since access to receptive females is limited, an impetus for combat exists in male groups. Rams appear to be strongly motivated to live in a predictable social environment throughout the year. This they create by combat, and maintain by display, minor overt aggressive interactions and probably through contact behaviour. The latter appears to be responsible for the evolution of short, pliable hairs on the face of sheep, rather than the long, brittle ones found on the body. The manifestation of a predictable social environment is the dominance hierarchy.

Since dominance is directly related to horn size, since large horns appear to deliver a more forceful clash, and since a horn display immediately follows a clash, rams can associate clash force with horn size, and hence predict a stranger's relative dominance rank from his horn size. Since horns, acting as rank symbols, can maintain a priori predictability of dominance relationships, rams can live in an open society.

Neoteny appears to be a product of selection for large horns in males.

Sheep evolution is linked to glaciation, for the further sheep moved into once glaciated areas, the more they increased in horn size, sexual dimorphism, rump patch size and clash specialization. This relationship appears to hold true for other caprids and cervine deer.

It is suggested that large horns and specialized fighting were selected for in populations colonizing new living space which followed in the wake of glaciers. Intense selection occurred in the expanding, high quality populations; it came to a halt once populations stabilized and the life expectancy of rams increased. In such populations the selective advantage of large horns could be counter balanced by the longer life expectancy of rams of smaller horn and body size. When populations stabilized they retained whatever social adaptations they had acquired; populations which arose further on, changed more. This could account for the geographic clines of Asiatic and American sheep.

In general, sheep evolution revolved about the perfection of a new combat type and secondarily about the indirect results it precipitated. Living socially in close proximity of others appears to be one such secondary result. Habitat and body care behaviour appears to evolve independently of social behaviour in sheep.

# LITERATURE CITED

Anonymous. Records of North American big game. Boon and Crocket Club. 1964 Ed. Holt, Rinehart & Wilson, New York.

Alexander, G. and E. Peterson. 1961. Neonatal mortality in Lambs. Aust. Vet. J. 37 (10) : 371 - 381.

Allee, W. C. 1951. Cooperation among animals. Schuman, New York, 256 pp.

Altmann, M. 1963. Naturalistic studies of maternal care in moose and elk. in: Maternal Behaviour of Mammals. H. L. Rheingold (editor). pp. 233 - 253. J. Wiley & Sons, New York.

Anderson, J. A. and J. B. Nenderson. 1961. Himalayan thar in New Zealand. N.Z. Deer Stalkers Association. Special Publication No. 2. 36 pp.

Ardrey, R. 1963. African Genesis. Dell Publishing Co. New York. 380 pp.

Backhaus, D. 1961. Beobachtungen an Giraffen in Zoologischen Gärten und freier Wildbahn. Inst. Parcs Nat. Congo et Ruanda-Urundi. Bruxelles. 202 pp.

Banks, E. M. 1964. Some aspects of sexual behaviour in domestic sheep, Ovis aries. Behaviour 23 (3-4) : 249 - 279.

Bonatti, E. 1966. North mediterranean climate during the last Würm glaciation. Nature 209 : 984 - 985.

Brandborg, S. M. 1955. Life history and management of the mountain goat in Idaho. Idaho. 142 pp.

Brehm, A. 1916. Brehm's Tierleben. Säugetiere 4.

Buechner, H. K. 1961. Territorial behaviour in Uganda kob. Science 133 : 698 - 699.

Cherniavski, F. B. 1962. On the reproduction and growth of the snow sheep (Ovis nivicola). Zoolo. Zhur. XLI (10) : 1556 - 1566 (Translation, Canad. Wildl. Service, Ottawa).

Clark, J. L. 1964. The great arc of the wild sheep. Univ. Oklahoma Press, Norman. 247 pp.

Cowan, I. McT. 1940. Distribution and variation in the native sheep of North America. Am. Midl. Naturalist 24 (3) : 505 - 580.

______________, A. J. Wood and W. D. Kitts, 1957. Feed requirements of deer, beaver, bear and mink for growth and maintenance. Trans. N. Am. Wildl. Conf. 22 : 179 - 188.

______________ and C. J. Guiguet. 1965. The Mammals of British Columbia (3 Ed.) Handbook No. 11 Victoria, B.C. 414 pp.

Des Meules, P. 1964. The influence of snow on the behaviour of moose. (Mimeographed excerpt from M. Sc. thesis, Ontario Agric. College, Guelph)

Eisenberg, J. F. 1966. The social organizations of mammals. Kükenthal-Krumbach Handbuch der Zoologie. Vol. 8, 10 (7) : 1 - 92.

Geist, V. 1963. On the behaviour of the North American Moose (*Alces alces andersoni*, Peterson 1950) in British Columbia. Behaviour 20 (3-4) : 377 - 416.

________________. 1964. On the rutting behaviour of the mountain goat. J. Mammal. 45 (4) : 551 - 568.

________________. 1966.(a) Validity of horn segment counts in aging bighorn sheep. J. Wildl. Mgmt. 30 (3) : 634 - 635.

________________. 1966.(b) Ethological observations on some North American Cervids. Zool. Beiträge 12 : 220 - 250.

________________. 1966.(c) The evolution of horn-like organs. Behaviour (in press).

________________. The evolutionary significance of mountain sheep horns. Evolution (in press).

________________. On fighting injuries and dermal shields in mountain goat. J. Wildl. Mgmt. (in press).

Geptner, W. G., A. A. Nasimovitch and A. G. Bannikov. 1961. The mammals of the Soviet Union. High School press. Moskow. (in Russian).

Gundlach, H. 1961. Beobachtungen bei Versuchen zur Wildschadenverhütung am Rotwild des Georg von Opel-Freigeheges. G. v. Opel Freigehege, Kronberg Jahrbuch 1960/61 : 116 - 128.

Gunn, R. G. and J. F. Robinson. 1963. Lamb mortality in Scottish Hill flocks. Anim. Prod. 5 (1) : 67 - 76.

Haas, G. 1958. Untersuchungen über angeborene Verhaltensweisen bei Mahnenspringern (Ammotragus lervia Pallas) Z. Tierpsych. 16 (2) : 218 - 242.

Hansen, G. S. 1965. Growth and development of desert bighorn sheep. J. Wildl. Mgmt. 29 (2) : 387 - 391.

Heusser, C. J. 1965. A Pleistocene phytogeographic sketch of the Pacific North West and Alaska. in: The Quaternary of North American. Wright, H. E. and Frey, D. G. (Ed.) Princeton Univ. Press. pp. 469 - 484.

Katz, J. 1949. Behavioural interactions in a herd of barbary sheep. Zoologica 34 (1) : 9 - 18.

Klein, D. R. 1964 Range - related differences in growth of deer reflected in skeletal ratios. J. Mammal. 45 (2) : 226 - 235.

________________. 1965. Ecology of deer range in Alaska. Ecol. Monog. 35 : 259 - 284.

Krumbiegel, I. 1954. Biologie der Säugetiere. Vol. I. Agis Verlag, Krefeld. 355 pp.

Kühme, W. 1965. Freilandstudien zur Sociologie des Hyanenhundes (Lycaon pictus lupinus. Thomas 1902). Z. Tierpsych. 22 (5) : 495 - 541.

Lindsay, D. R. 1965. The importance of olfactory stimuli in the mating behaviour of the ram. Anim. Behav. 13 (1) : 75 - 78.

Lydekker, R. 1898. Wild oxen, sheep and goats of all lands. Rowland Ward Ltd. London. 318 pp.

________________. 1913. Catalogue of the Ungulate mammals. Vol. I. Artiodactyla. British Museum, London. 249 pp.

Moser, C. A. 1962. The bighorn sheep of Colorado. Dept. of Game and Fish. Colorado. 48 pp.

Munroe, J. 1962. A study of the milk yield of three strains of Scottish blackface ewes in two environments. Anim. Prod. 4 (2) : 203 - 213.

Murie, A. 1944. The wolves of Mount McKinley. Fauna Series No. 5 U.S. National Parks. Washington, D.B. 238 pp.

Ogren H. A. 1965. Barbary sheep. New Mexico Dept. of Game and Fish. Santa Fe. 117 pp.

Petzsch, H. 1957. (a) Reflexionen zur Phylogenie der Capridae im allgemeinen und der Hausziegen im besonderen. Wissenschaftl Zs. M. Luther Universität. Halle-Wittenberg VI (6) : 995 - 1019.

______________. (b) Lebender ♀ - Bastard aus Ammatragus levia Pall. - ♂ x Capra hircus L. - ♀ im Berg - Zoo Halle - S. geboren. Zool. Anzeiger 159 (11/12) : 285 - 290.

Purser, A. F. and G. B. Young. 1959. Lamb survival in two hill flocks. Anim. Prod. 1 (1) : 85 - 91.

Rammell, C. G. and G. Caughley. 1964. Composition of thar's milk. N.Z.J. Sci. 7 (4) : 667 - 670.

Romer, A. S. 1962. The vertebrate body. W. B. Saunders, Phila. 627 pp.

Ryder, M. L. 1960. A study of the coat of the mouflon Ovis musimon with special reference to seasonal changes. Proc. Zool. Soc. London 135 (3) : 387 - 408.

Schaller, G. B. 1963. The Mountain Gorilla. Univ. of Chicago. 431 pp.

Schinkel, P. G. and F. B. Short. 1961. The influence of nutritional level during pre-natal and early post-natal life of adult fleece and body characteristics. Aust. J. Agric. Res. 12 (1) : 176 - 202.

Schloeth, R. 1961. Das Socialleben des Camargue - Rindes. Z. Tierpsych. 18 (5) : 574 - 627.

Schmitt, J. 1963. Ammotragus lervia Pallas. Mähnenschaf oder Mähenenziege? Zs. Säugetierkunde 28 (1) : 7 - 12.

Slen, S. B., R. D. Clark and R. Hironaka. 1963. A comparison of milk production and its relation to lamb growth in five breeds of sheep. Can. J. Anim. Sci. 43 : 16 - 21.

Stokes, W. L. and K. C. Condie. 1961. Pleistocene bighorn sheep from the Great Basin. J. Paleontology 35 (3) : 598 - 609.

Thenius, E. and H. Hofer. 1960. Stammesgeschichte der Säugetiere. Springer Verlag. Berlin. 322 pp.

Ulmer, F. 1941. On the weights of Dall sheep. J. Mammal. 22 (4) : 448 - 449.

Wallace, R. L. 1948. The growth of lambs before and after birth in relation to the level of nutrition. J. Agric. Sci. 38 : 93 - 153, 243 - 302, 367 - 401.

Walther, F. 1958. Zum Kampf und Paarungsverhalten einiger Antilopen. Z. Tierpsych. 15 : 340 - 380.

__________________. 1960. Beobachtungen zum Sozialverhalten der Sasin (Hirschziegenantilope *Antilope cervicapra* L.) G. v. Opel Freigehege, Kronberg Jahrbuch 1959/60 : 64 - 78.

__________________. 1961. Enige Verhaltensbeobachtungen am Bergwild des Georg von Opel-Freigeheges. G. v. Opel Freigehege, Kronberg Jahrbuch 1960/61 : 53 - 89.

__________________. 1964. Einige Verhaltenbeobachtungen an Thomson gazellen (*Gazella thomsoni* Günther, 1884) im Ngorogoro-Krater. Z. Tierpsych. 21 (4) : 871 - 890.

Watson, R. H., C. S. Snapsford, and J. McCance. 1956. The development of testis, epididymis and penis in the young Merino ram. Aust. J. Agric. Res. 7 : 574 - 590.

Welles, R. E. and F. B. Welles. 1961. The bighorn of Death Valley. Fauna Series No. 6. U.S. National Park Service. Washington, D.C. 197 pp.

Wood, A. J., I. McT. Cowan, and H. C. Nordan. 1962. Periodicity of growth in ungulates as shown by deer of the genus *Odocoileus*. Can. J. Zool. 40 : 593 - 603.

Woodgerd, W. 1964. Population dynamics of bighorn sheep on Wildhorse Island. J. Wildl. Mgmt. 28 (2) : 381 - 391.

Zannier-Tanner, E. 1965. Vergleichende Verhaltensuntersuchungen über Hinlegen und Aufstehen bei Huftieren. Z. Tierpsych. 22 (6) : 696 - 723.

Zedwitz, Graf. F. X. 1937. Die Gemse. Monog. der Wildsäugetiere, Schöps. Leipzig. 80 pp.

FIGURE 1. A 14 year old Stone's ram, D-ram, from the Spatisi study area. Oct. 1962.

FIGURE 2. A Dall's ram, 8 years old or older, from Kluane Lake, Yukon. Note the preorbital gland, the dark markings about the eye and gland, and the thin, wide spreading horn with distinct horn segments. Nov. 1965.

FIGURE 3. An old bighorn ram, 12 - 15 years old, from the Palliser Range, Banff National Park. Note the heavy horns and their broken (broomed) ends so characteristic of this species. April, 1965.

FIGURE 4. Variations in the coat patterning and horn form of Stone's rams. Note the lighter face and neck colouration, the white muzzle on the dark ram, the belly band on the lower ram and variations in the shape of the rump patch. Individual differences in these characteristics permitted identification of individuals.

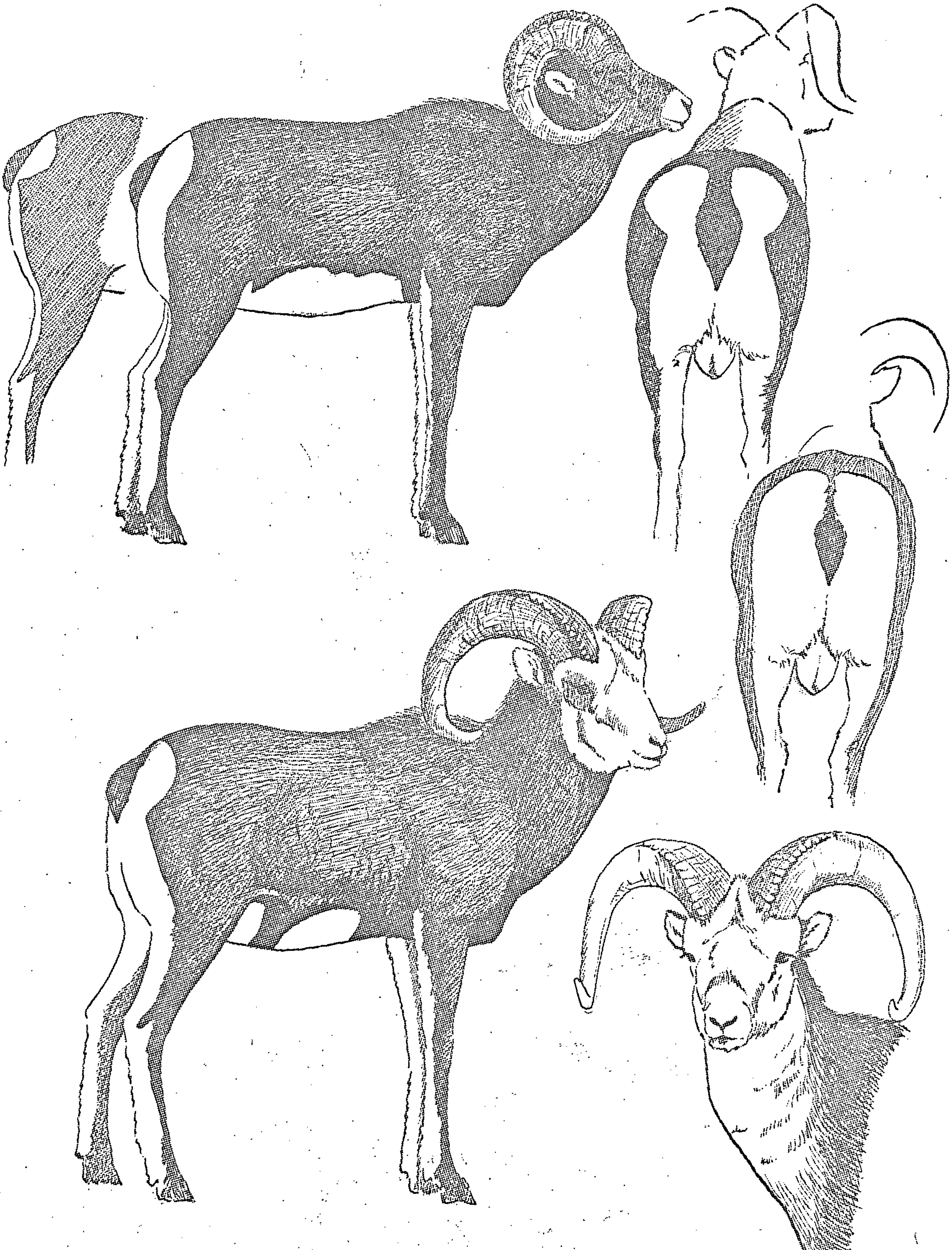


FIGURE 5. A six months old bighorn lamb ( ♂ ) showing fair to good development. It is in its dark adult-like wintercoat and has clearly visible horns. Late October, 1964.

FIGURE 6. A six months old Dall's lamb ( ♂ ) , in October 1965. Unlike the bighorn lamb of equal age, it has almost no visible horns.

FIGURE 7. Sex-age classes of bighorn sheep arranged from a - h in order of resemblence.

(a) Lamb ( L.) - smallest in horn and body size with short juvenile face.

(b) Yearling female ( )(12-24 months of age) next largest in horn and body size to lamb; still retains a short juvenile face.

(c) Adult female ( ) (2-24 years of age) Exceeded in horn and body size only by equal aged males. This class forms the standard others are compared by. (Note the tufts of broken hair stuck in the fields of newly growing ones).

(d) Yearling ram ( ) (12-24 months of age), is very similar in horn-and body size as well as coat patterning to adult ewes. The horns however, tend to diverge slightly more in the yearling rams, and are thicker at the base.

(e) Class I ram (I) (2-3 years old). These rams surpass adult ewes and yearling rams in horn-and body size. The horns form less than 1/2 circle.

(f) Class II ram (4-6 years old). The horns form about 1/2 circle and are much larger than those of the preceding class. This class tends to be more massive in body than Class I.

(g) Class III ram (6-8 years old). Horns form about 3/4 of a circle and are quite massive. The facial features are those of older rams. The horn tips tend to be intact.

(h) Class IV ram (7-17 years of age). Horn growth and body development reach a maximum. The horns form a complete circle; these rams are also termed full curls. No noticeable difference in body size exists between these and Class III rams.

a

b

c

d

e

f

а

б

FIGURE 8. A group of adult bighorn sheep, three ewes and two yearling rams. The great similarity between these two classes is apparent. The lower pawing sheep is a ram and so is the one behind his rear. Note the ram's white belly; it turns dark with age. December 1964

FIGURE 9. A well developed yearling Dall's ram. The wide spreading horns distinguish it as a male. October 1965.

FIGURE 10. Two bighorn ewes and a Class I ram (2-1/2 years old, October 1964). The ram is typically larger and darker than the ewes and has a distinct, white muzzle. This ram class is often found in ewe bands.

FIGURE 11. A mule deer buck in a resting position often used by deer but not sheep. The buck lies full on his side, legs extended sideways. Sheep support themselves on hip and elbows.

FIGURE 12. A resting Class III bighorn in the normal resting position. The ram is dozing and its eyes are partially closed.

FIGURE 13. Sheep commonly rest closely together in a group. The animals rest in shallow depressions or beds which are pawed by them. This is a band of Dall's ewes, except for subadults and one 2-1/2 year old ram (in centre of picture).

FIGURE 14. A bighorn ewe and her lamb. Latter typically rests in close contact uphill from the ewe. The female is in moult.

FIGURE 15. Moose --unlike sheep--take advantage of the insulating properties of deep, soft snow. This bull has his extremeties well buried, and only about half his body protudes above the snow. January 1965.

FIGURE 16. An old Dall's ewe cleaning a much used bed before lying down. Such beds become covered with rocks which have rolled down the slope. Note (a) how many rocks are in the bed before the ewe pawed. In (b) the ewe is removing a large rock with her front leg. The clean bed is seen at (c).



FIGURE 17. Pawing is often used by sheep to dislodge companions from a resting place. Here it is done by a Class IV ram on an old ewe.

FIGURE 18. In winter, sheep paw craters in the snow to reach covered vegetation. Sheep with injured legs have rather apparent difficulties in reaching covered forage. This is a yearling ram. January 1965.

FIGURE 19. A female bighorn in the late stages of moult. Matted hair hangs like towels from her body and will eventually be lost as one or several large patches.

FIGURE 20. A Class I ram scratching his withers with a horn tip. On small horned sheep this activity bares the withers.

FIGURE 21. The results of extensive horn scratching by a ewe. Her withers are almost bare of old hair. Circular marks are locations where ticks engorged. Scabs are seen on the very top of the withers. Rubbing has broken off hair and left others standing in clumps. Short, dark brown hair is growing on some of the exposed area.

FIGURE 22. A Class II Stone's ram stretching itself after getting up. The ram is in the short summer coat. Note the dorsal stripe, the shape of the rump patch compared to bighorn sheep, and the head and neck colouration.

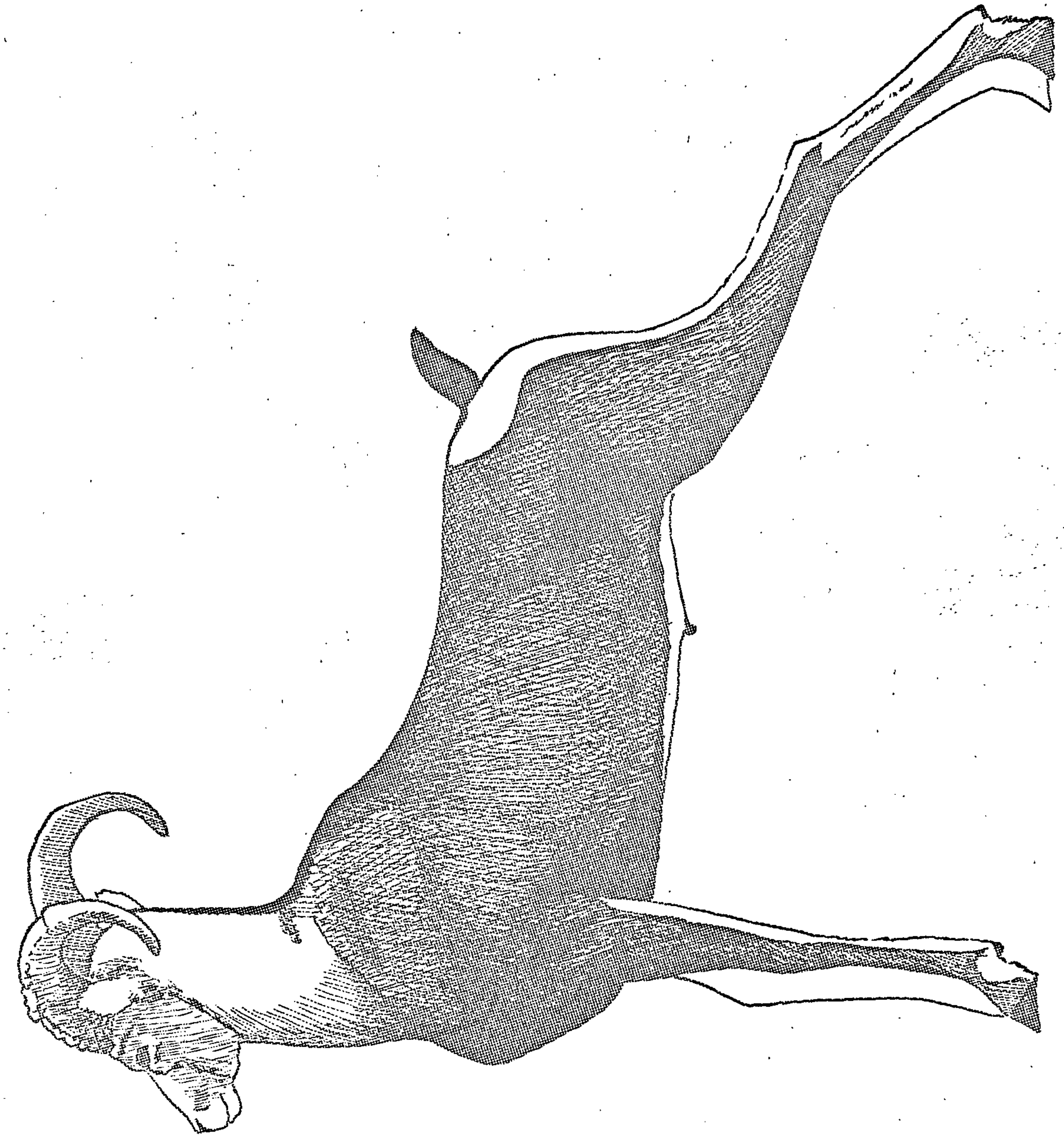


FIGURE 23. A urinating bighorn ewe in the typical crouched posture. The female has partially shed her old coat. June 1964.

