SOCIAL BEHAVIOR OF THE AOUDAD (*AMMOTRAGUS LERVIA*) IN HONDO VALLEY, NEW MEXICO

By

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ABSTRACT

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Since its introduction in the Hondo Valley in the early 1940s the aoudad population has expanded and dispersed into much of southeastern New Mexico. Despite its ability to occupy new ranges, the population has not been studied previously on its original range.

A population estimate by direct count was made on 12 randomly-selected plots. The calculated mean density of 6.4 animals/km^2 indicated a total of 615 animals on the 96 km^2 study area. A complementary Lincoln-Petersen census in January-February 1982 yielded a similar density of 5.8/km^2. The sex ratio of 42.5 adult males per 100 adult females, obviously was much skewed toward females. While the disproportionate sex ratio may partially reflect the effects of hunting, it may more reasonably be a result of male emigration.

Between September and November, males of all age classes were present on the rutting grounds. A total of 22 aggressive and sexual patterns were recognized. The hypothesis that interactions among the various sex-age

classes occurred at random and was independent of group composition was rejected. In the presence of dominant rams, subordinate males were effectively inhibited from interacting with females. A system of linear hierarchy based on horn size was established with the large-horned males enjoying a reproductive advantage and contributing importantly to the gene pool.

The behavioral repertoire of the aoudad included patterns common to both goats and sheep. Based on its behavioral characteristics, the aoudad evidently is in an intermediate position between the two groups.

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INTRODUCTION

The aoudad (Ammotragus lervia) was introduced in the Hondo Valley, New Mexico in the early 1940s. Originally released in the 770 ha. McKnight game pasture the animals have escaped from the fenced area on a regular basis and have established a free-ranging population in the Hondo Valley. Although scattered throughout the valley on several private ranches, the population is mainly concentrated on the South Ranch of the Diamond A Cattle Company (Figure 1).

Displaying exotic vigor and finding conditions suitable for expansion, the species has dispersed into many parts of southeastern New Mexico. Despite its ability to expand rapidly in newly occupied ranges, the aoudad population in the Hondo Valley has not been studied previously.

The aoudad has physical attributes related to both goats (Capra) and sheep (Ovis). In discussing the morphological and behavioral characteristics of the aoudad Geist (1971, p. 329) stated: "Ammotragus could serve not only as an exemplary ancestor of sheep, but also make a passable ancestor for goats, at least the round-horned forms... Ammotragus combined a number of goatlike characteristics and can be linked with intermediate forms not only to the argalis but also to ibex".

In general behavior, the various species of the Caprini tribe seem to behave in much the same way. When specific display and other sexual and aggressive traits are compared, however, certain differences in their behavioral repertoire appear to distinguish the two main Caprini genera. The aoudad diverged from the goat stock sometime in the Pliocene when it occupied the Atlas massif of North America. Radiating into the monotypic Ammotragus genus, it retained certain characteristics common to both Capra and Ovis while developing certain unique traits.

Previous work on the aoudad social behavior has been restricted to studies of captive herds (Katz 1949, Haas 1959, Hamdy and Schmidt 1972). To complement these investigations with an analysis of the behavior of a free-ranging aoudad population, the present research was undertaken. The principal objectives of the study were 1) to assess population size and structure 2) to study the qualitative and quantitative aspects of aoudad behavior patterns which govern social status, and 3) to undertake ethological comparisons between Ammotragus and other Caprid species.

STUDY SITE

Location

Since their release in the Hondo Valley four decades ago, aoudads have spread throughout the Hondo Valley system but the main portion of the population is located in the 22,400 ha. South Ranch of the Diamond A Cattle Company. Under a grant generously provided by Mr. Robert O. Anderson, the aoudad population of this area was studied from July 1981 to December 1982.

The study site lies 70 km. west of Rosewell at 33°15' north latitude and between 105° and 105°15' east longitude on rolling hills south of the Hondo River (Figure 1). The site lies in the southeastern corner of Lincoln county in southeastern New Mexico. Elevations on the area range from 1520 m. in valley floors to 1700 m. on ridge summits.