FIGURE 24. The posture of an undisturbed, walking sheep. The animal is relaxed, its eyes are partially closed and its head is lowered. (The coat has been bleached so much that a rump patch is no longer visible).

FIGURE 25. The alarm posture. The head is sharply raised, ears are pinned back, eyes wide open while the hindlegs are tensely crouched.

FIGURE 26. The alarm posture of elk is similar to that of sheep.

FIGURE 27. The alert posture. The yearling rams have noted something interesting. Other members of the band, noting the behaviour of the rams, turn towards the source of interest.

FIGURE 28. A full curl (IV) horning the branches of a pine.

FIGURE 29. A small lodge pole pine (_Pinus contorta_) shows the typical effects of frequent and long horning by sheep. Note the thin stem cleaned of branches, the damaged bark, dead limbs and twisted trunk. Such damaged pines are common at tree line.

FIGURE 30. Orientations of a dominant and subordinate ewe in an encounter. Subordinate ewe (left) looks away from the dominant.

FIGURE 31. A comparison of the orientations of four six-week old lambs in the presence and absence of a yearling ewe. They turned their rear towards the ewe and pull back their ears towards the female.

FIGURE 32. A typical social interaction on a bedding site (a) and the resulting bedding positions (b). A dominant Dall's ewe displaces another ewe from a bed; dominant in low-stretch subordinate looking away. The dominant 3-1/2 year old ram looks on. When at rest (b) sheep are oriented in such a manner that the subordinate do not face a dominant directly. The bedding site is typical, a small elevated platform offering good visibility all around.

FIGURE 33. The low-stretch (Class IV) and the horn threat (Class II). Both rams act typically for their dominance rank.

FIGURE 34. The present, a horn display from the elevated head. The rams have just clashed and froze into a present. Note the stiff, tense stance. The subordinate ram (lower) has closed his eyes, hence does not look directly at the dominant.

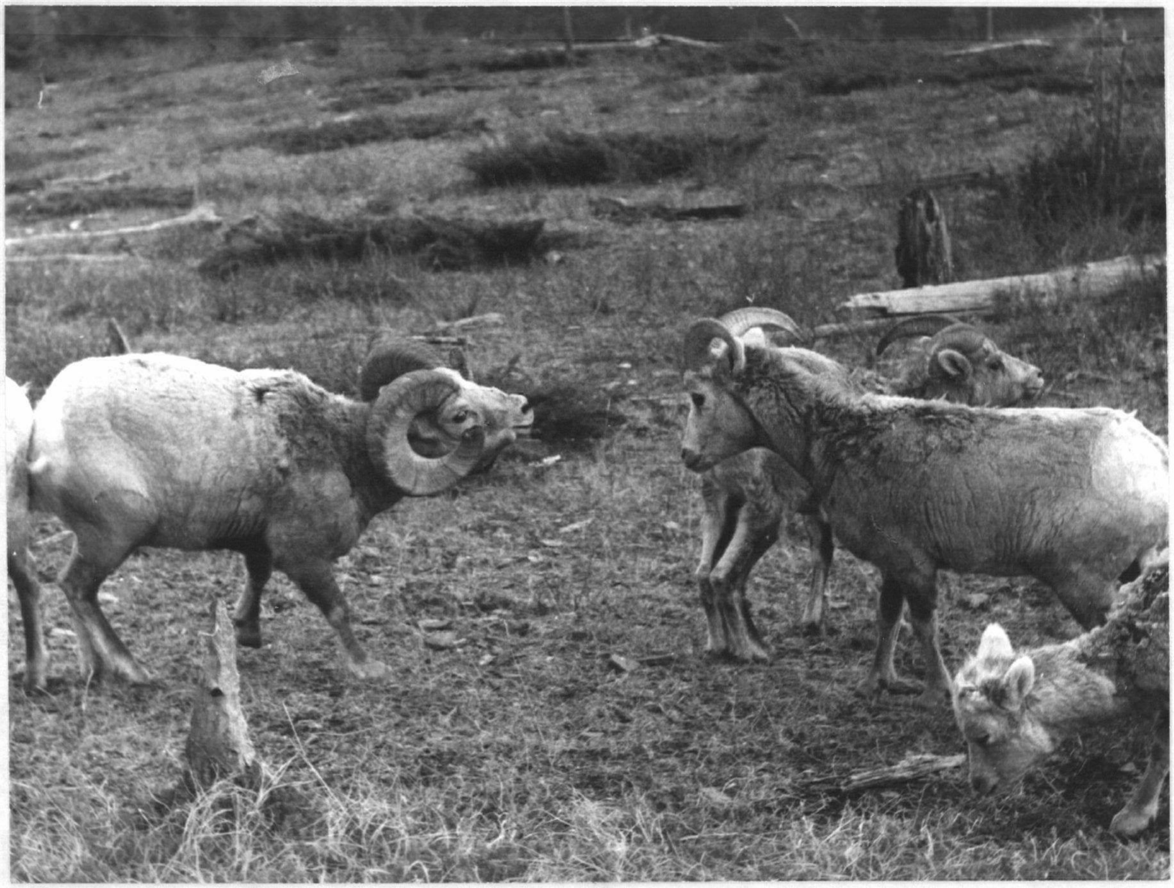


FIGURE 35. The positioning of horns and body during a horn-display.

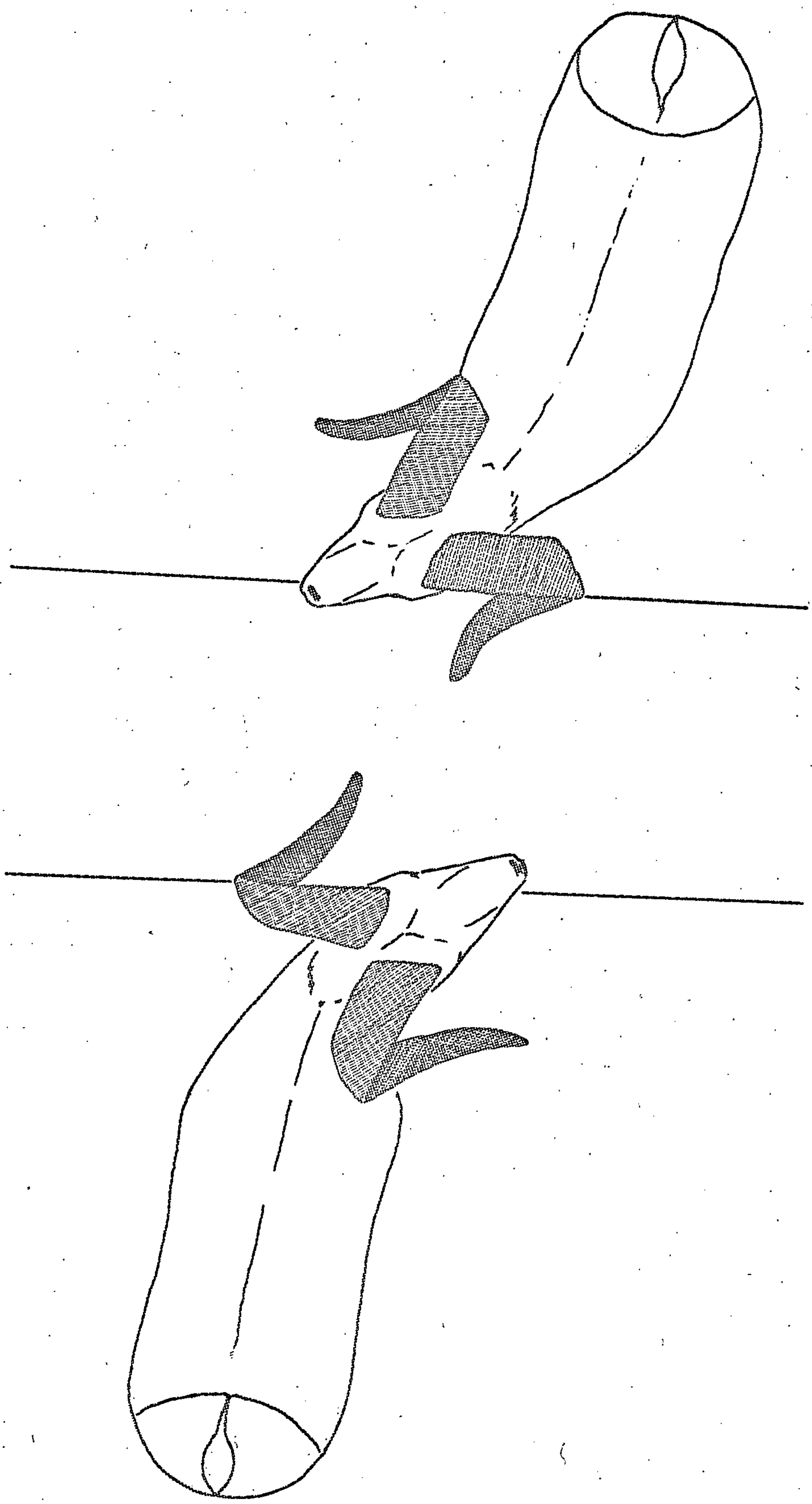


FIGURE 36. A horn display from the low stretch shown by a Class IV ram towards a threat-jumping Class II ram. The full curl displays his left horn most favourably. Both rams act typically for their respective ranks, the larger displays, the smaller threatens.

FIGURE 37. Mutual horn displaying is performed by rams of equal horn size. Two Class II rams display to one another. The small two year old ram in foreground is too small to enter in a display. His sharply reclined ears are a prelude to a horn threat, the behaviour one would expect from so small a ram.

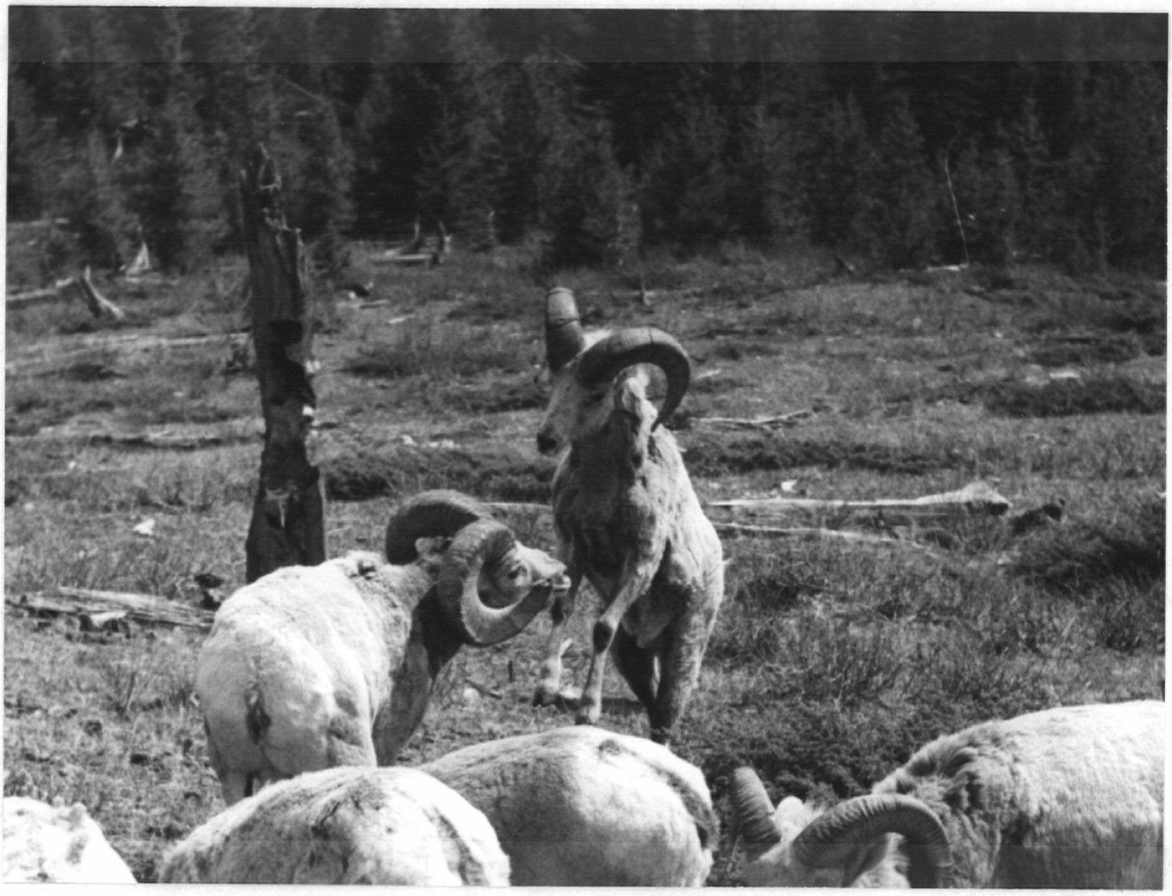


FIGURE 38. A crouched low-stretch is occasionally shown to females. This posture form is not common.

FIGURE 39. A low-stretch to a young female by a Dall's ram. The slight crouch and tipped up nose are more commonly assumed by Dall's than bighorn sheep.

FIGURE 40. The twist and tongue-flicker are shown here by a courting Dall's ram. The ram suddenly pulls forward, twists and then returns to a normal posture. He twists alternatively left and right. This type of courtship is commonly done by young rams towards ewes approaching estrus.

FIGURE 41. The front-kick performed by a dominant on a subordinate ram. During a kick, the dominant may dig in his muzzle into his opponents side.

FIGURE 42. The front-kick may land anywhere on the body. It lands however, only exceptionally on the chin.

FIGURE 43. The neck fight is a vestegial behaviour pattern of sheep, though it is common in primitive caprids. In sheep it proceeds apparently no further than the placing of head and neck over the opponents shoulder. This is a rare behaviour pattern.

FIGURE 44. The mount is typically performed by the larger on the smaller. Note that the smaller performs lordosis.

FIGURE 45. Ejaculation (auterotic), left by a bighorn - right by a Stone's ram (from photo, a 16 mm. film).

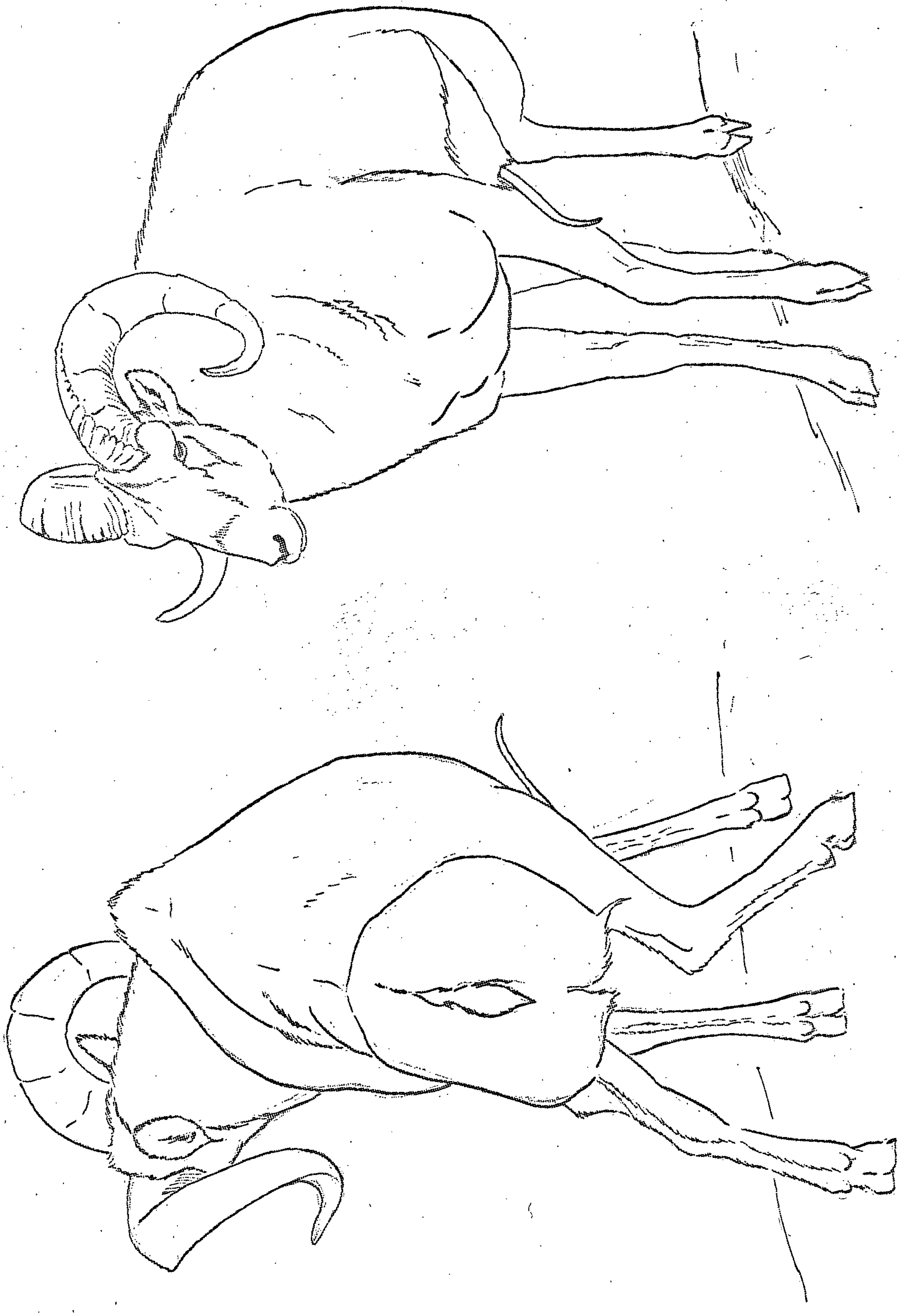


FIGURE 46. Rams initiate courtships in low-stretch. Here are two courting the same ewe without any display of hostility. Hostile interactions take place about the estrous ewe. Both rams attempt to investigate the vulva.

FIGURE 47. Ewes tend to urinate in response to courting rams.

FIGURE 48. After a ewe urinates, rams lick and nuzzle the urin and performs a Lipcurl. Here two Class IV rams lipcurl over the urin of one ewe. There is no hostility; any ram may come and lipcurl over a females urin.

FIGURE 49. A ram twisting to a non-estrous ewe. None of the other rams pay any attention. Non-estrous ewes are not defended.

FIGURE 50. Rubbing (a) and horning (b) are the most common social behaviour patterns which small rams perform on larger ones. The subordinate quickly changes from one to other behaviour.

a

b

FIGURE 51. A Class IV ram butts a Class III ram. This pattern is used almost equally frequently by dominant on subordinate rams as vice-versa.

FIGURE 52. The rush or horncharge is commonly used by large rams in chasing smaller ones away. Ewes use it more commonly than rams.

FIGURE 53. (a) The clash, preparatory phase initiated from the normal stance. The hindlegs are cocked, the back is arched, the head slanted sideways, and the eyes turned towards the opponent.

(b) Two 11 months old lambs initiate the clash from a more extreme bipedal stance. All sex-age classes of sheep clash similarly.

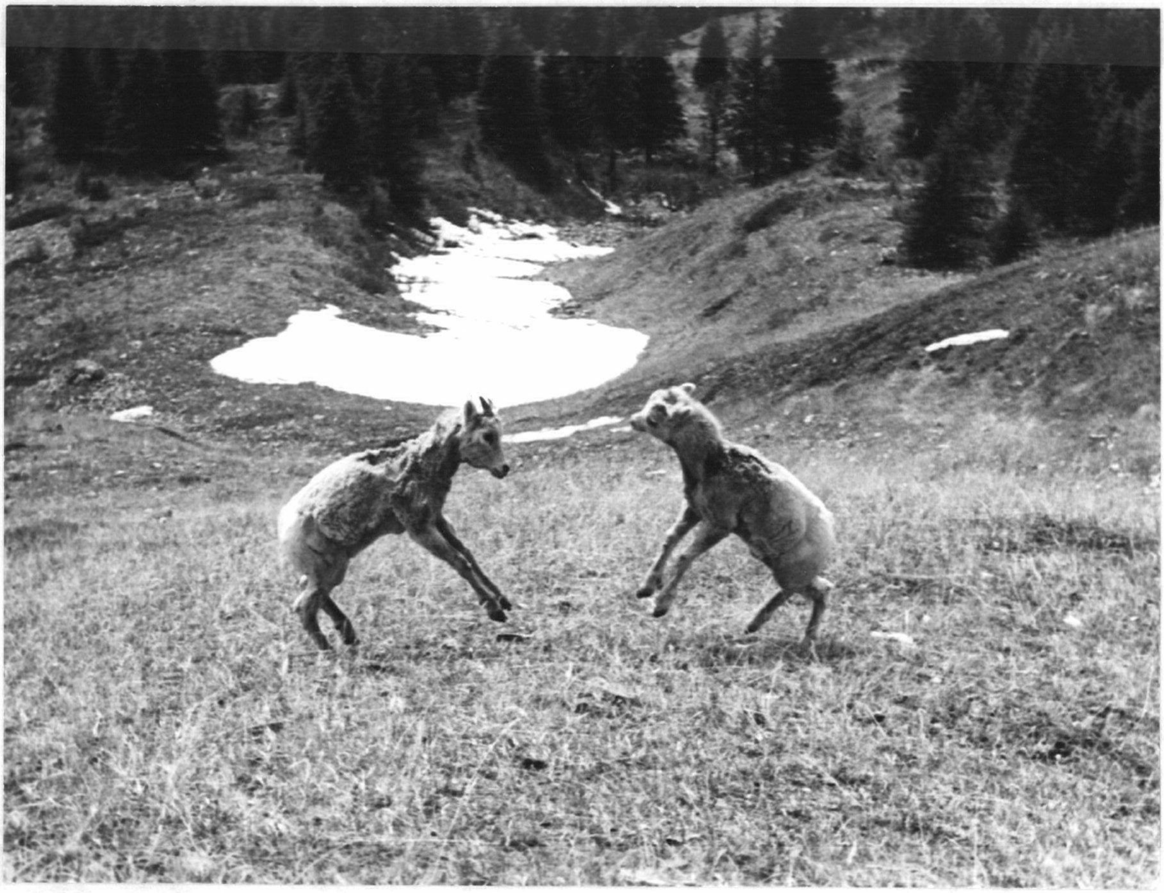


FIGURE 54. The clash, contact is made with the opponent. Both rams close their eyes. The horns of the combatans are often crossed, though not in this instance. The horns have been thrown forward.

FIGURE 55. Rams in successive phases of a clash. From 16 mm film, 24 frames/second. Numbers indicate frame number (i.e., 8 is the eighth frame or 0.3 seconds removed from frame one).

A, clash from the bipedal stance. Note (a) the downward blow of the horns, (b) the fall of the body, (c) the projection of the left horn, (d) the rotations of the skull after contact which allows the second horn to make contact.

B, note in addition, the propulsion of the ram and his manner of catching himself.

C, the ram rotates while clashing, thus he almost reverses his position from framel -28 by almost 180°. Note the four components of the clash force, (1) propulsion forward of the body, (2) fall of the body due to gravity, (3), blow with the head achieved by rapidly lowering the neck, (4) the blow with the horns achieved by throwing these forward.

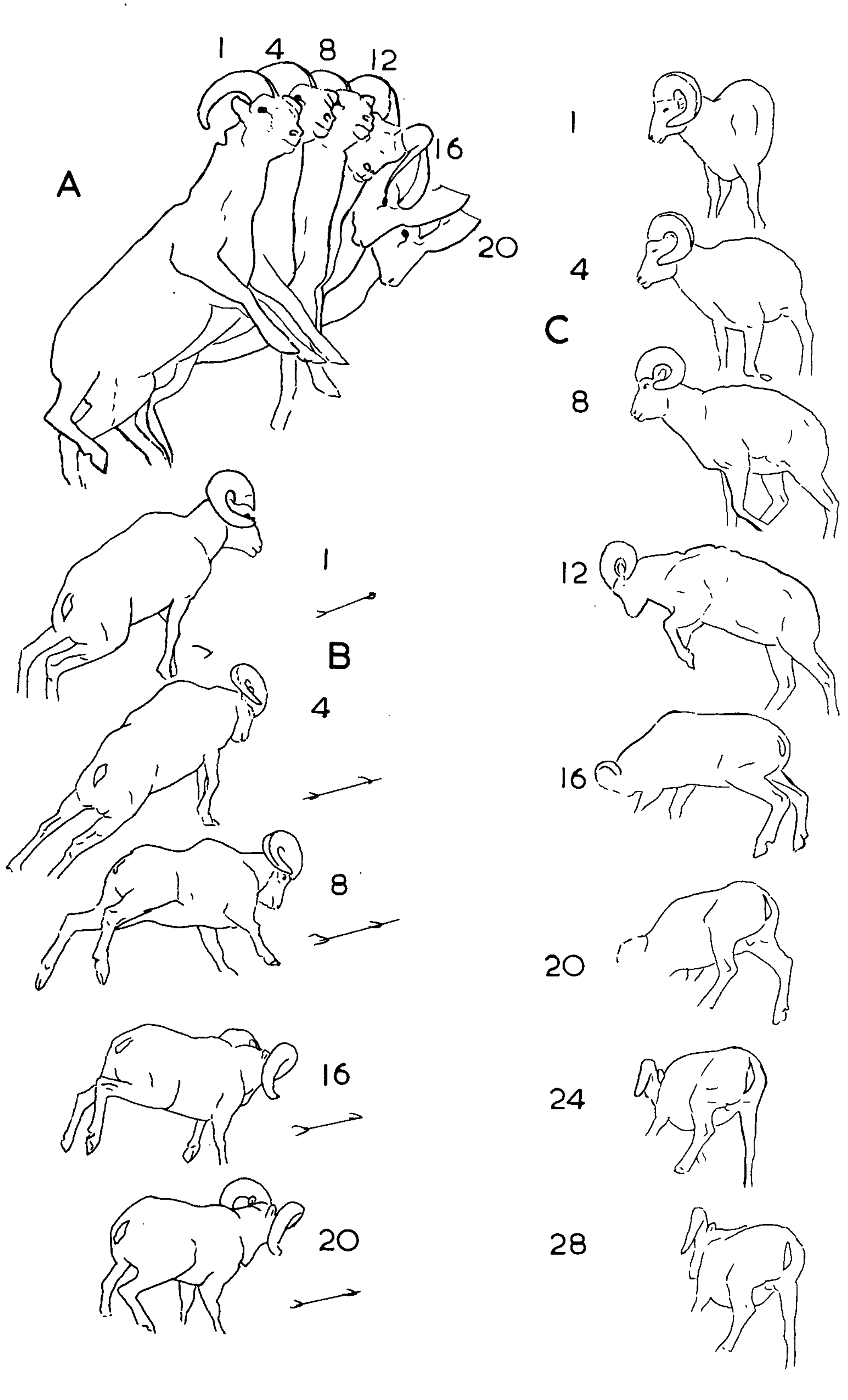

A
1
4
8
12
16
20
B
1
4
8
16
20
C
1
4
8
12
16
20
24
28

FIGURE 56. After contact is made, the downward push with the head continues. In this clash, the ewe on the right pivots her body about the right shoulder. Neck and body are held rigid by the ewe and she rises in the rear and one the left side of the body.

FIGURE 57. This is a second method of continuing the downward blow with the head. The female on the right pivots her body about the acetabulum, collapses the front legs and crouches in the rear. She adds the force of her descending body to the clash.

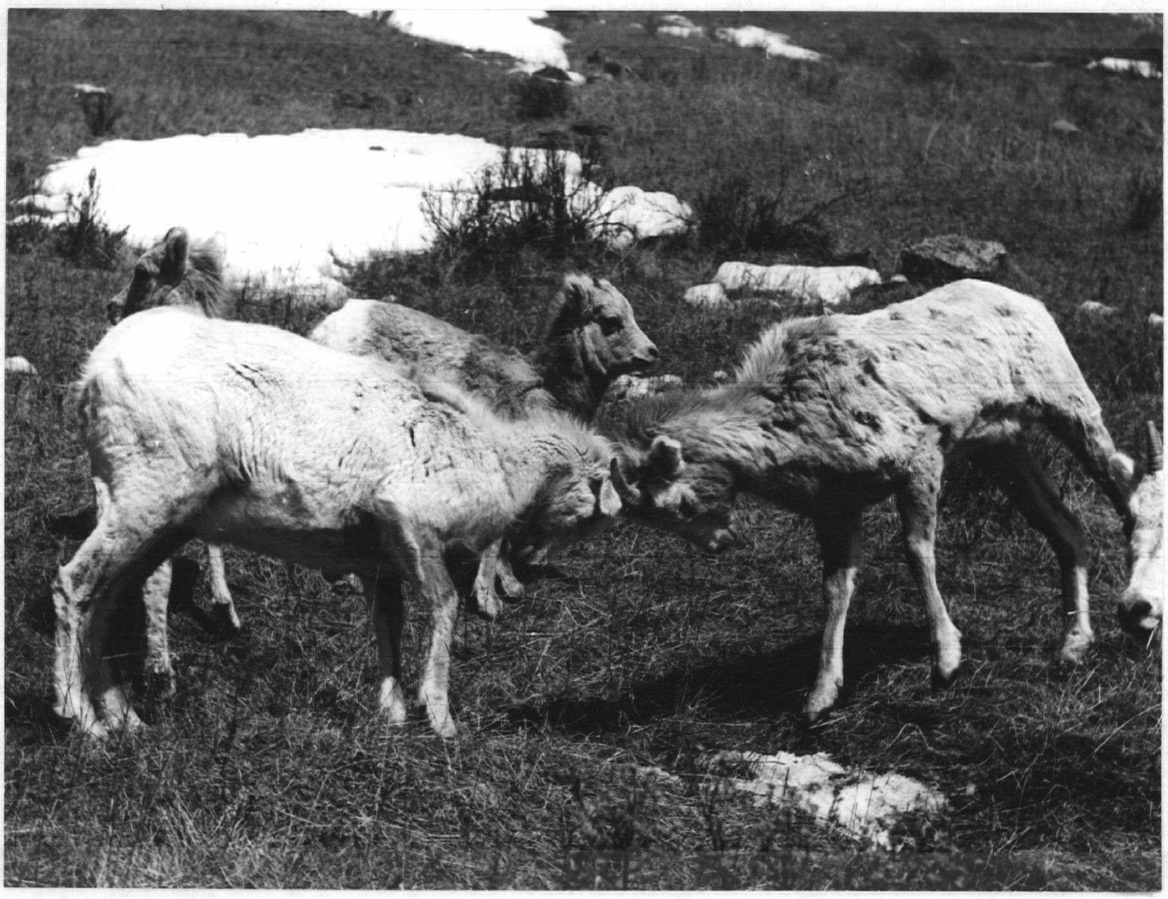
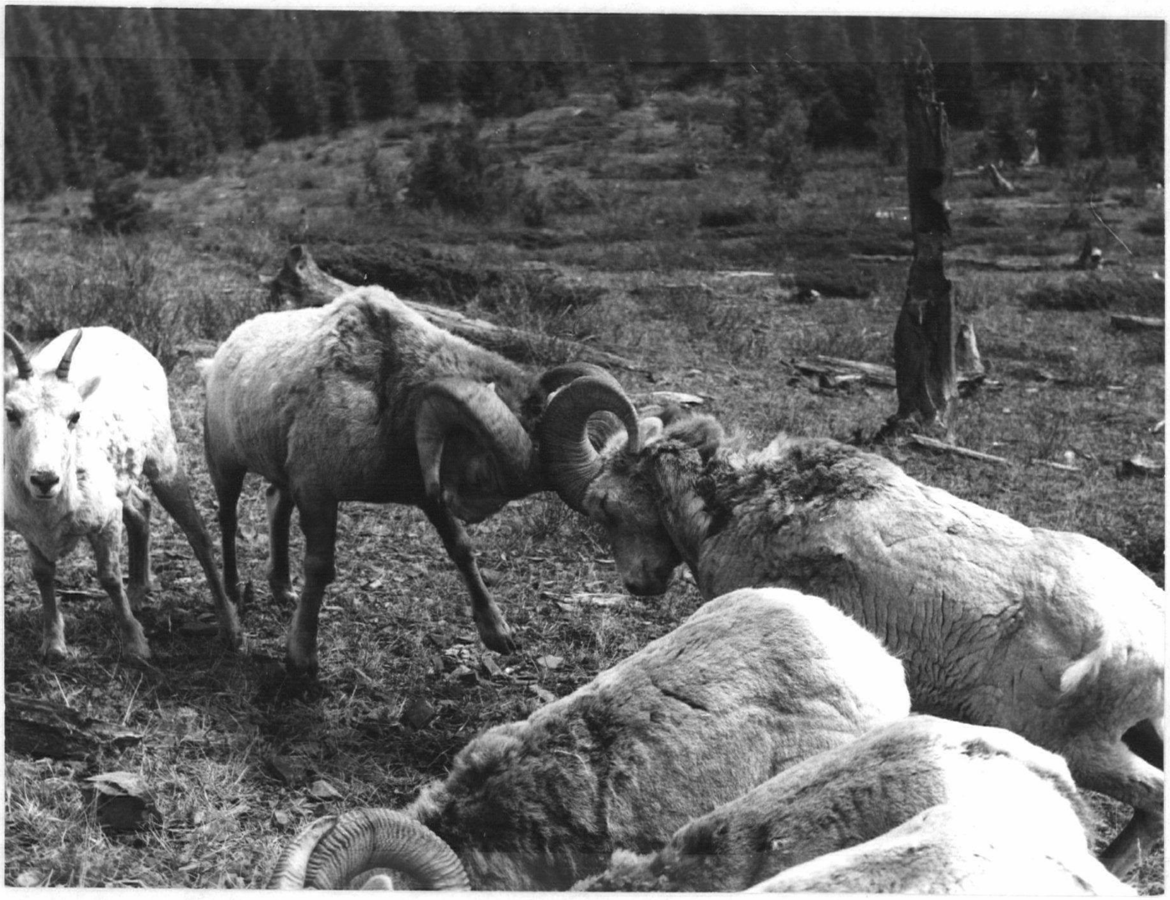


FIGURE 58. A clash that missed. The small opponent jumped aside. This photo shows how the ram caught his fall and it illustrates that the clash is a downward blow with the horns. The Class II ram in foreground has thrown his horns forward as if to catch the clash.

FIGURE 59. The clash is variable. The front legs or hindlegs must be off the ground. The IV ram has the front legs off the ground at contact.

FIGURE 60. The horns of the opponents slipped. The ram on the right is shown one split second before his head crashes into the ground. He has lost footing with both frontlegs.



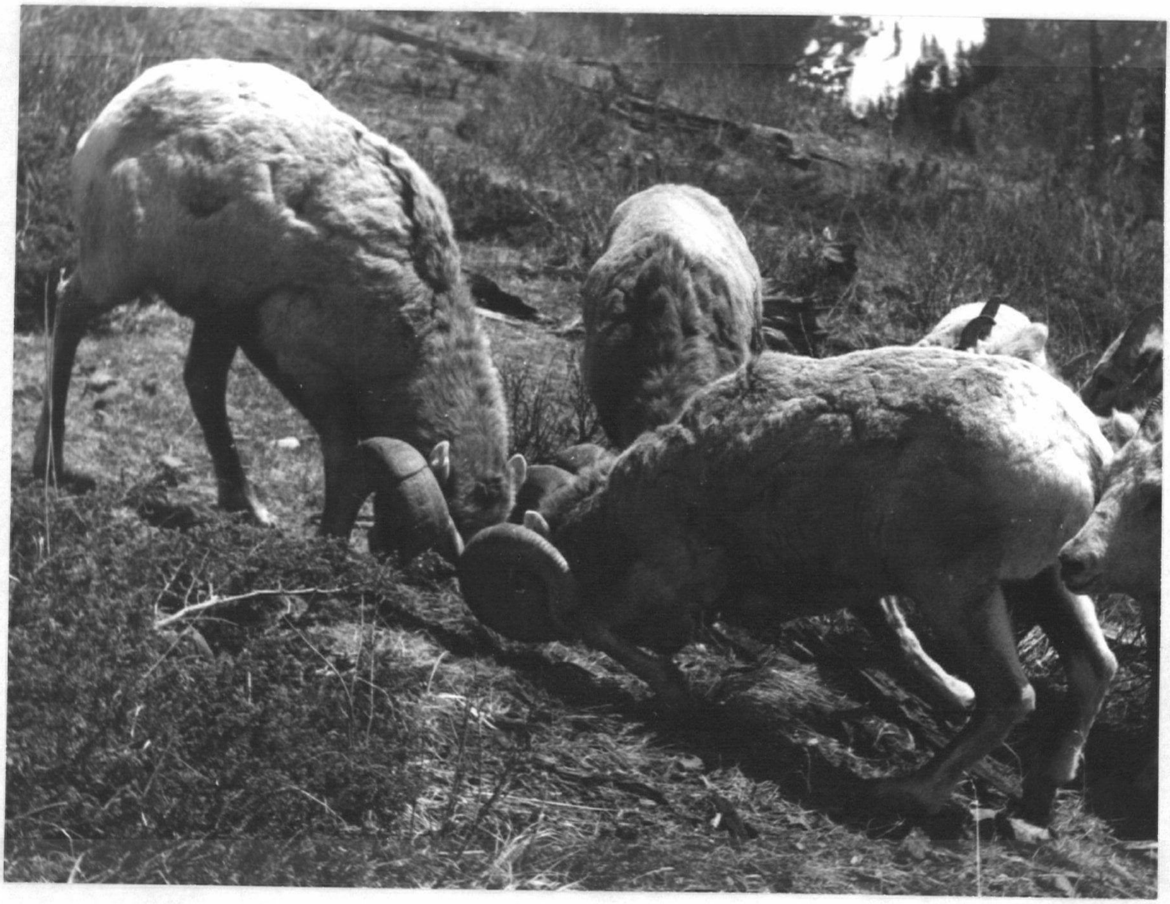


FIGURE 61. (a) The effect of the clash. The ram on left is "telescoped" by the force of the clash.

(b) A large Class IV ram is forcefully executing a clash. Compare its posture with that of the ram in part (a). The smaller ram on the left has his head twisted down and sideways and has been pushed back.

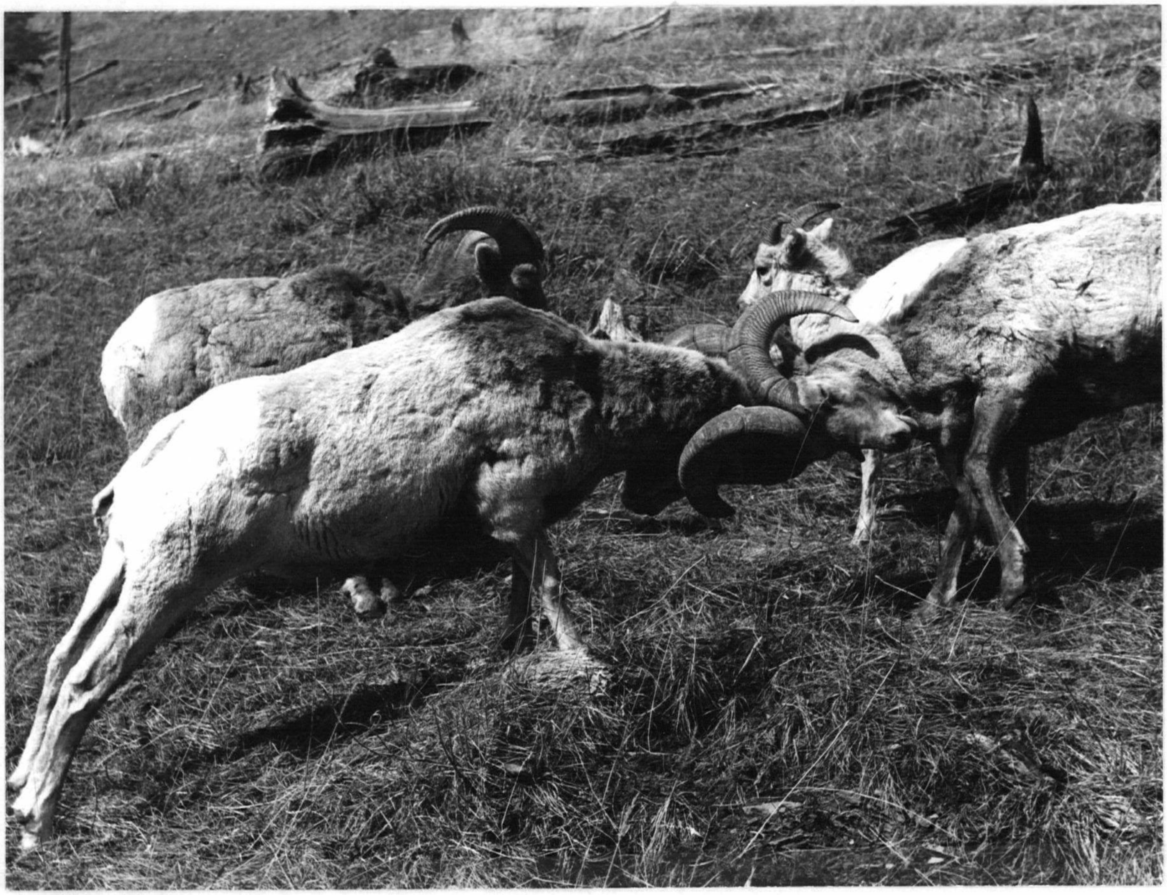


FIGURE 62. The effect of the clash. Note the chunk of horn gouged out of the ram's right horn, the scarred nose, the broken horn tips, the hair torn from an opponents body and the broken hair covering the ram's horns.

FIGURE 63. This old ram has lost most of his left horn, probably due to clashing and faulty growth of horn.

FIGURE 64. A defense against horn blows, is to catch them and let them work harmlessly against the tension of the neck. The Class I ram on right is striking downward. The ewe anticipates the blow with lowered head and is quickly orienting her body in line with the blow. The rams butt would depress the ewe's neck against the tension of the neck.

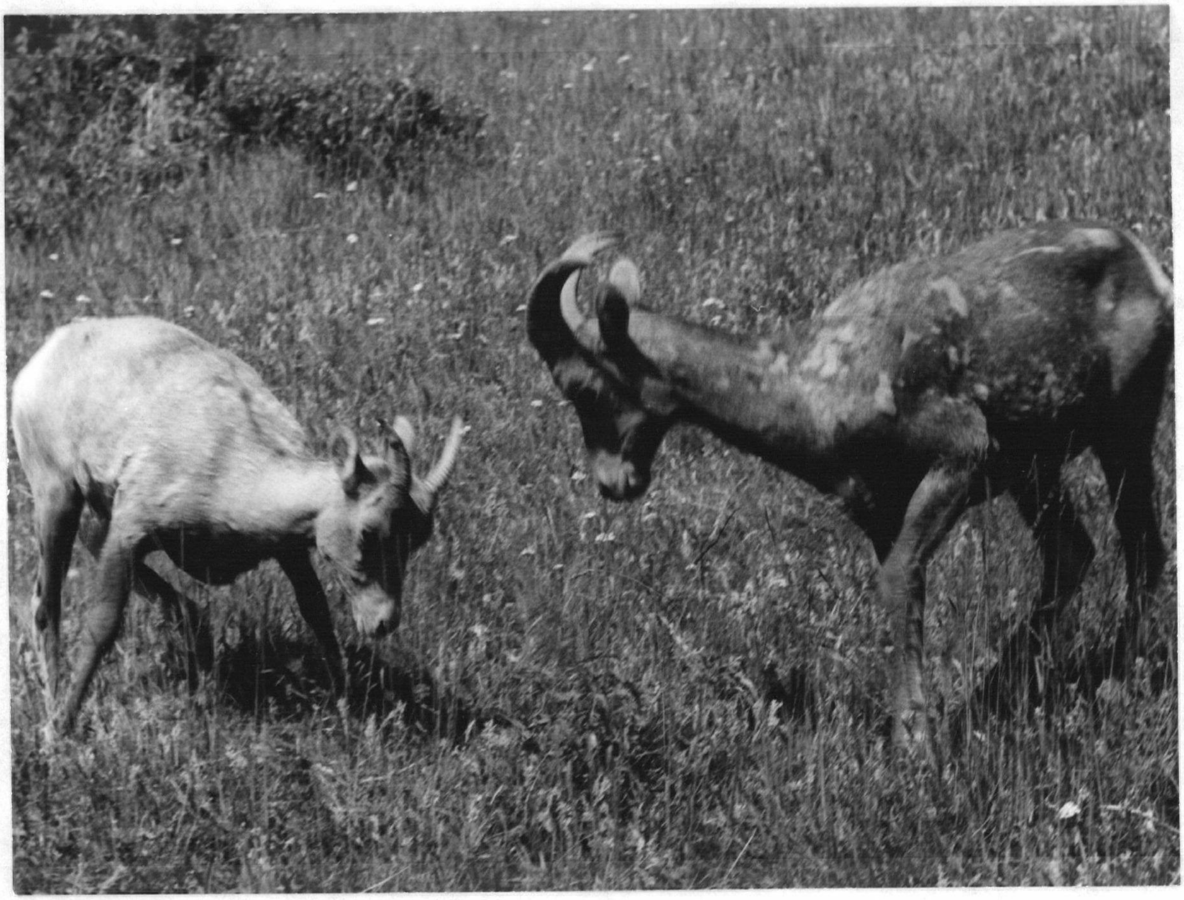
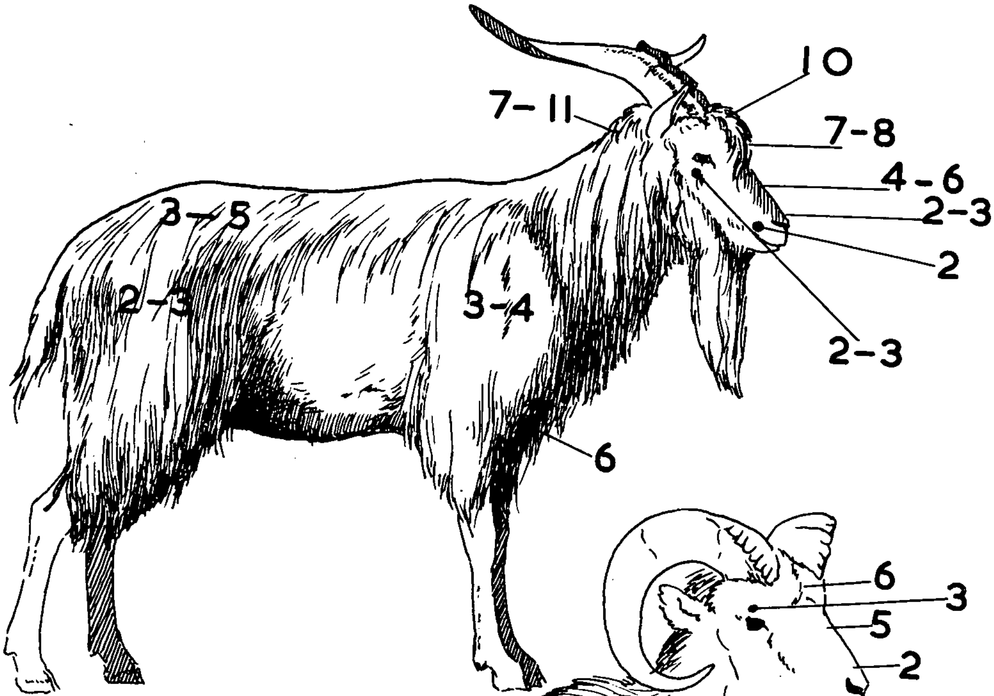
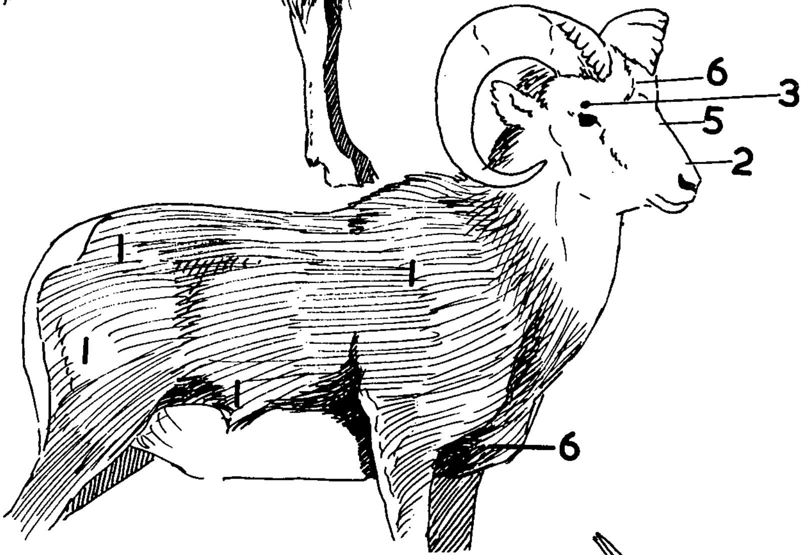


FIGURE 65. Skin thickness measurements (in mm) on feral male domestic goats (upper), a Stone's ram (centre), and a male mountain goat (lower). Note the thick hide on the heads of the large horned species and the heavy dermal shield on the rump of the mountain goat.