Prior to the introduction of cattle in the Hondo Valley in mid 1960s, much of the land was established in apple orchards. With a change in ownership, the orchards were abandoned and devoted to cattle pastures. Except for three months in winter, the fields are irrigated using water from the Rio Hondo and a number of deep wells. About 1000 cattle (H. Talley pers. comm.) of the Diamond A Cattle Company occupy the ranch. The majority are restricted to the Hondo Valley but some are seasonally grazed on the valley floor of Casey Canyon (Figure 2). About 4000 domestic

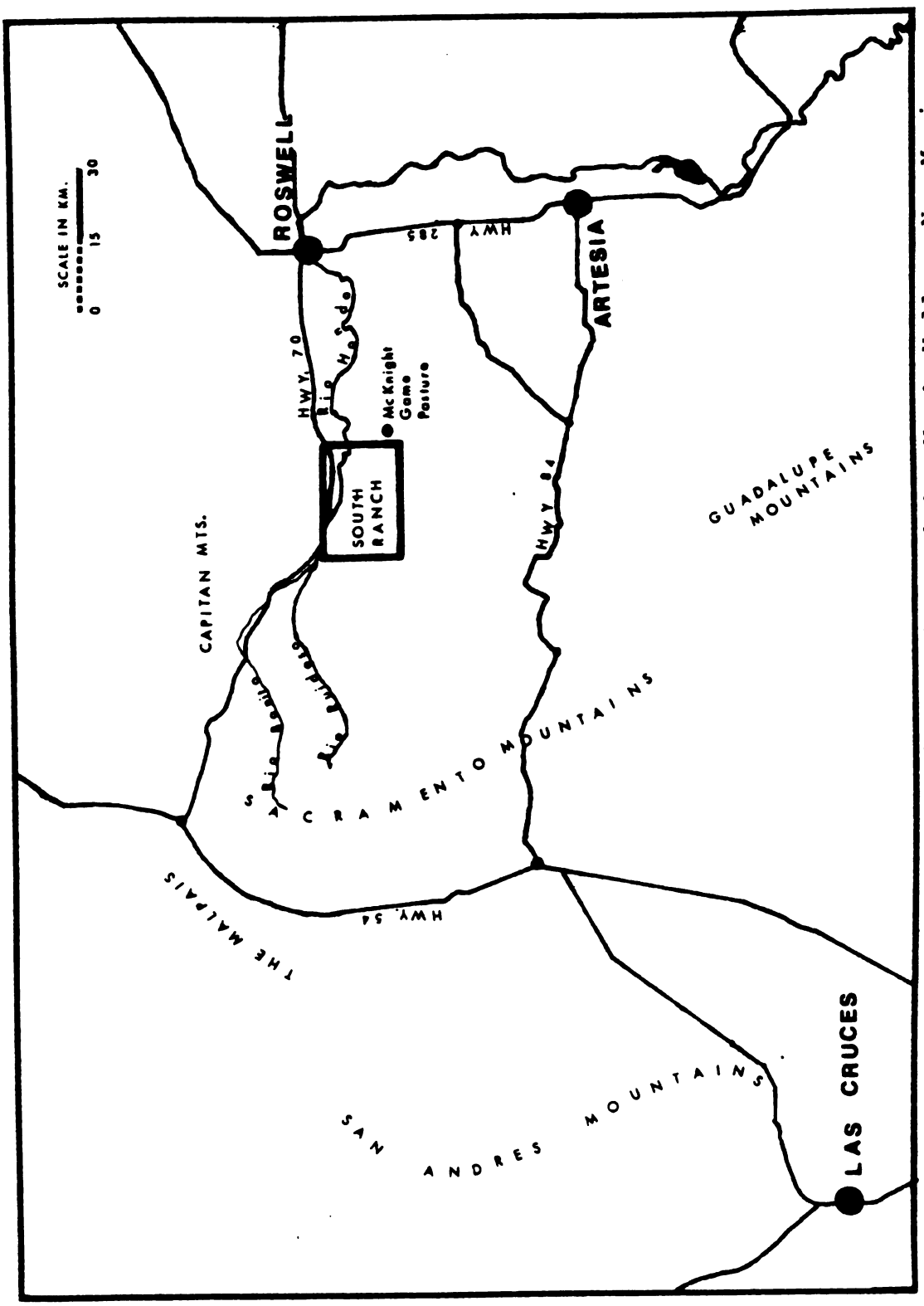

Figure 1. Map of study site location of the aoudads, Hondo Valley, New Mexico.