10
7-11
7-8
4-6
2-3
3-5
2
2-3
3-4
2-3
6


6
3
5
2
1
1
1
1
6

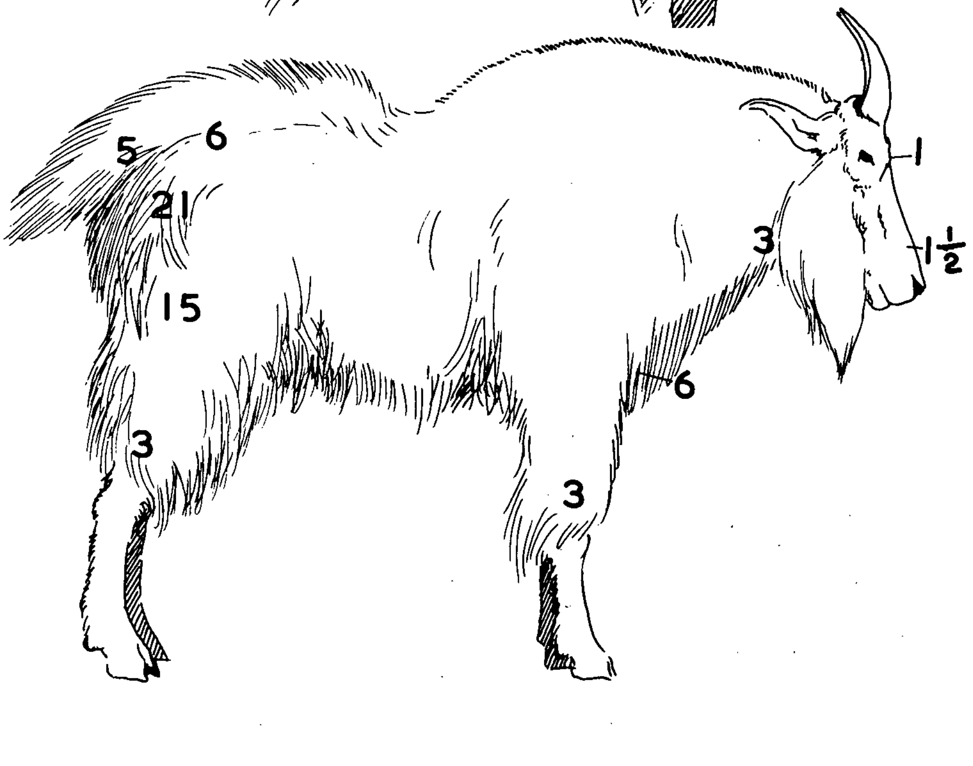
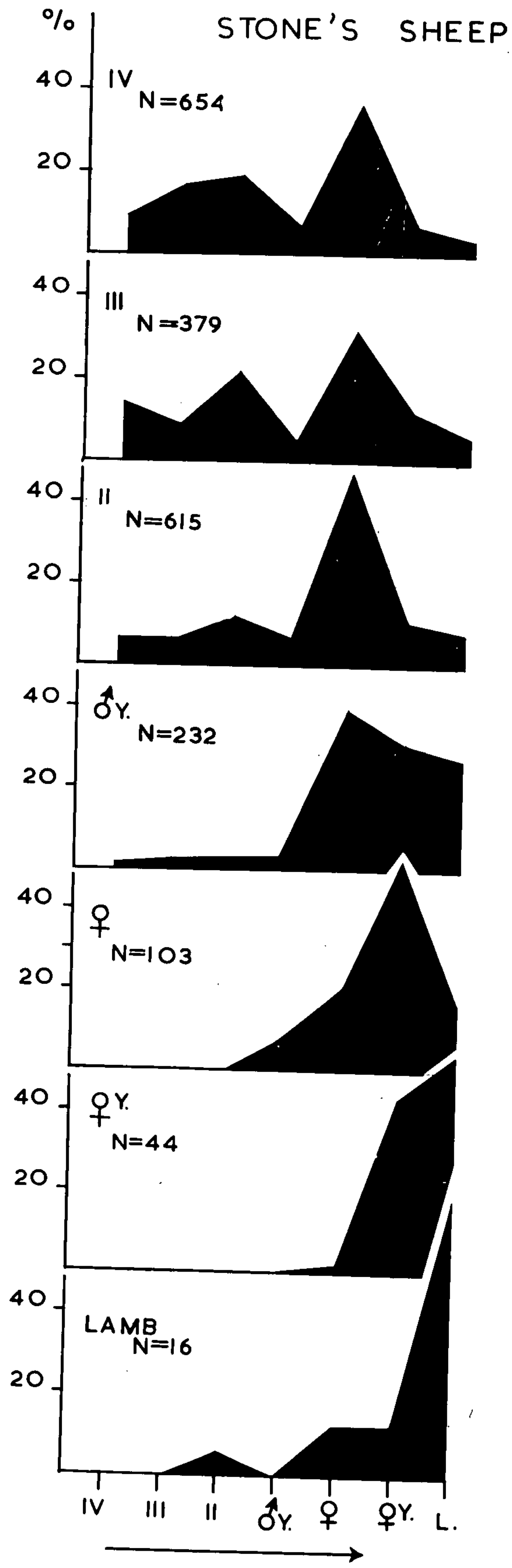

5
6
1
21
3
1 1/2
15
6
3
3

FIGURE 66. The threat jump is shown by a Class I rams towards a II ram. This group of ram is playing. An old, barren ewe (left) has joined in the race and is now chased by a I ram.

FIGURE 67. The distribution of social interactions by sheep on other sheep of all sexes and sizes. Abscissa, sex-age classes of sheep. Ordinate, percent frequency of social interactions. IV to Lamb identifies various sex-age classes. N, stands for the number of interactions which I observed each age class perform. Thus, I observed Class IV rams in 645 interactions with other sheep. Almost 40% of these interactions were initiated on females ( ♀ ) and only about 5% on Lambs ( L. ).



STONE'S SHEEP
%
40
20
IV
N=654
III
N=379
II
N=615
♂Y.
N=232
♀
N=103
♀Y.
N=44
LAMB
N=16
IV
III
II
♂Y.
♀
♀Y.
L.

FIGURE 68. Interaction preferences of rams on other sheep. Abscissa, sex-age classes of sheep. Ordinate, preference index (see p. 66 ) or number of patterns dealt out per interaction (o, open circle). The solid circles (•) stand for Stone's sheep preference index data, as the solid line (–) does for bighorns. The first heavy, vertical bar stands for the acting classes of rams; the second bar stands for females. These two bars draw attention to the two classes of sheep which acting rams prefer i.e. Class III rams prefer other III rams and ewes. Preference usually to the same or the next closest ram class.

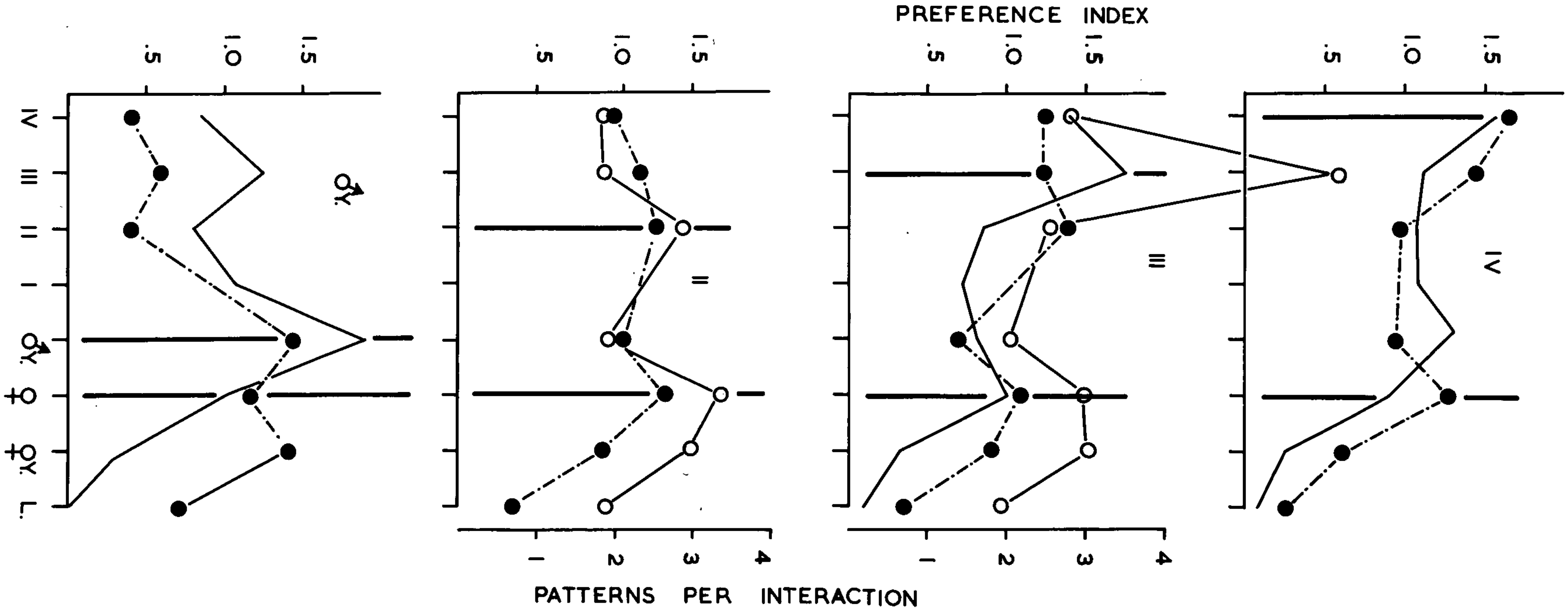
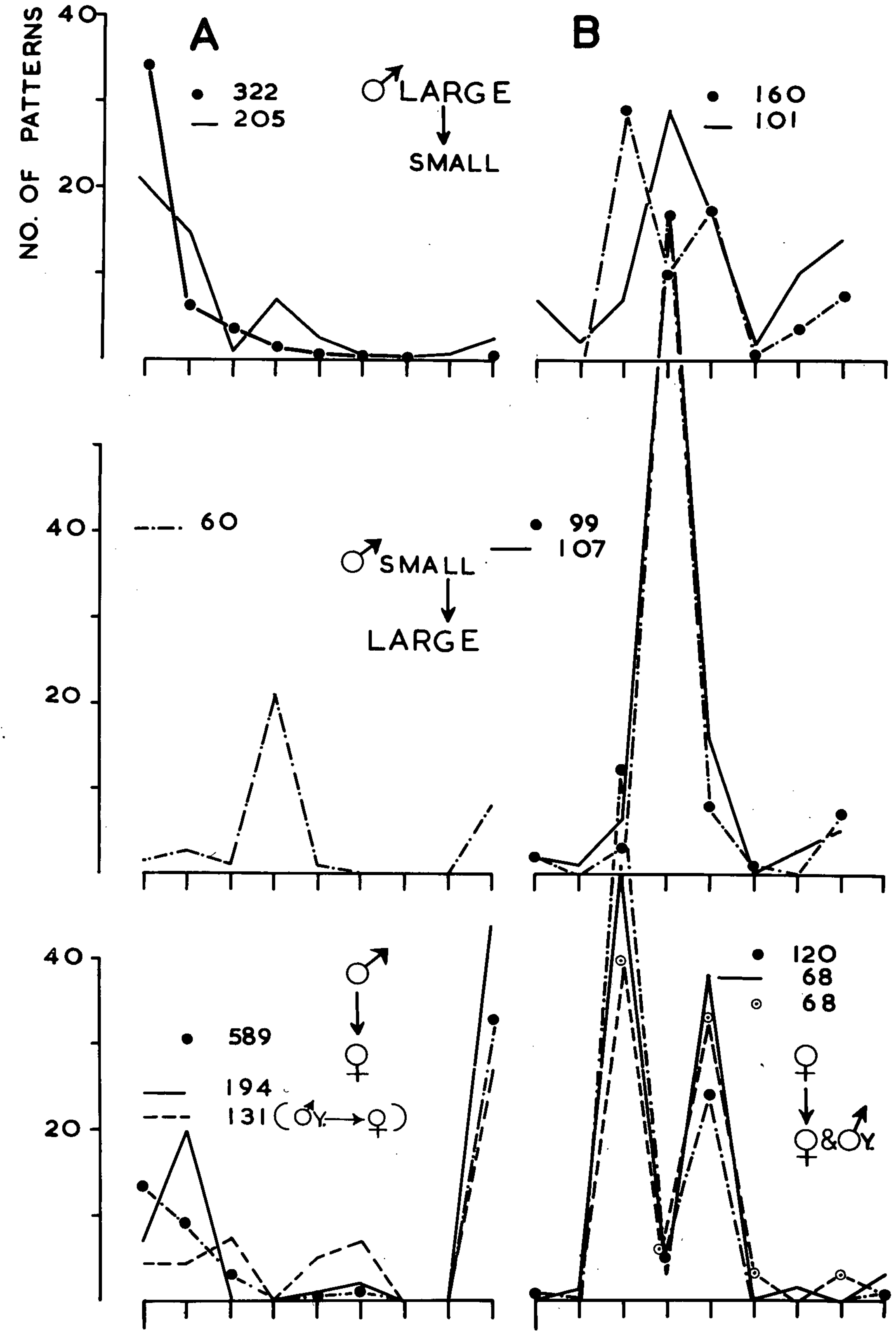
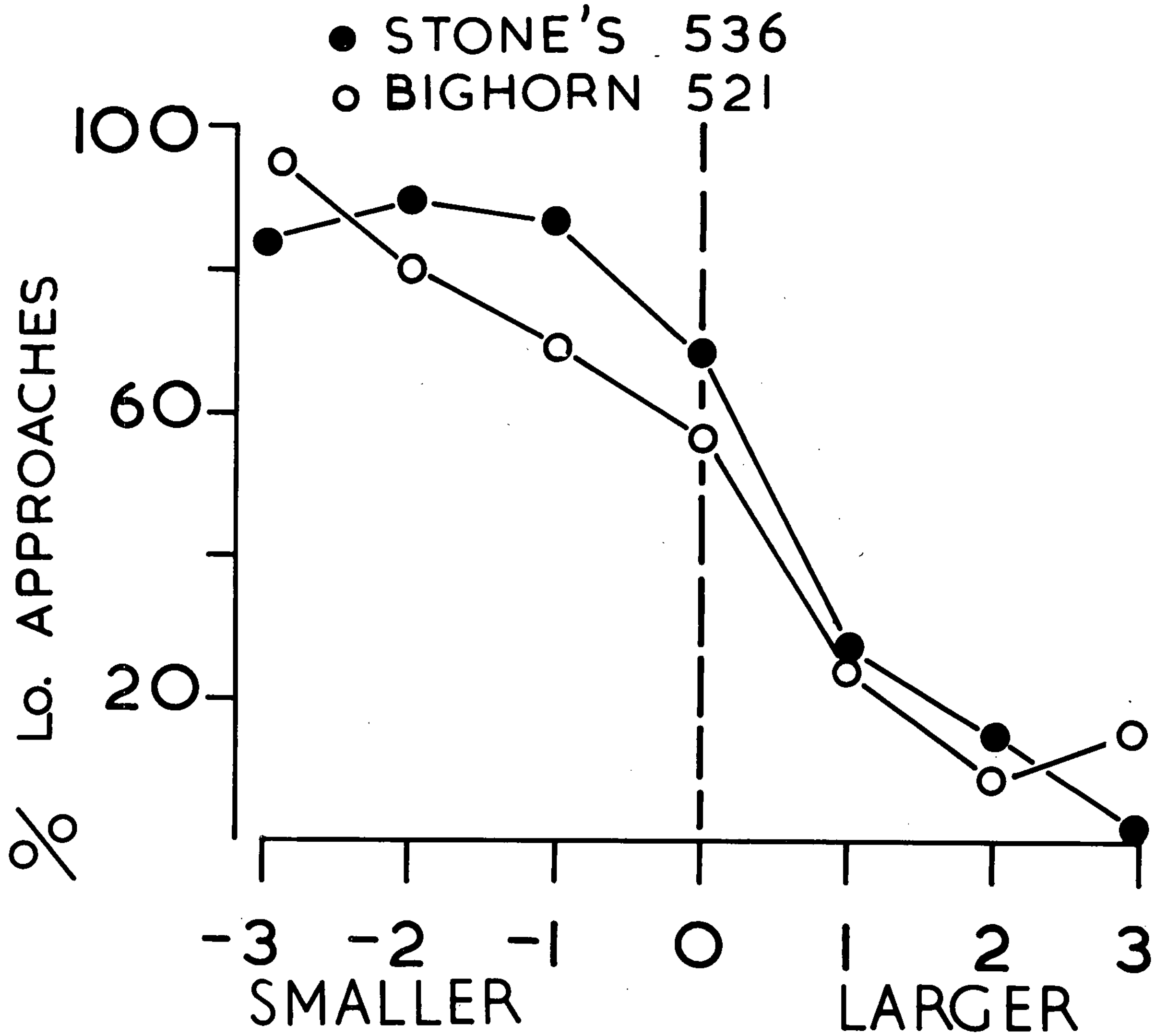

PREFERENCE INDEX
PATTERNS PER INTERACTION

FIGURE 69. Comparison of frequencies with which rams of two species of sheep approach smaller, equal and larger opponents in a low-stretch. Abscissa, horn size gradient of rams. Here o stands for the <u>same</u> class as the acting ram; -3 and +3 stand for rams three horn size classes smaller and larger respectively, than the acting ram. Ordinate, percent frequency with which acting rams approach in a low-stretch. For instance, bighorn rams (o) approach rams of their own size class in 58% of all interactions in low-stretch, but rams three classes smaller are approached in low-stretch 98% of all interactions.



NO. OF PATTERNS
A
B
322
205
♂ LARGE
SMALL
160
101
60
99
107
♂ SMALL
LARGE
589
194
131 (♂Y → ♀)
♀
120
68
68
♀ & ♂Y
L T H R B M C TH. S

FIGURE 70. Frequency with which various behaviour patterns occur as the first pattern after the initiating sheep has closed the distance and stands beside its opponent. Abscissa, patterns ranked in the order of frequency with which they follow a low-stretch initiation by large Stone's rams on smaller ones. Ordinate, frequency with which a given pattern followed in 100 initiations. Graphs under A refer to approaches in which the initiating sheep used a low-stretch; under B, approaches in which the initiating animal did not use a low-stretch. LARGE ——→ SMALL refers to the social situation, in which the larger approaches the smaller one. Solid (o) and open circles (o) stand for Stone's sheep data; solid line only (——) stands for bighorn data; broken line only (---) refers to Stone's and bighorn data combined. Numbers refer to the number of approaches each graph is based on i.e. in 322 approaches in low-stretch (A), Stone's rams (o & o ) which were larger than their opponents, delivered a front kick ( L ) 38 times right after the low-stretch in 100 approaches.



● STONE'S 536
○ BIGHORN 521
100
60
20
% Lo. APPROACHES
-3
-2
-1
0
1
2
3
SMALLER
LARGER

FIGURE 71. Frequency of behaviour patterns as they occur within interactions. Abscissa, patterns ranked in the order of frequency with which they are used by large bighorn rams interacting with small ones in the "normal" situation (p. 62). Patterns S. Rv. and F. are outside the rank order (see p.63). Ordinate, patterns per 100 interactions). Upper graph, actions of larger sheep (cross hatched) lower graph, actions of smaller sheep.

A, interactions initiated by large rams on small ones;

B, interactions initiated by small rams on large ones;

C, interactions between ewes. Vertical heavy bars, actions of Stone's sheep; solid line, actions of bighorn sheep; broken line, actions of Stone's sheep yearling females. Numbers above each graph show the number of interactions each graph is based on. For explanation of symbols Lo. -F. see p.

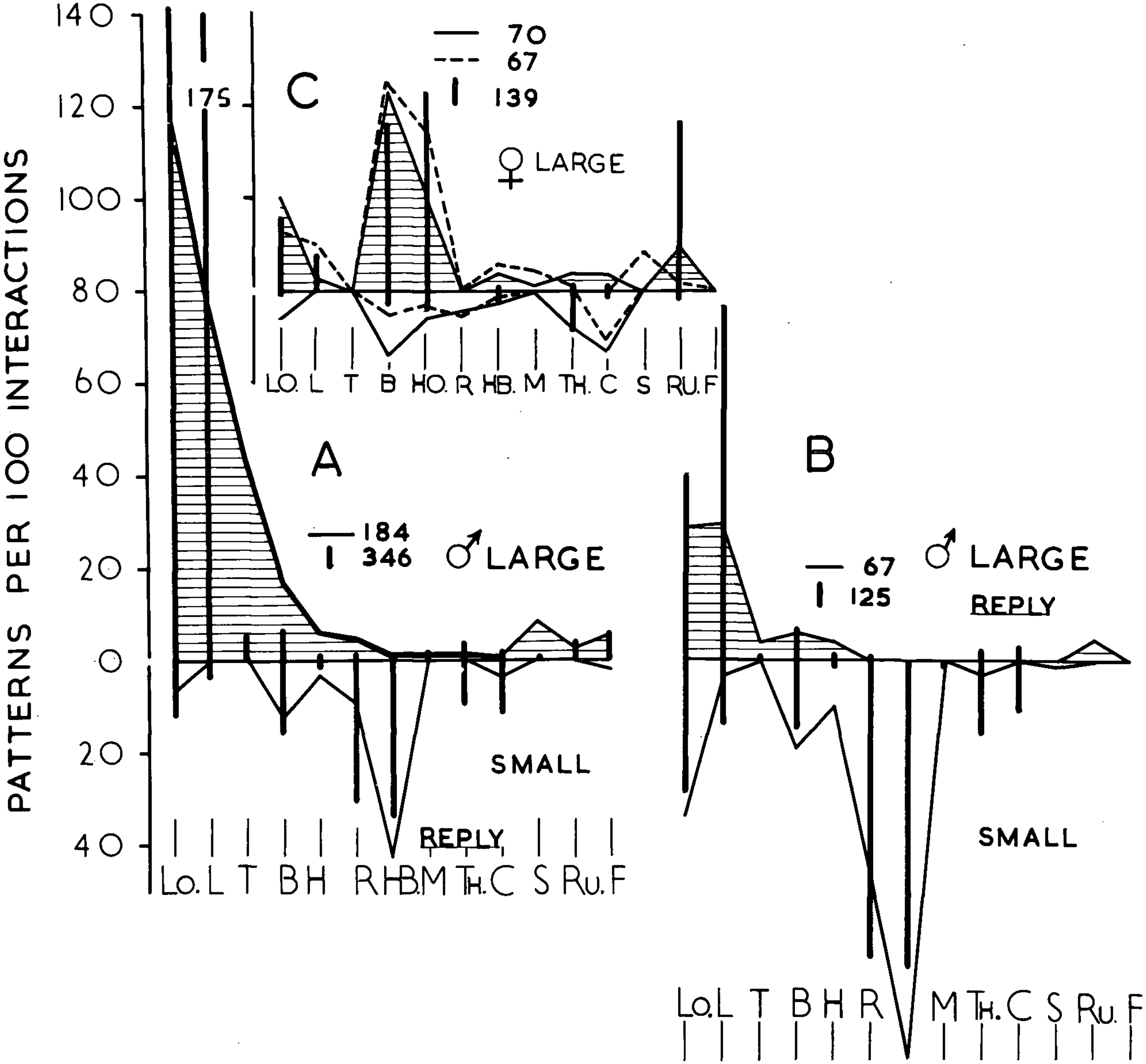
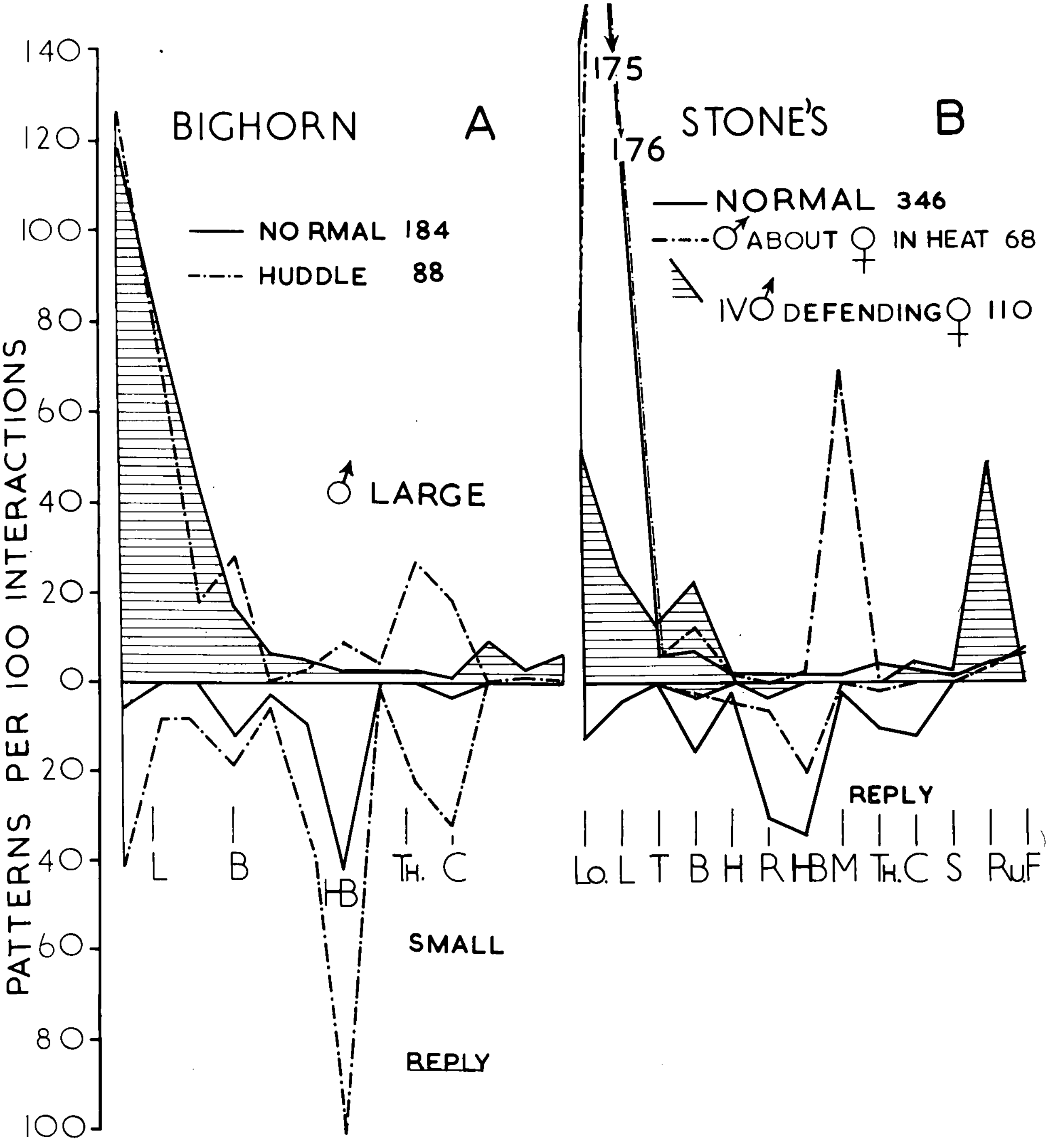
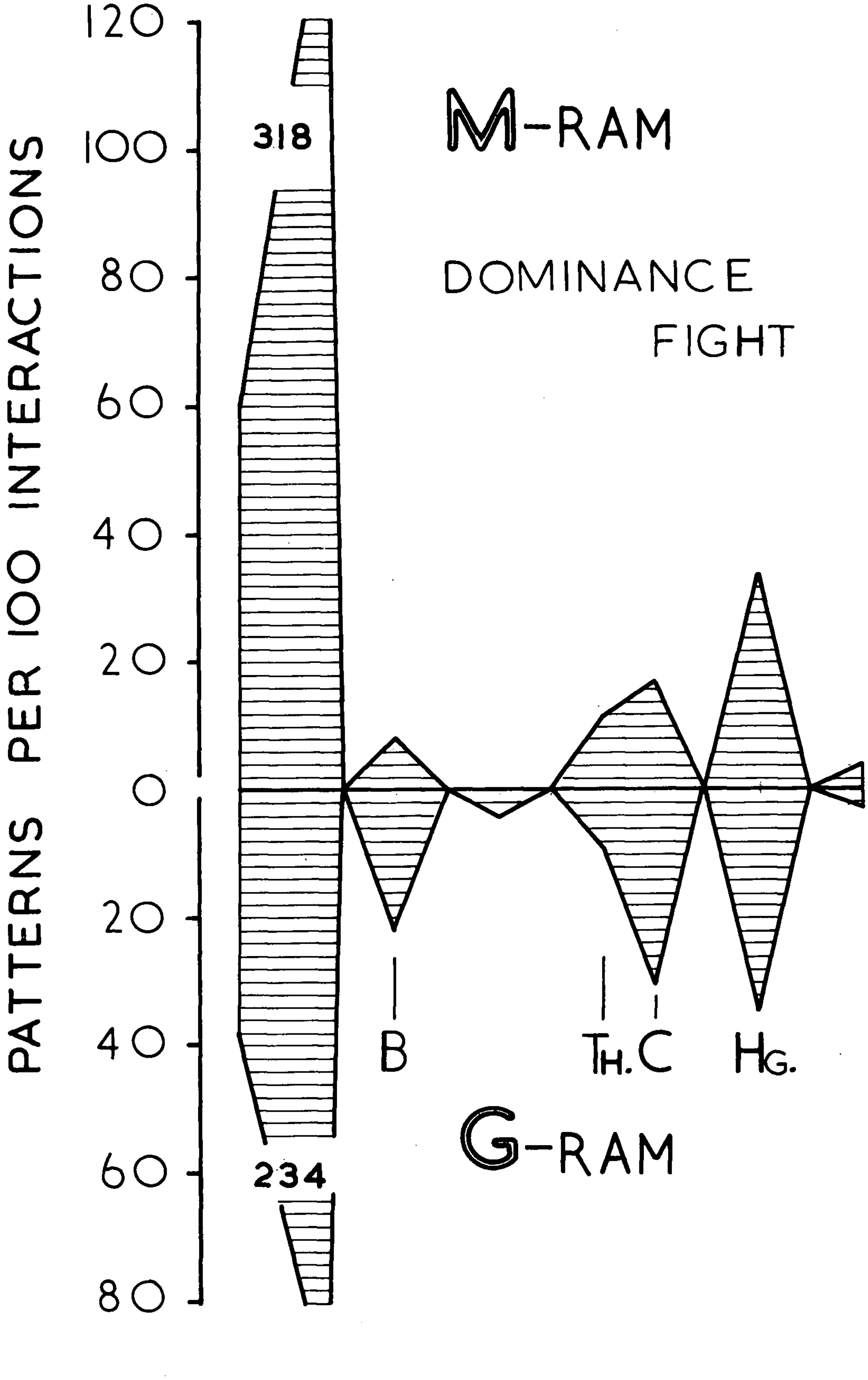

PATTERNS PER 100 INTERACTIONS
140
120
100
80
60
40
20
0
20
40
175
C
70
67
139
♀ LARGE
LO. L T B HO. R HB. M TH. C S RU. F
A
184
346
♂ LARGE
SMALL
REPLY
Lo. L T B H R HB. M TH. C S RU. F
B
67
125
♂ LARGE
REPLY
SMALL
Lo. L T B H R M TH. C S RU. F

FIGURE 72. Abscissa, and ordinate as well as arrangement of graphs is the same as in Fig. 82. The frequency with which behaviour patterns occur in the "normal" situation is compared with that from other situations.



BIGHORN A
NORMAL 184
HUDDLE 88
♂ LARGE
SMALL
REPLY
PATTERNS PER 100 INTERACTIONS
140
120
100
80
60
40
20
0
20
40
60
80
100
L B HB TH. C
STONE'S B
175
176
NORMAL 346
♂ ABOUT ♀ IN HEAT 68
IV♂ DEFENDING ♀ 110
REPLY
Lo. L T B H R HB M TH. C S Ru. F

FIGURE 73. Frequency of behaviour patterns in a dominance fight between two Class III Stone's rams. Abscissa and ordinate same as Fig. 82, except that horning of the ground (Hg) replaces sniffing of rear (s). The numbers 318 and 284 stand for the number of frontkicks dealt out by M- and G-ram respectively. Observation period, eight hours.



PATTERNS PER 100 INTERACTIONS
120
100
80
60
40
20
0
20
40
60
80
318
234
M-RAM
DOMINANCE FIGHT
G-RAM
B
TH. C
HG.

FIGURE 74. Frequency of behaviour patterns in interactions of rams with non-estrous ewes. Solid line in A stand for bighorn data, broken line for Stone's sheep data; B, is based on combined bighorn and Stone's sheep data. A, interactions initiated by class II - IV rams; B, yearling rams interacting with ewes.

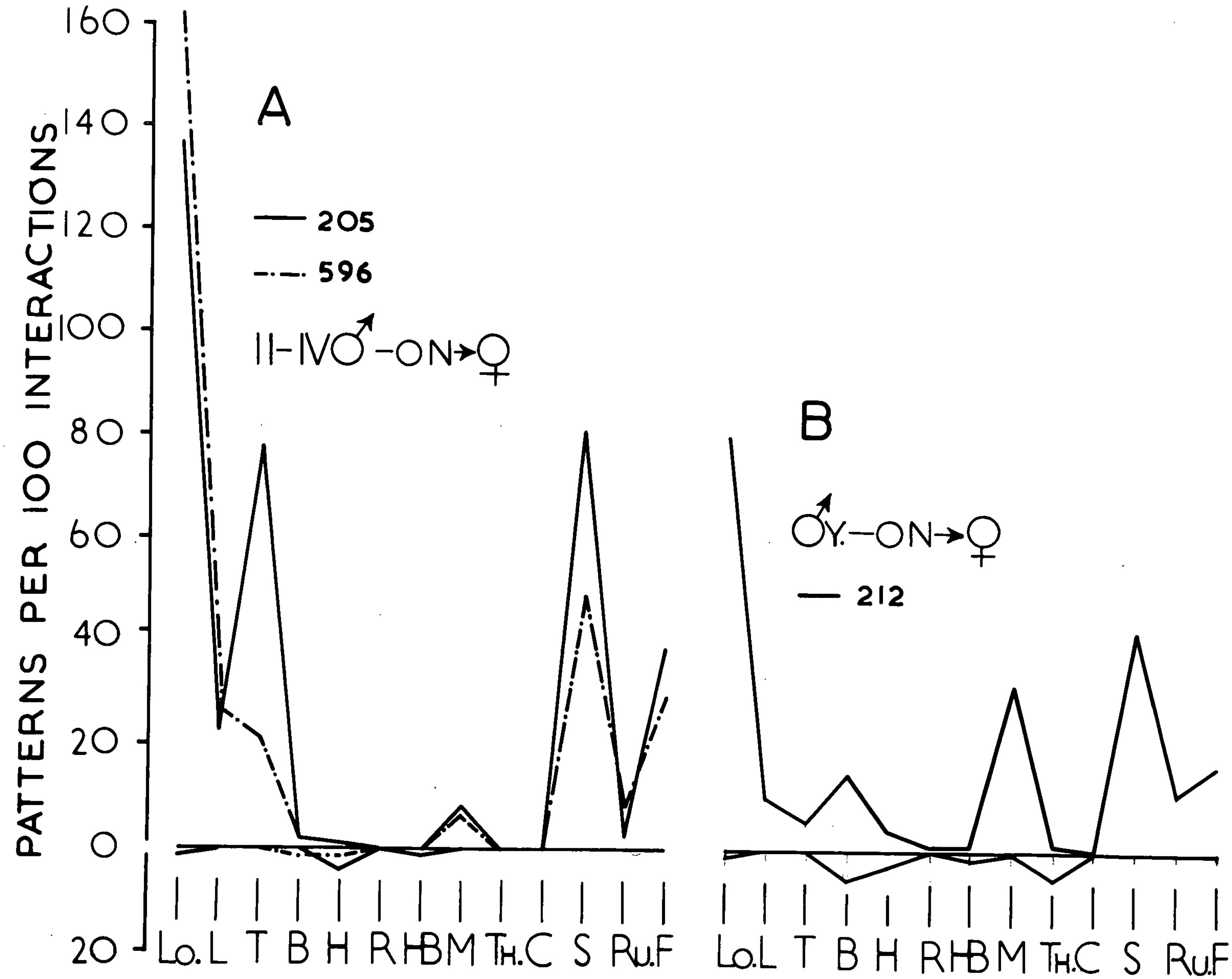

PATTERNS PER 100 INTERACTIONS
160
140
120
100
80
60
40
20
0
20
A
205
596
II-IV♂-ON→♀
B
♂Y.-ON→♀
212
Lo.L T B H R H-B M Th.C S Ru.F
Lo.L T B H R H-B M Th.C S Ru.F

FIGURE 75. A comparison of frequencies of behaviour patterns in interactions of large, guarding rams with estrous ewes (solid line) and large, subordinate rams on smaller rams in the presence of an estrous ewe. The numbers 99 and 68 stand for the number of interactions each set of graphs is based on. Lower graph, solid line stands for the actions of the estrous ewe.

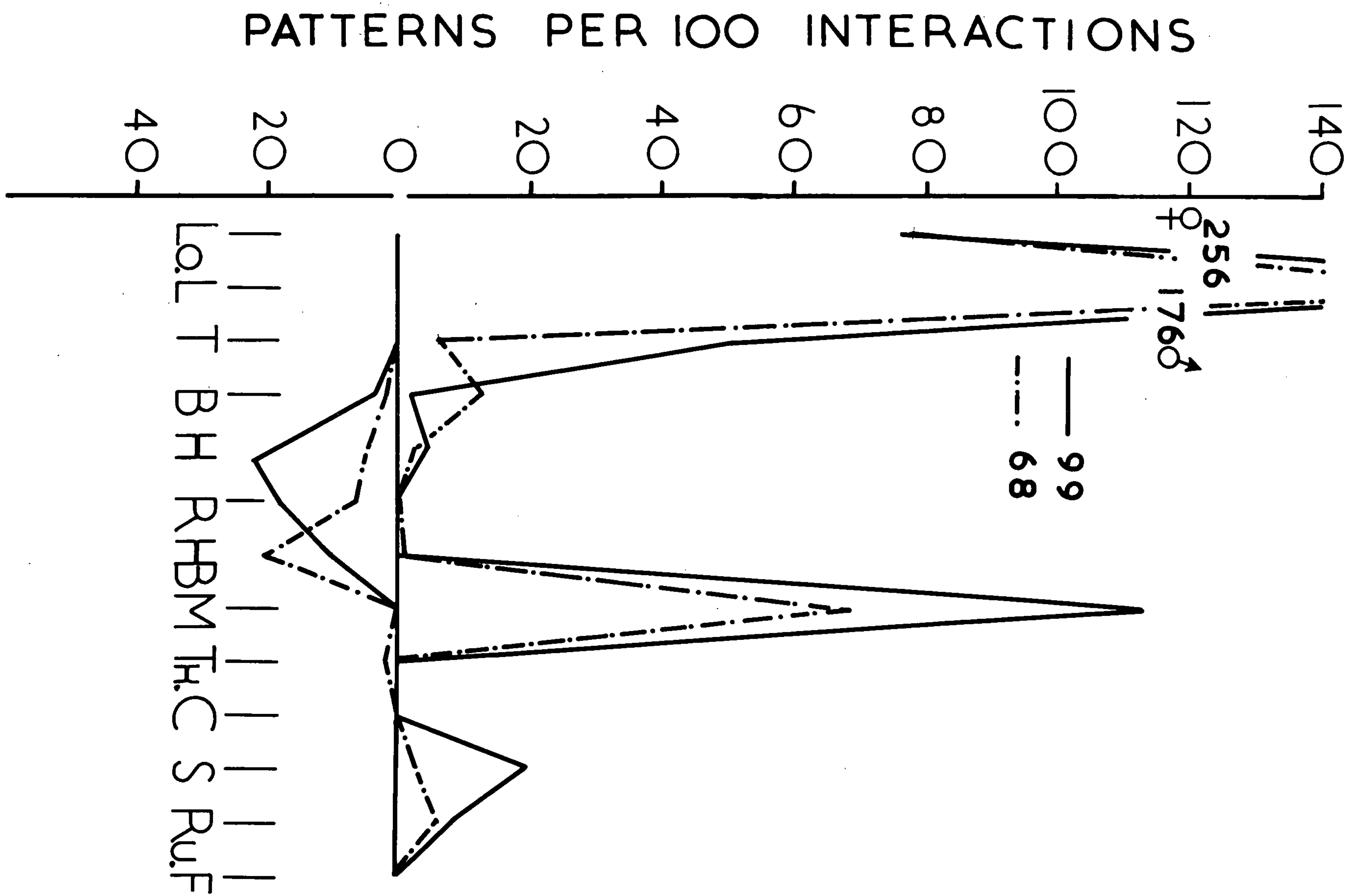

PATTERNS PER 100 INTERACTIONS
40 20 0 20 40 60 80 100 120 140
♀ 256
176 ♂
99
68
LoL T B H R HBM ThC S RuF

FIGURE 76. Frequency of sexual patterns within every 100 interactions initiated by Class IV-II rams on other sheep classes. Abscissa, sex-age classes of sheep.

A, frequency with which rams sniffed and nuzzled the rear of other sheep.

B, frequency with which rams mounted other sheep. The more sheep resembled a ewe in outside appearance, the more frequently they were treated sexually by rams.