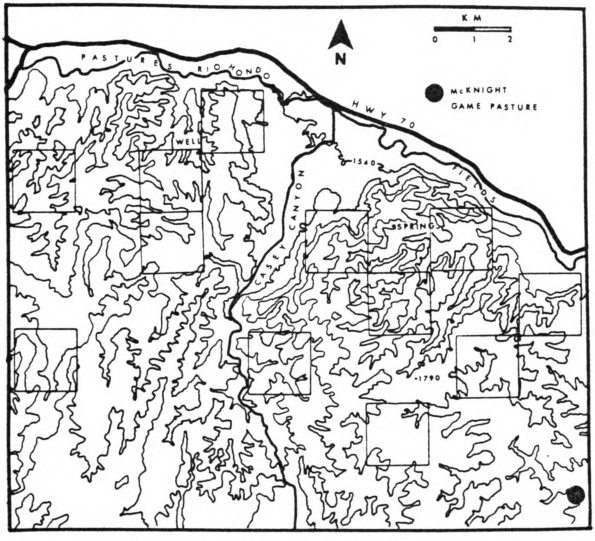

Figure 2. Map of study site, Hondo Valley, New Mexico. Squares show the plots where direct counts were made.

sheep are raised on upland portions of the ranch and share the range in sympatry with aoudad and mule deer.

Climate

The area has a semi-arid climate with hot summers and relatively mild winters. Most precipitation takes place as rain during July-September (Figure 3). During rest of the year, the climate is dry with relatively low humidity. Snow occasionally occurs during winter months but usually melts within 2-3 days. Average temperatures in the area range from 8-19 ^{o}C with high winds during the spring months. Mean precipitation is 30-40 cm. with the higher elevations receiving more rainfall than the low-laying valley floors. The frost free period range is 150-190 days annually.

Topography and Soils

On the study site, hills rise 200-300 m. from the valley floor. They are incised by streambeds which are dry throughout the year and harbor only occasional flash floods during the main rainy season. Slope grades on hillsides vary between 15 and 50^{o}. Rock outcrops increase toward the hill summits and in some places form steep bluffs. Little vegetation grows on these outcrops.

Rio Hondo, the main stream draining the area is formed by the junction of the Rio Bonito and Rio Ruidoso. These rivers have headwaters in the Sacramento mountains west of