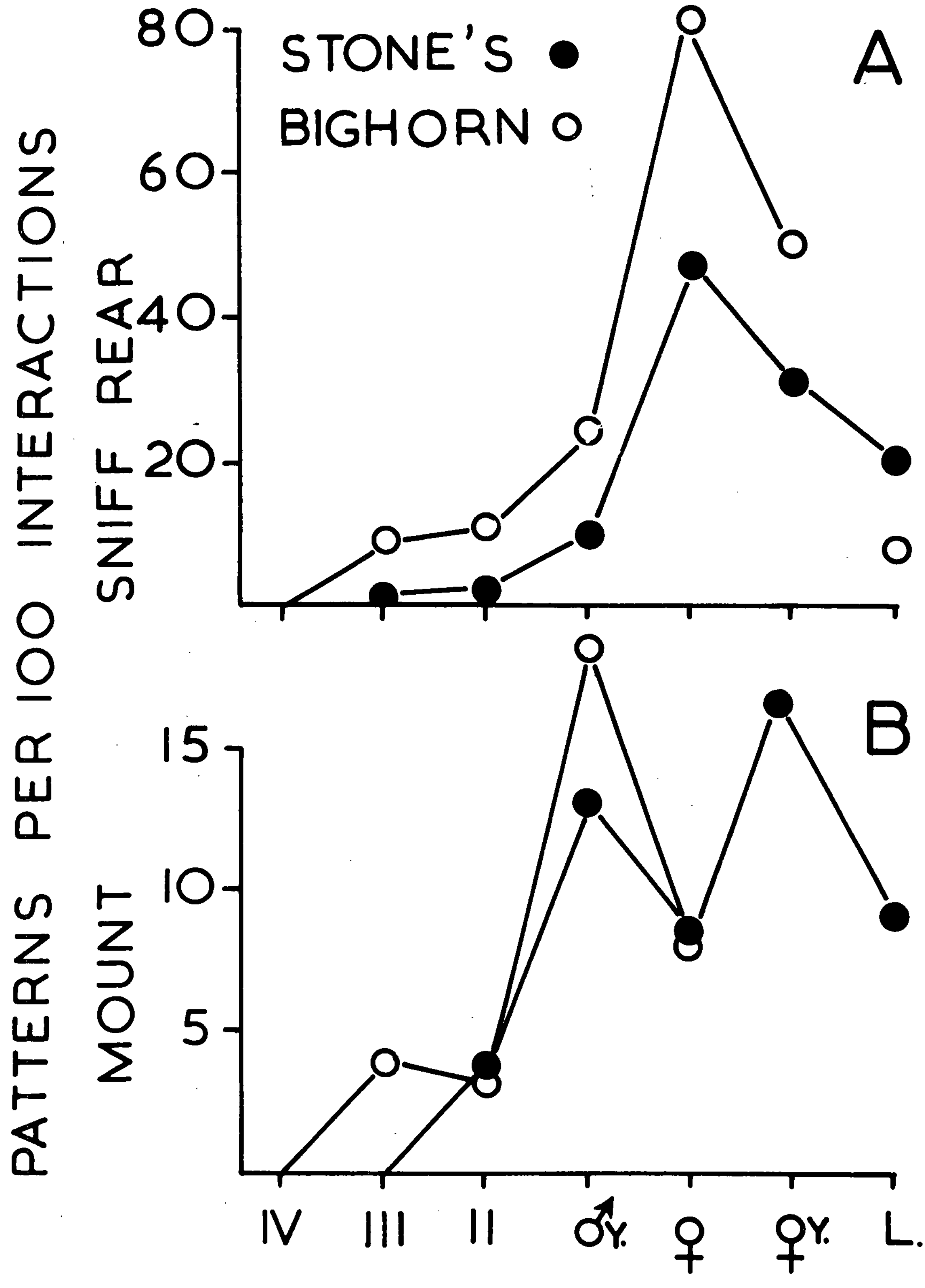
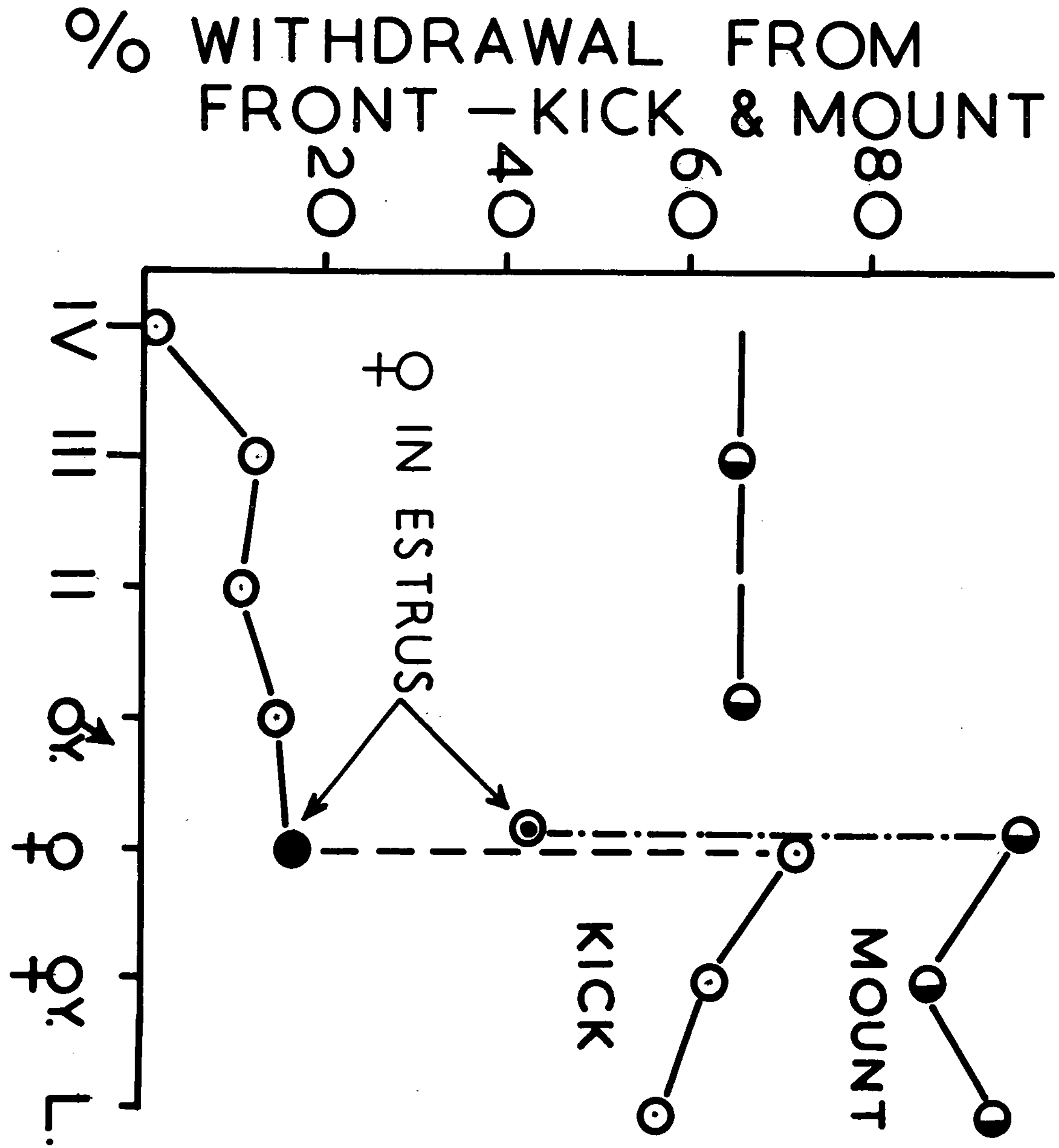

STONE'S ●
BIGHORN ○
A
B
PATTERNS PER 100 INTERACTIONS
SNIFF REAR
MOUNT
80
60
40
20
15
10
5
IV
III
II
♂Y.
♀
♀Y.
L.

FIGURE 77. Withdrawal frequency of sheep from the mount (o & o) and from the kick (o & o). Abscissa, sex-age classes of sheep. Ordinate, percent of instances in which sheep withdrew rather than stood when mounted or kicked. The non-estrous ewe is similar in her reactions to sub-adults; the estrous ewe resembles rams in her response.



% WITHDRAWAL FROM FRONT – KICK & MOUNT
20
40
60
80
IV
III
II
♀ IN ESTRUS
KICK
MOUNT
L.

FIGURE 78. During feeding, rams are usually widely dispersed.

FIGURE 79. A group of three rams led by a full curl enter another ram band. The full curl enters the ram band in low-stretch.

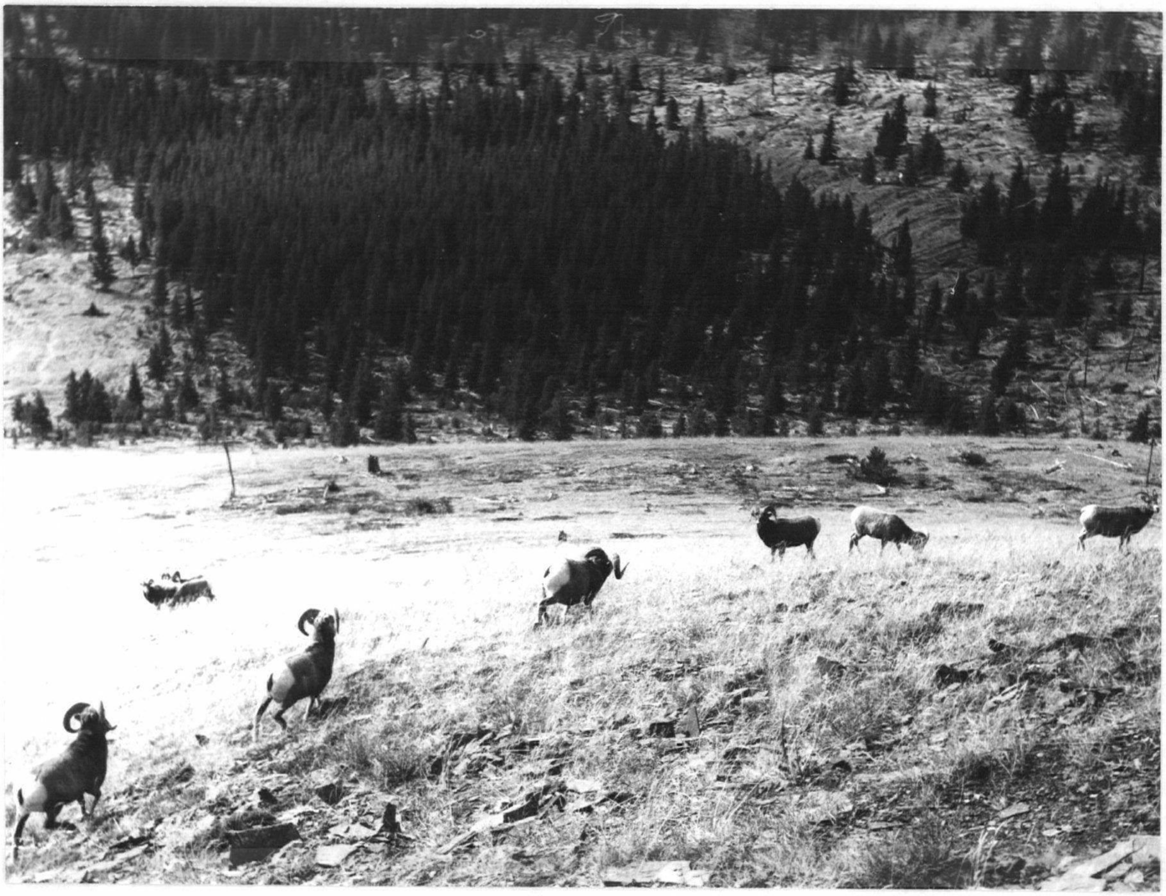


FIGURE 80. Bighorn rams in a huddle. Rams display and usually horn, rub and nuzzle each others head and horns.

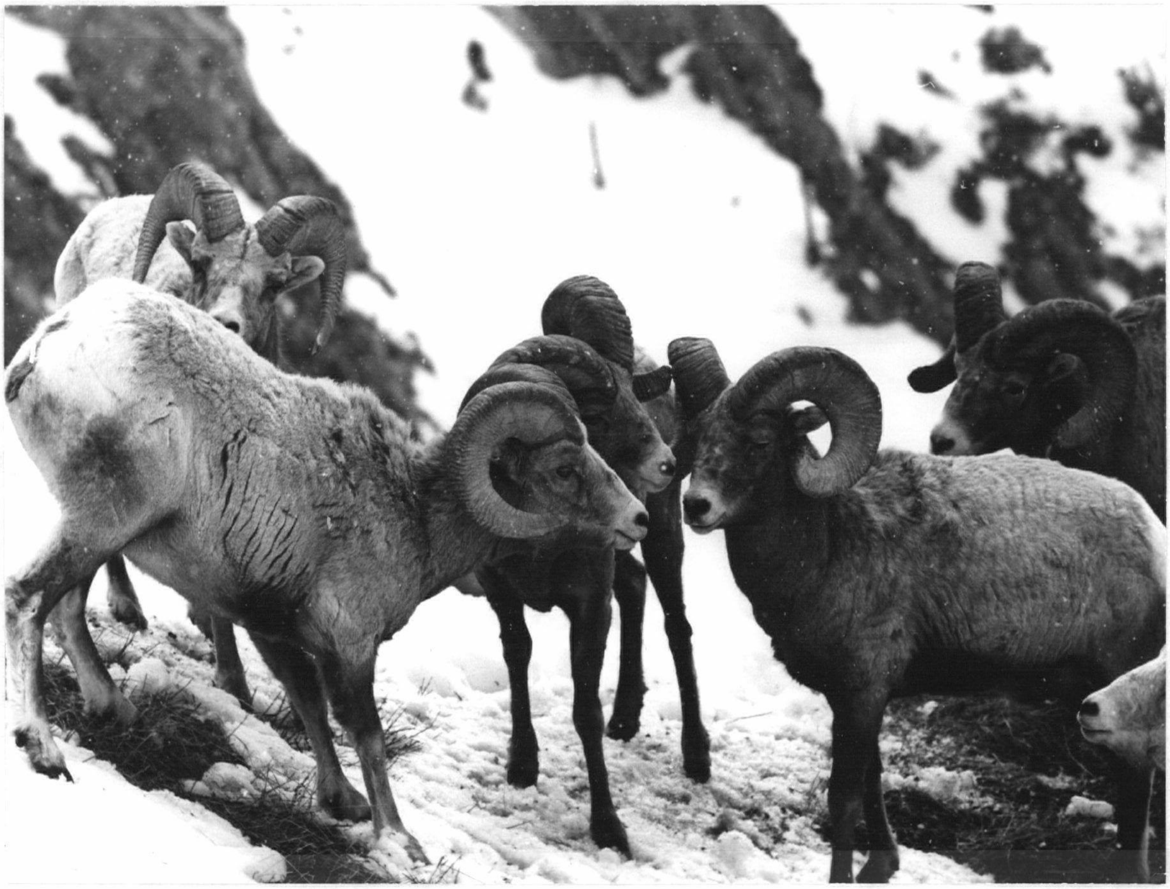


FIGURE 81. Young rams at play in spring. The lead ram whirled and rose into a threat jump on a small, barren piece of flat ground. It was a common huddling place.

FIGURE 82. Rams during exuberant play. The II ram on left is not threat jumping but frolicking, two full curls in rear are about to clash. The full curl in centre is whirling around.

FIGURE 83. Behaviour phases of rams in a dominance fight.

A, initiation of interaction, in low-stretch.

B, kick phase in which rams deliver kicks and present to each other.

C, disengagement in low-stretch signalling the impeding threat jump or clash.

D, bipedal run by ram on left (threat jump). Ram on right gets ready to receive the clash.

G, rams feed side by side for a short while before one or the other approaches in low-stretch.

(A) to begin another cycle.

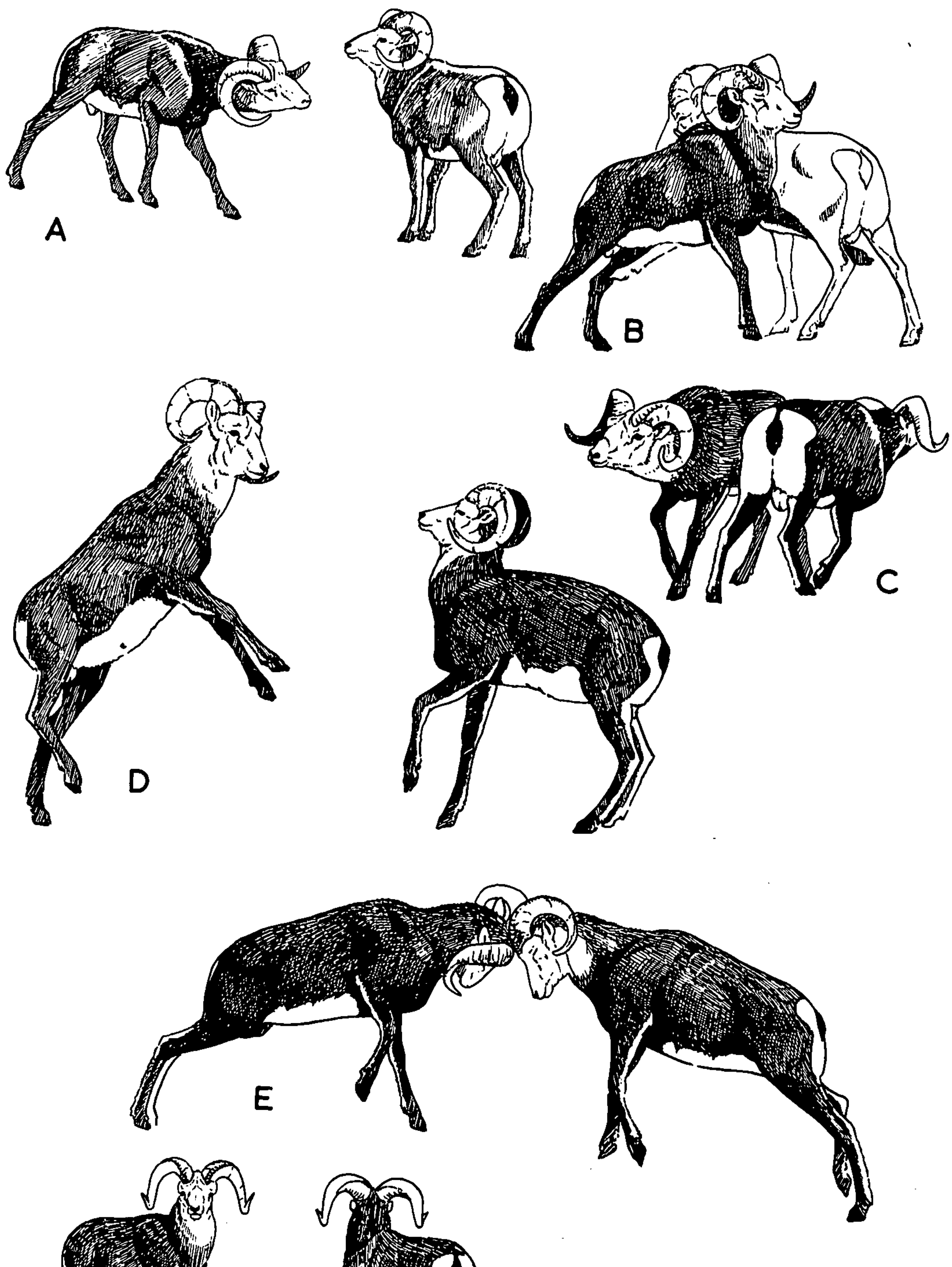

A
B
C
D
E
F
G

FIGURE 84. Rams in a vicious fight. Ram on right hits sideways with his horns. Ram on left moves sideways attempting to keep his opponents flank in front of him and to deliver a blow.

FIGURE 85. Rams in a vicious fight. The two opponents push each other about with their shoulders, neck and horns.

FIGURE 86. Two rams accidentally locked horns. This occurs rarely and opponents usually free themselves quickly.

FIGURE 87. A 12 months old ram interacting with a yearling ewe, which he repeatedly begins to mount.

FIGURE 88. The same ram approaches the same ewe in low-stretch. From their first birthday on, yearling rams systematically engage females until they dominate her.

FIGURE 89. During fall, short but vicious fights may errupt between ewes and yearling rams. Rams have gained dominance when ewes withdraw rather than attack.

FIGURE 90. A group of rams chasing an estrous ewe. The largest horned ram is behind the ewe and prevents subordinate rams from passing.

FIGURE 91. During a chase, a III ram managed to mount the ewe. The photo was taken a split second before the dominant IV ram crashed into him and knocked him off the ewe.

FIGURE 92. When the chase ends, the largest horned ram positions himself between the ewe and his subordinates. The subordinates usually interact with each other.

FIGURE 93. A Class I ram got close to the guarded ewe and is chased off by the full curl.

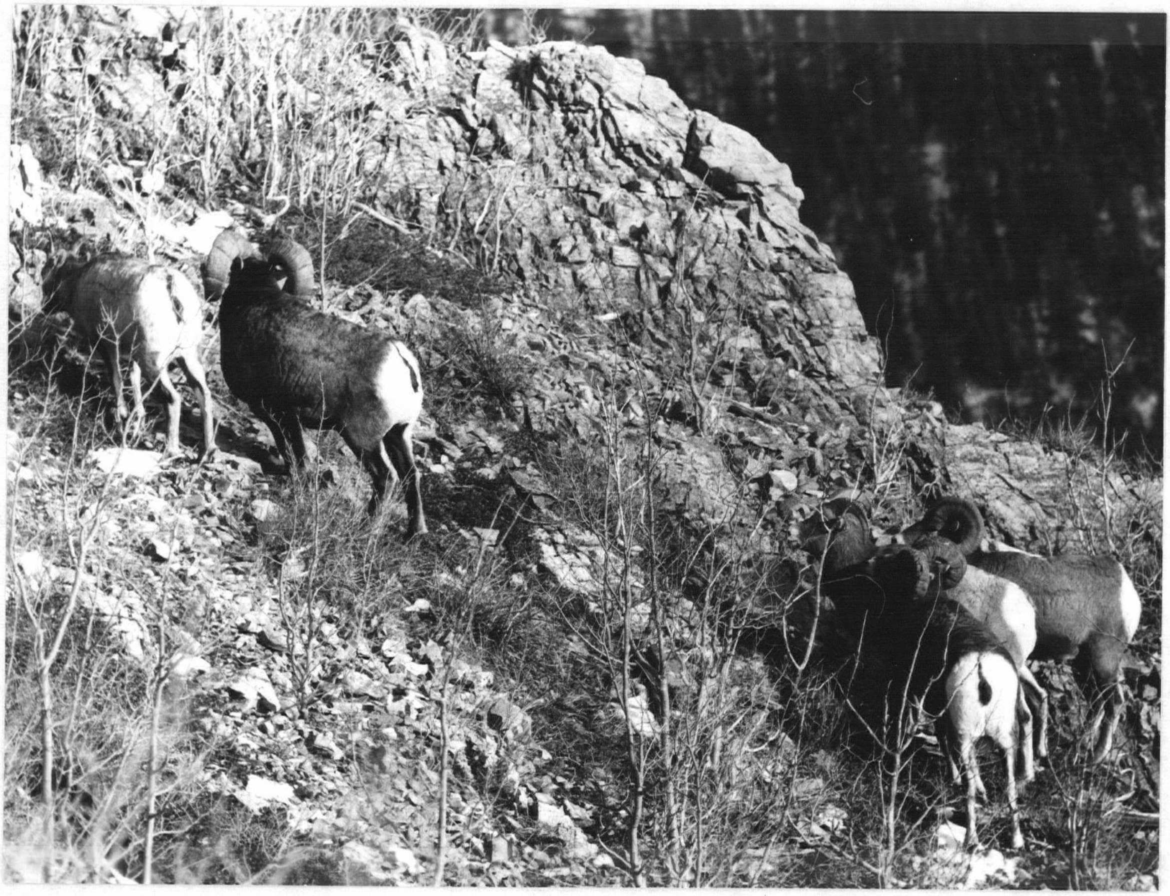


FIGURE 94. Courtshipby the estrous ewe.

A, the ewe suddenly bounds away in a coquet run, which triggers the ram into running after her for a few jumps.

B, the ewe turns and while horn threatening prances back to the ram.

C, she butts and horns the rams chest, neck, face or horns.

D, she slips under his chin and rubs her body along his chest.

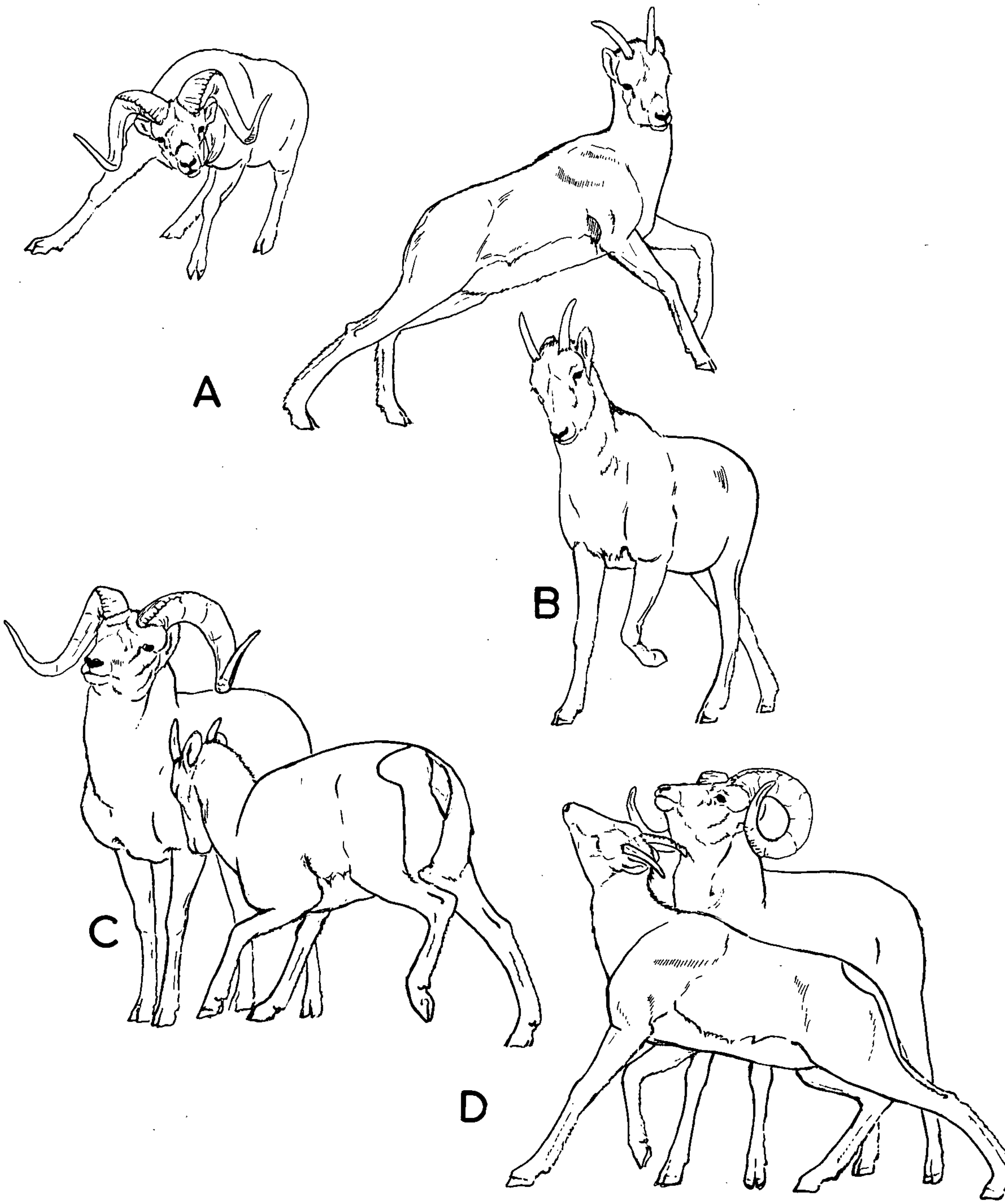
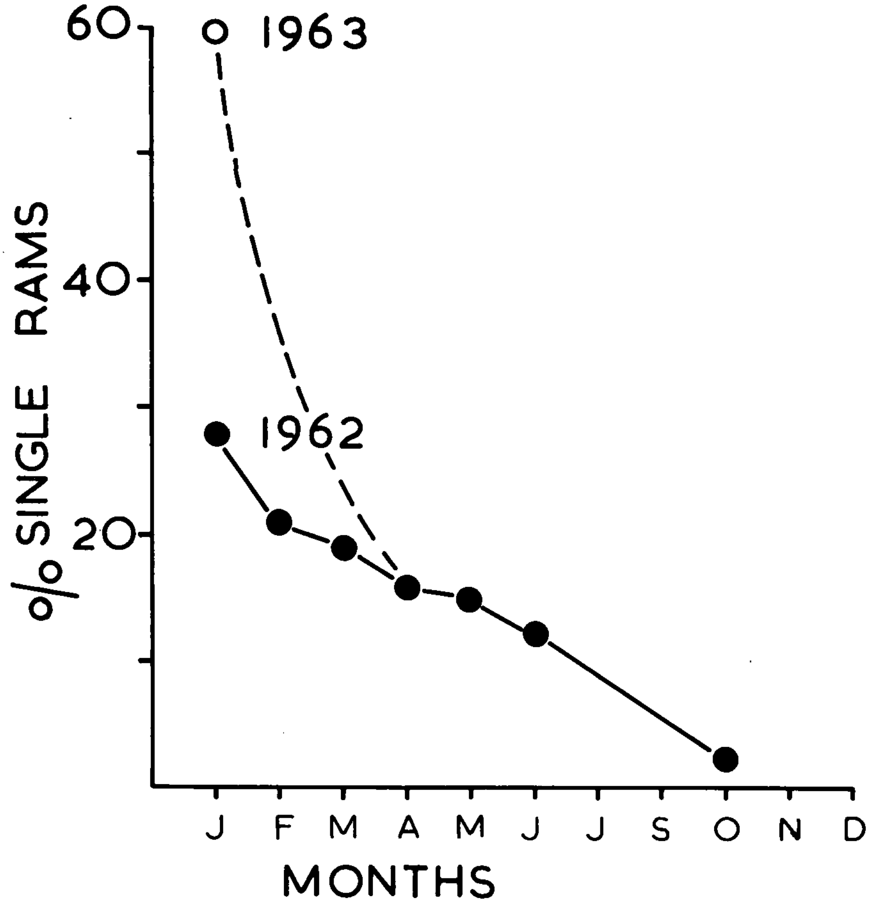
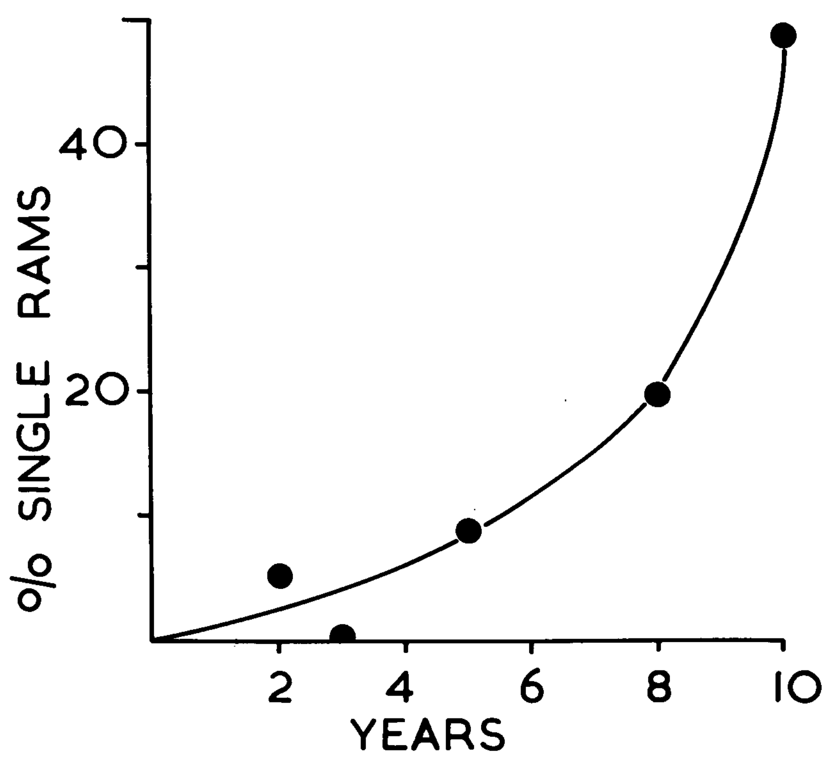

A
B
C
D

FIGURE 95. Rams become progressively less solitary as winter advances. Solid circles, data for Stone's rams 1962; open circles data for the very same rams in January 1963. The winter of 1961/62 was one of deep snow; in January 1965 little snow lay on the ground. It appears, that when little snow lay on the ground, the rams dispersed more and were more solitary than when confined by deep snow. Since in March-April 1962, hard snow did allow dispersal, the points for that time and January 1963 are comparable. The broken line illustrates the probable true social tendencies of rams during winter.

FIGURE 96. The older rams get, the more frequently they are seen alone. Data for Stone's rams from January - May 1962.



60
40
20
% SINGLE RAMS
1963
1962
J F M A M J J S O N D
MONTHS

40
20
% SINGLE RAMS
2 4 6 8 10
YEARS

FIGURE 97. Goat-like caprids assembled in order of resemblance. Bottom, Ammotragus male and female. Above them is Capra cylindricornis, a young male and female. To the left is a male Capra caucasica. Above latter are a Capra ibex male and female. (After Petzsh 1957).

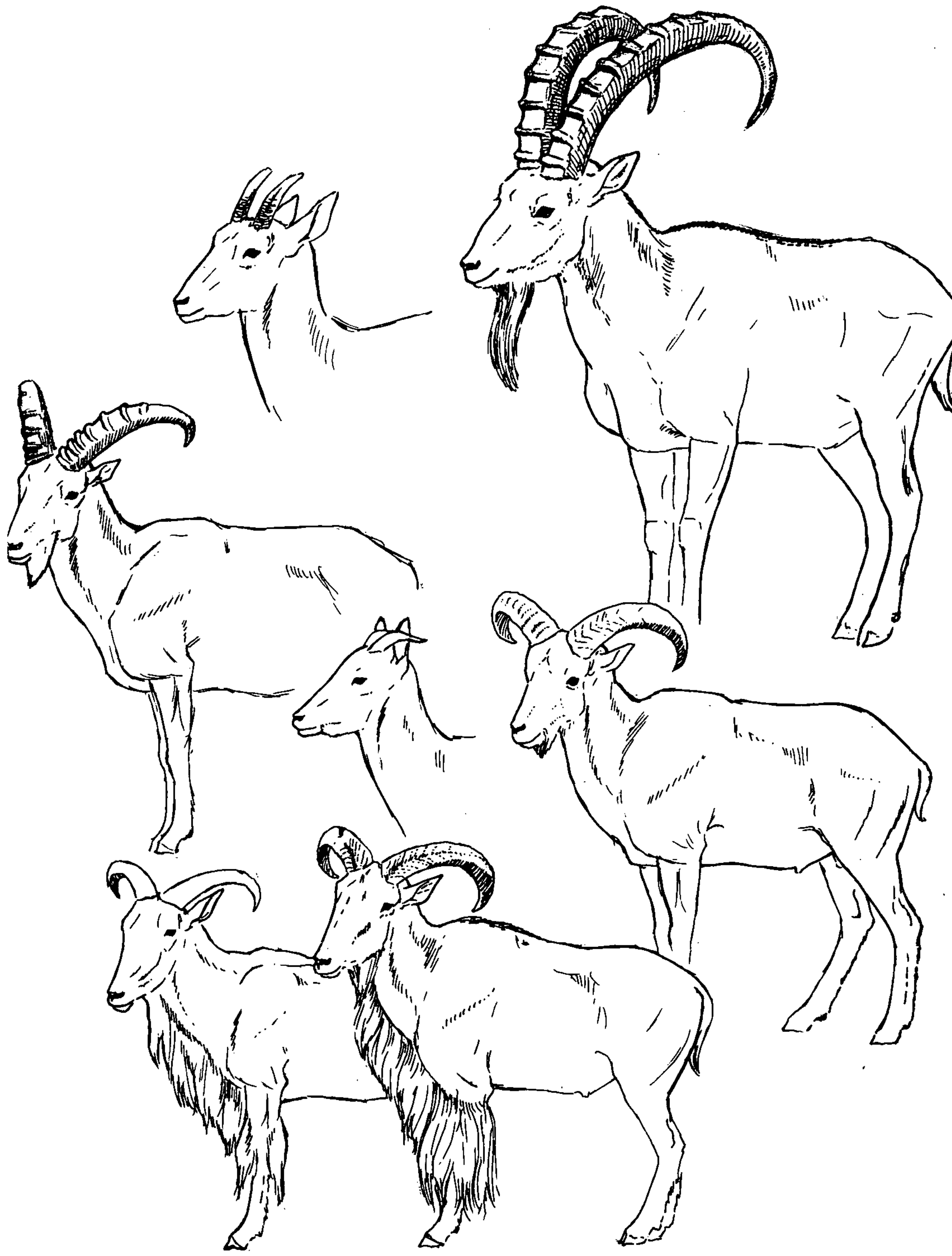


FIGURE 98. <u>Ammotragus</u>, and the Asiatic <u>ammon</u> sheep assembled in order of resemblance.

1 <u>Ammotragus</u>

2 <u>Ovis ammon gemelini</u>

3 <u>orientalis</u>

4 <u>cycloceros</u>

5 <u>severtzovi</u>

6 <u>poli</u>

7 <u>karelini</u>

8 <u>ammon</u>

Please note the changes in horn shape and size, reduction of ventral neck ruff, changes in ear length and shape. In <u>karelini</u> (7), the lateral horn edge shifted medianly. Not drawn to size.


8
7
6
5
4
3
2
1

FIGURE 99. The movements and distribution of sheep. On the North American continent all names refer to subspecies of sheep; on the Eurasian continent all names refer to species; in North Africa, Ammotragus refers to the genus. The figures 1-9 denote subspecies of Ovis ammon, as in Fig. 98 except figure 9. This refers to O. ammon darwini from Mongolia. Broken lines indicate probably migration routes of ancestral American sheep. Movement in Asia would be probable before the Riss glaciation; movement of ancestral sheep in North American is probably pre-Wisconsin, during the sangamon. Post Wisconsin dispersal in North American is shown in heavy lines.

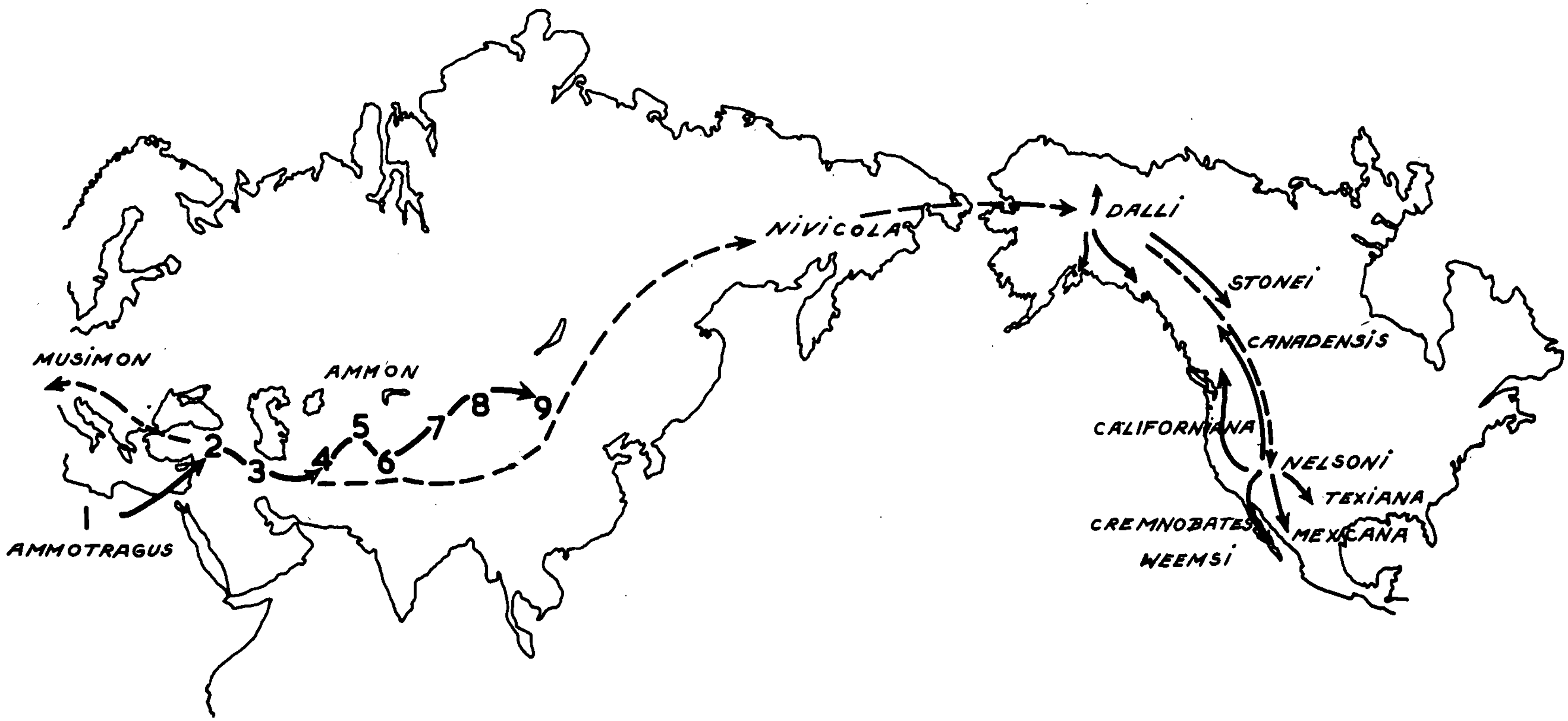

MUSIMON
AMMON
1
2
3
4
5
6
7
8
9
AMMOTRAGUS
NIVICOLA
DALLI
STONEI
CANADENSIS
CALIFORNIANA
NELSONI
TEXIANA
CREMNOBATES
MEXICANA
WEEMSI

FIGURE 100. Two subspecies of *Ovis ammon*. Lower, *orientalis* male and female; upper, *poli* male and female (after Walther 1961). Please note the shape and size of the rump patches; please compare these with those of American sheep (Fig. 101).

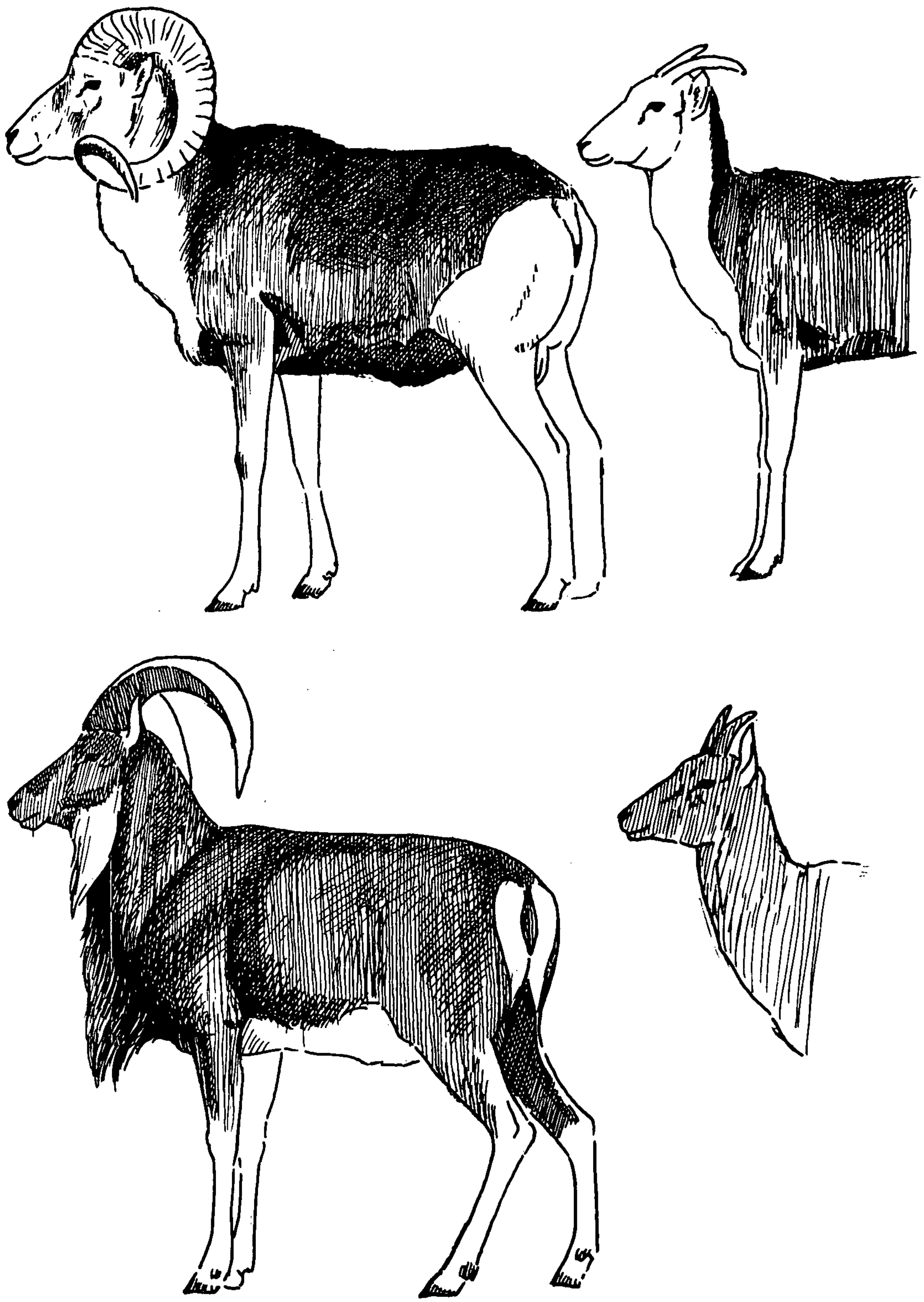


FIGURE 101. American sheep. Lower, _O. nivicola_ from Siberia. Next to it the white Dall's sheep (_O. dalli dalli_); to its left is the Stone's sheep (_O. stonei_). Above and to the right of the Dall's sheep is Nelson's bighorn (_O. canadensis nelsoni_) and the upper most sheep is the northern bighorn sheep (_O. canadensis canadensis_). It is the highest evolved _canadensis_ form, while _stonei_ represents the most advanced _dalli_ form. Both live in the formerly glaciated area. Note changes in rump patch, tail and horn size as well as the amount of white on the legs.

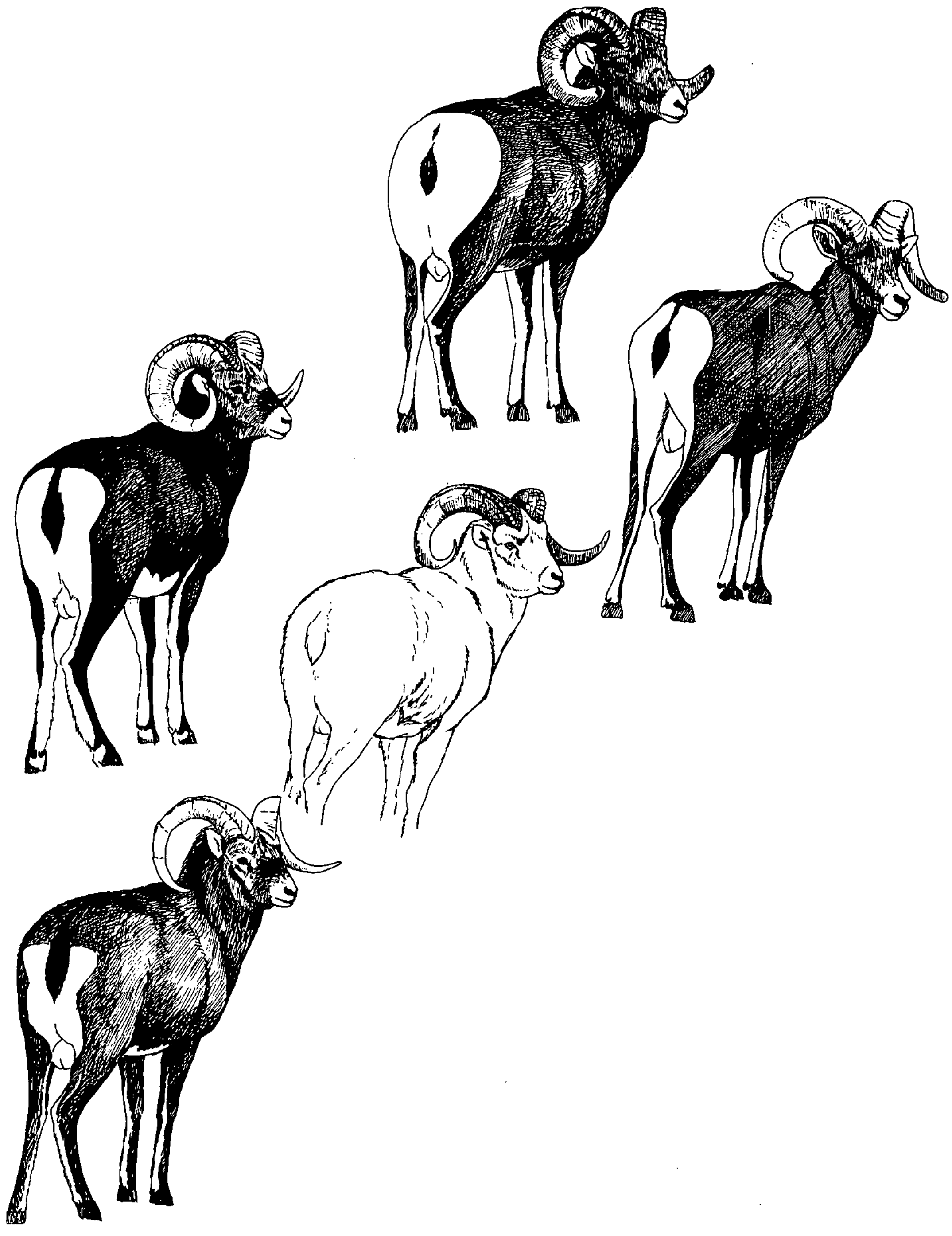


FIGURE 102. Frequency of butts and mounts per 100 interactions performed by males of various classes on females. As the males grow older, they butt and mount females less frequently; Lambs butt and mount most.

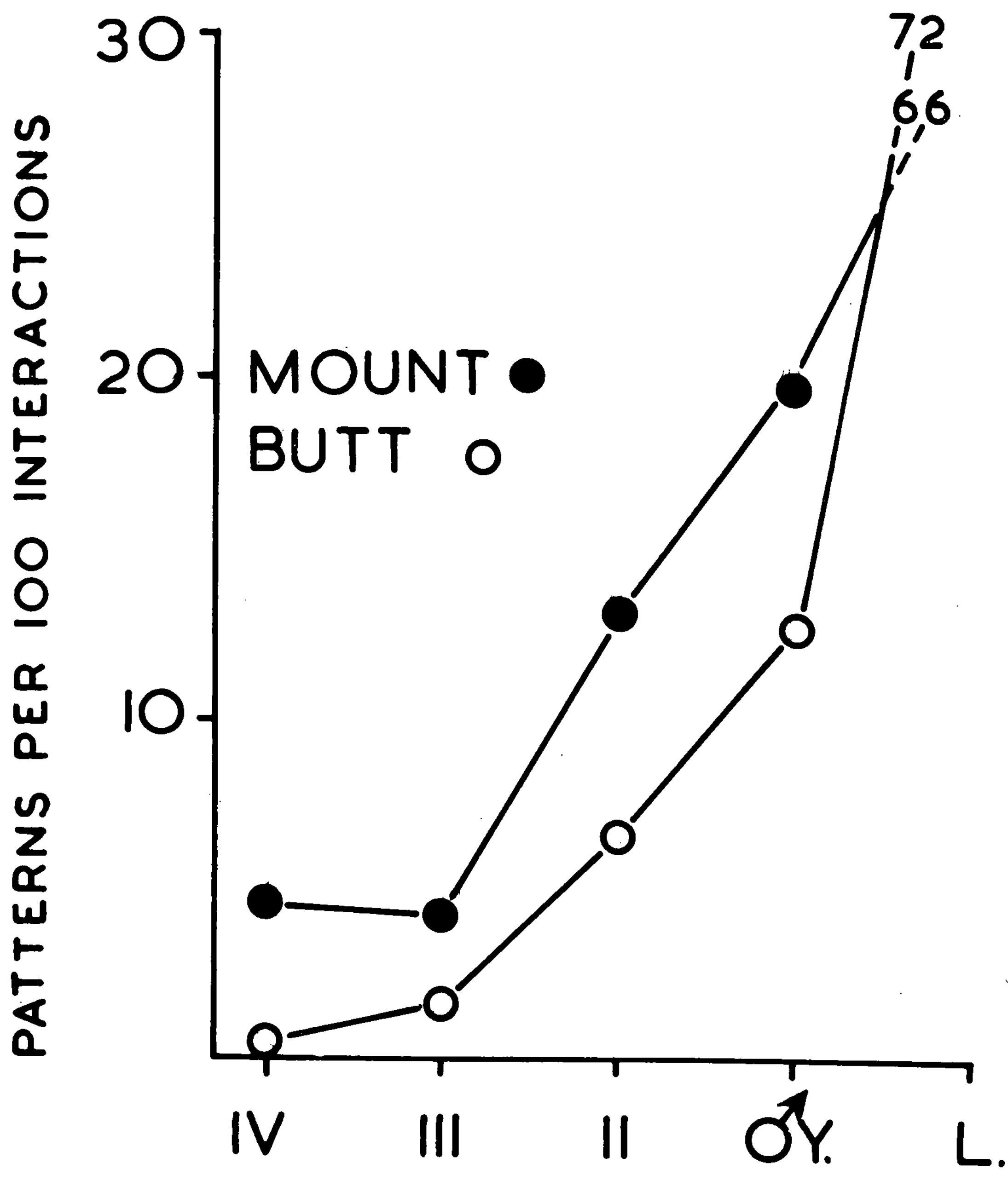
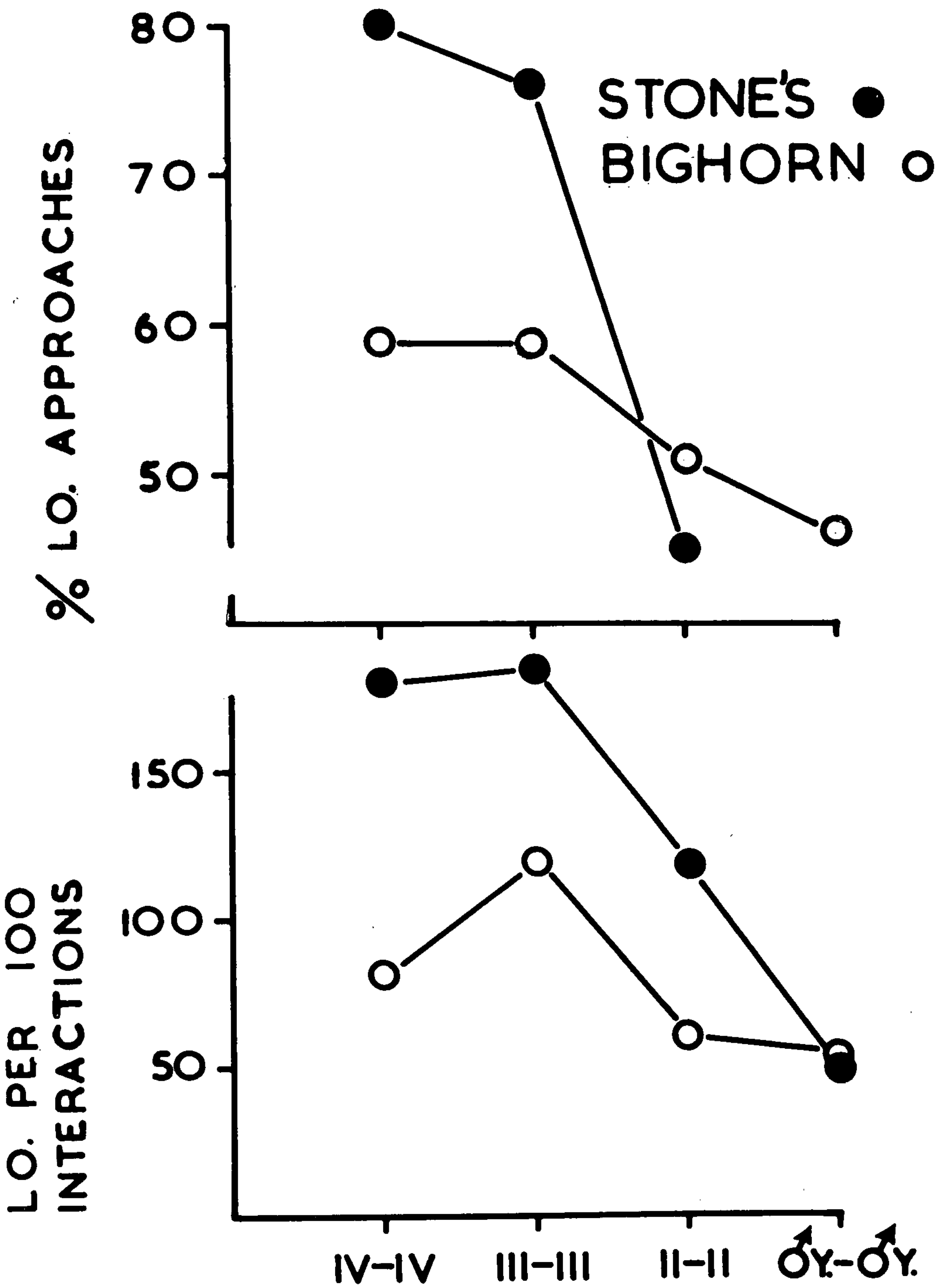

PATTERNS PER 100 INTERACTIONS
30
20
10
MOUNT ●
BUTT ○
72
66
IV
III
II
♂Y.
L.

FIGURE 103. A. Frequency of front kicks per 100 interactions performed by courting males on females. As rams grow older, they make greater use of the front kick.

B. same as A, except that it illustrates the use made of the twist. Rams use the twist increasingly more frequent with age. Please note that bighorn sheep used the twist more frequently than did Stone's sheep.



STONE'S ●
BIGHORN ○
% LO. APPROACHES
80
70
60
50
LO. PER 100 INTERACTIONS
150
100
50
IV–IV
III–III
II–II
♂Y.–♂Y.

FIGURE 104. A. Percent frequency with which rams of various size classes approached rams of their own size class in a low-stretch. Older rams approached their equals more frequently in low-stretch than did young rams.

B. Frequency with which low-stretches were performed within interactions of equal sized rams. Note that bighorn rams interacted less intense than Stone's sheep.

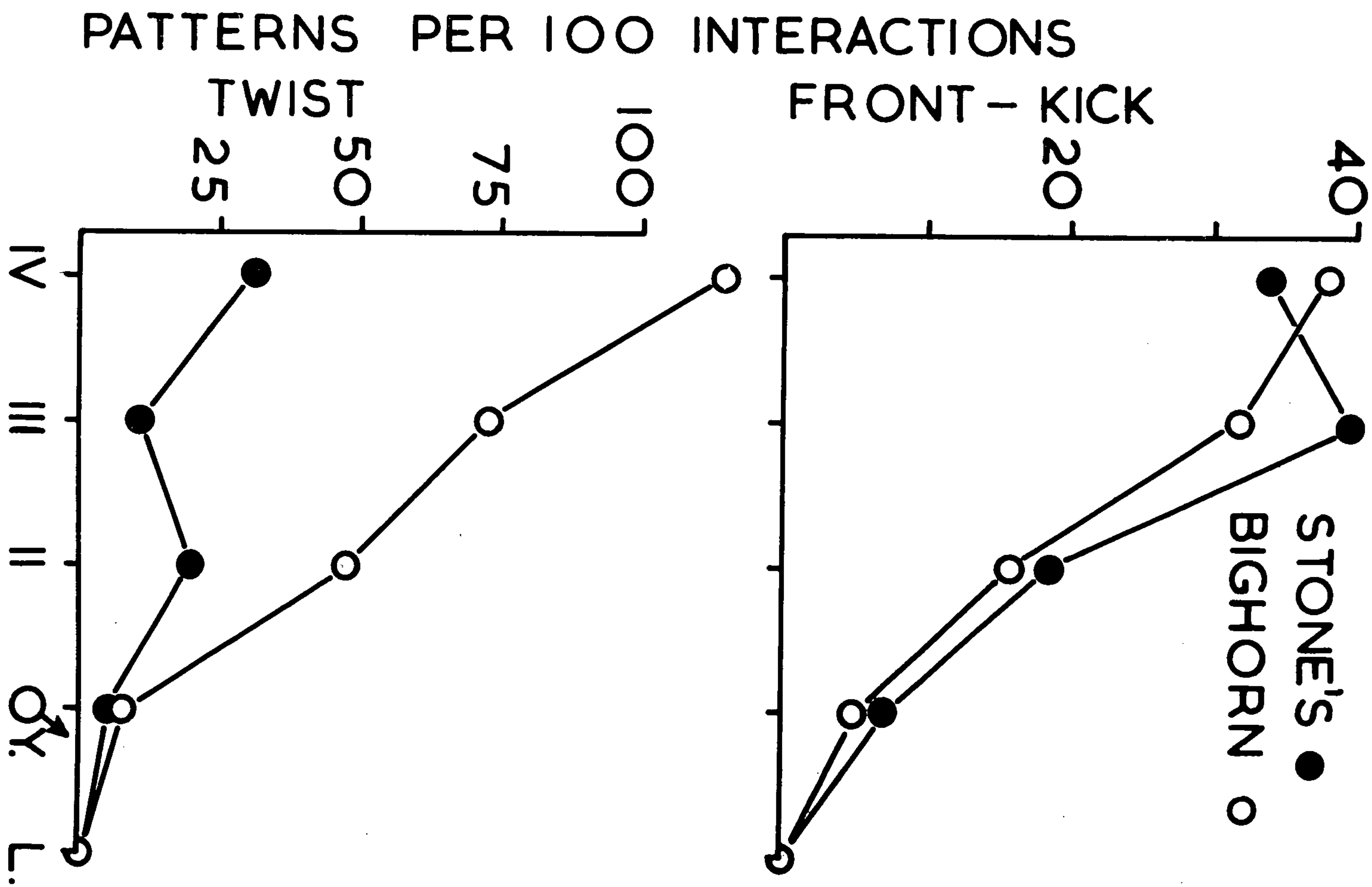

PATTERNS PER 100 INTERACTIONS
TWIST
FRONT-KICK
100
75
50
25
40
20
IV
III
II
Y.
L.
STONE's ●
BIGHORN ○

FIGURE 105. Horn segment growth on a Dall's ram (from Murie 1944) and a bighorn ram. The Dall's ram grows most horn early in life, the bighorn grows it a little later.

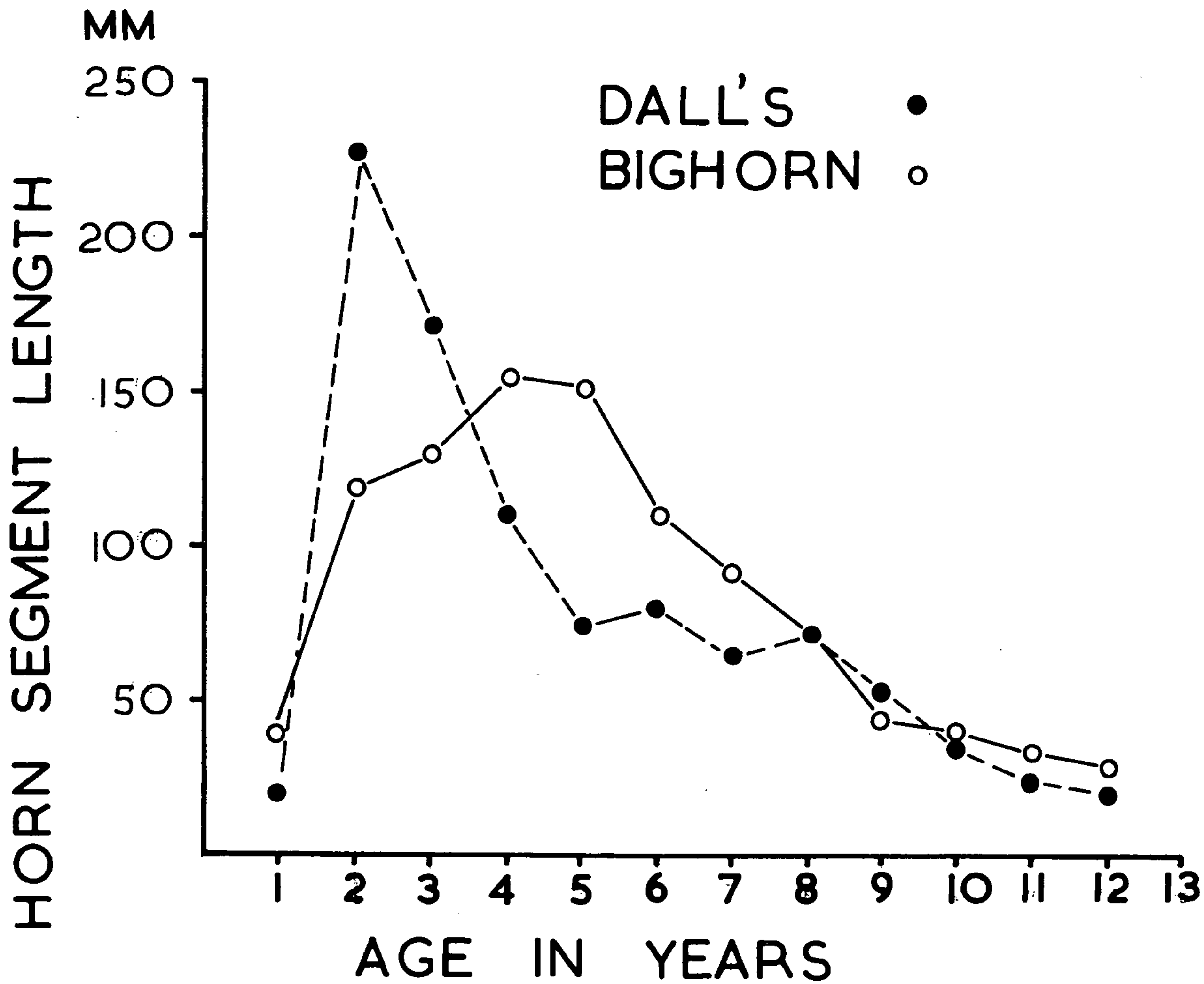

MM
250
200
150
100
50
HORN SEGMENT LENGTH
DALL'S
BIGHORN
1
2
3
4
5
6
7
8
9
10
11
12
13
AGE IN YEARS

FIGURE 106. Intensity of social interactions as indicated by the frequency of front kicks, in the interactions of equalsized rams. The 6-8 year old III rams interacted most vigorously.

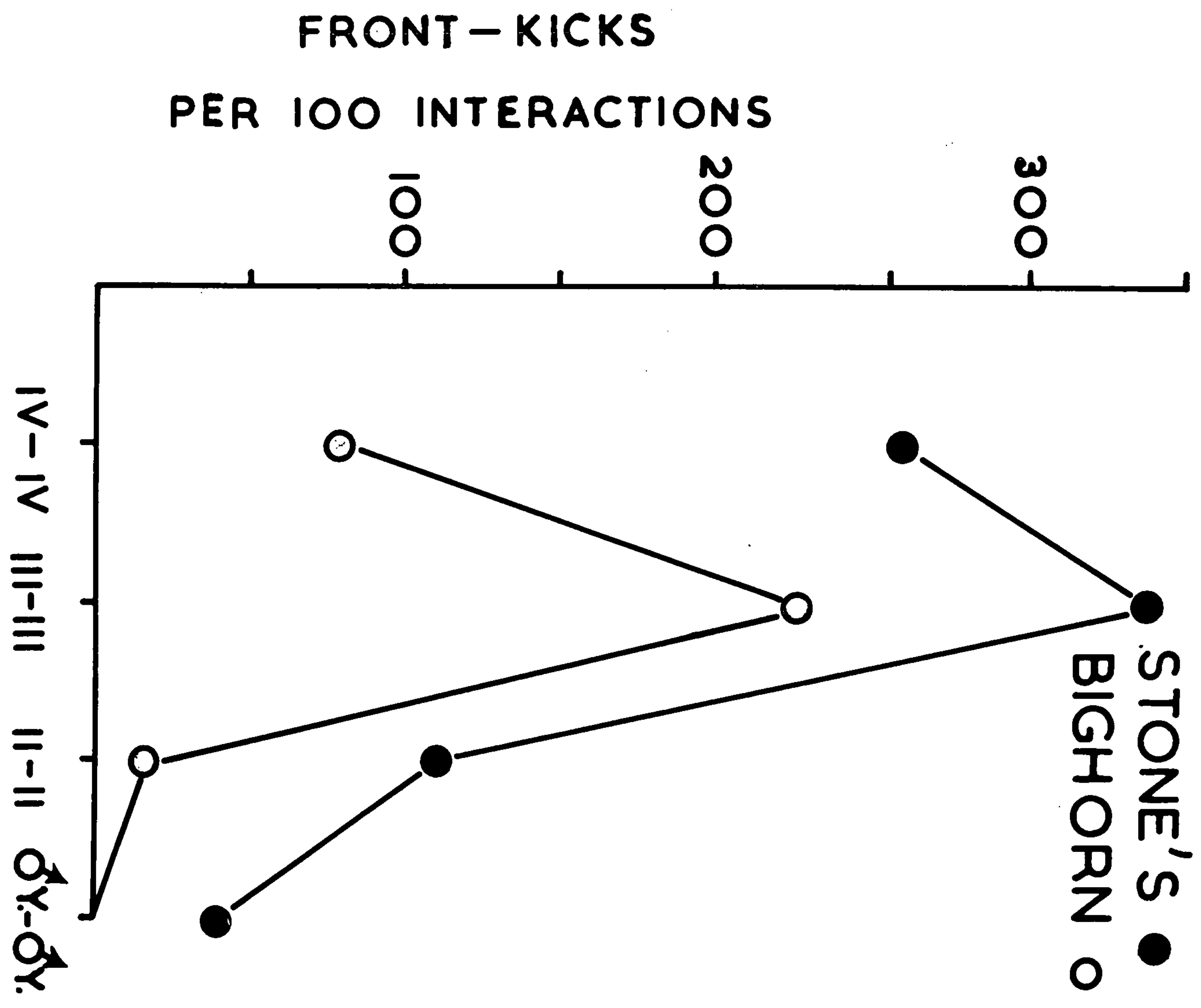

FRONT-KICKS
PER 100 INTERACTIONS
100
200
300
IV-IV
III-III
II-II
♂Y.-♂Y.
STONE'S ●
BIGHORN ○

TABLE I. Weights and measurements from two Stone's sheep. (p. 6)

| | Age Yrs. | Live Weight | Total Length | Hind Foot | Tail | Ear | Shoulder Height | Chest Girth |
|---|---|---|---|---|---|---|---|---|
| RAM | $6\frac{1}{2}$ | 170 lb. | 58" | $17\frac{1}{4}$ | 4 | $3\frac{3}{4}$ | 40 | 44 |
| EWE | 16+ | 135 lb. | 51" | $15\frac{1}{4}$ | 4 | $3\frac{3}{4}$ | 35 | 40 |

TABLE II. Frequency with which members of various sheep classes were seen without company. (p. 144)

Bighorn sheep (Banff Park - 1964-65, all season)

| Class | IV | III | II | I | oy | o |
|---|---|---|---|---|---|---|
| Average age (in yrs.) | 11 | 7 | 5 | 3 | 1 - 2 | ---- |
| Total no. seen | 1796 | 985 | 1880 | 366 | 410 | 1907 |
| No. seen single | 116 | 56 | 71 | 9 | 7 | 29 |
| % seen single | 6.5 | 5.75 | 3.8 | 2.4 | 1.75 | 1.52 |

TABLE III. Leadership in bighorn rams (Banff Park, 1963-65) Based on 95 bands of rams (543 individuals) observed during major movements (p. 144)

| Classes of rams | IV | III | II | I |
|---|---|---|---|---|
| Number of bands containing the following classes (A). | 73 | 59 | 82 | 33 |
| Number of bands in which rams of the following classes were leading (B). | 71 | 15 | 7 | 2 |
| % of bands in the following classes were leading ($\frac{A}{B}$ x 100) | 97.5 | 25.0 | 8.5 | 6.0 |
| Number of rams led by the following classes (C) | 437 | 81 | 20 | 5 |
| % of rams led by the following classes ($\frac{C}{543}$ x 100) | 80.5 | 15.0 | 3.8 | 0.9 |
| Average size of band following leaders of the following classes ($\frac{C}{B}$) | 6.15 | 5.4 | 2.9 | 2.5 |

TABLE IV. Frequency of aggressive patterns in the interactions of large rams on small ones in the "normal" situation. A Comparison of Stone's and bighorn sheep. (Agressive patterns quantified = clash, butt, horn-threat and threat jump). (p. 146)

| Classes | Stone's sheep | Bighorns |
|---|---|---|
| | (all rams except yearlings) | |
| Number of interactions | 420 | 228 |
| Number of aggressive patterns | 72 | 66 |
| Number of patterns per 100 interactions | 17.1 | 29.0 |

(t = 3.7, difference in proportions extremely significant $P < .001$)