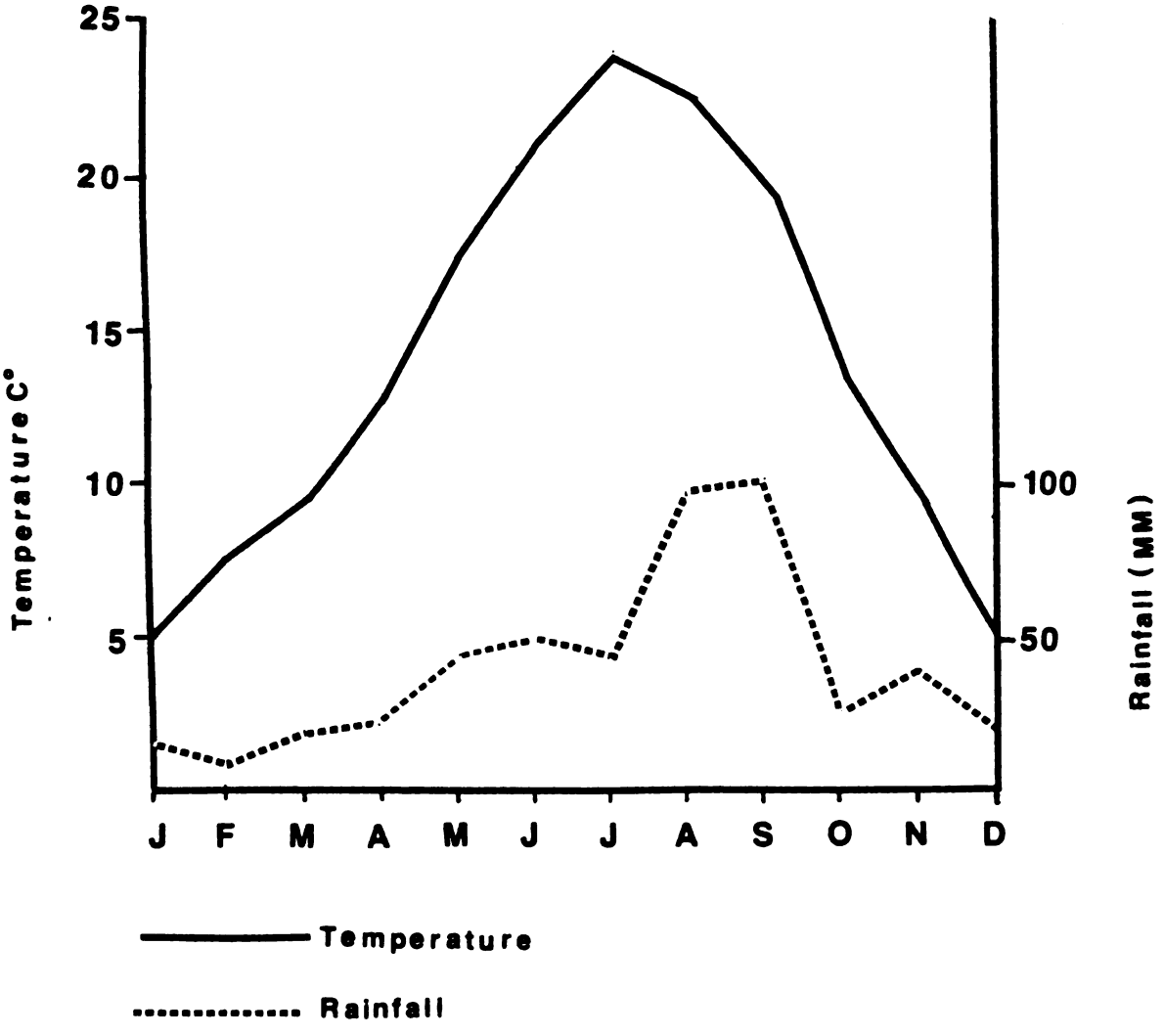

Figure 3. Average monthly temperatures and precipitation (1976-1981), Hondo Valley, New Mexico. (Climatological data, Vol. 80-85. United States Department of Commerce).

the study site. The Capitan mountains to the north contribute relatively little water to the Hondo. The study site lies on layered San Andreas limestones of Permian age. An underlying formation of rocks also of Permian age is exposed in the stream valleys (Hall 1964).

Deama loam is the soil type predominating in the area and covers 15-50% of the slopes. This soil is well-drained and only about 17 cm. deep. Hazards from water runoff is high but the danger of wind erosion is slight. Other major soil types are Harvey, Dioxice and Pena present on hillsides and valley floors. The topsoil on summits is Pastura (Sprankle 1980).

Vegetation

The study site was vegetated largely by the desert grassland association (Martin 1964). These grasslands, growing mainly between 1370 and 1820 m. elevation, were almost treeless but supported a number of shrub species and many forbs. On the slopes, a mixed shrub-grass cover type included mountain mahogany (Cercocarpus montanus) which dominated the slopes. Wavyleaf oak (Quercus undulata), beargrass (Nolina texana), sotol (Dasylirion wheeleri) and several leguminous shrubs including catclaw acacia (Acacia greggii) and sagebrush (Artemesia filfolia) also were present. Threeawns (Aristida spp.), hairy grama (Bouteloua hirsuta), sideoats grama (Bouteloua curtipendula), sand

dropseed (Sporobolus cryptandrus), metcalf muhly (Muhlenbergia metcalfei), green sprangletop (Leptochloa dubia) and plains lovegrass (Eragostis intermedia) were the main grasses found on slopes. Broom snakeweed (Xanthocephalum sarothrae) was a common broad-leaved herb.

On the valley floors, streambeds were bordered by dense thickets of such shrubs as skunkbush sumac (Rhus trilobata), little-leaf sumac (Rhus aeromata), honey mesquite (Prosopis glandulosa), four-winged saltbush (Atriplex canescens), Apache plume (Fallugia paradoxa), prairie mimosa (Mimosa desmanthus), barberry (Berberis haematocarpa) and netleaf hackberry (Celtis reticulata). Clustered among the shrubs were coarse clumps of alkali sacaton (Sporobolus airoides). These were 2 m. tall in some places.

Cane cholla (Opuntia imbricata) and Englemann pricklypear (Opuntia phaeacantha) formed dense cactus thickets on disturbed sites, ridge summits and near water sources in valley floors. Mat muhly (Muhlenbergia richardsonis) grew beneath the cacti.

Grasses were abundant throughout the range but were mixed with shrubs. Only a small portion of the valley floors were covered mainly with grasses and only a few scattered shrubs. Such areas were dominated by sixweeks grama (Bouteloua barbata), sideoats grama, blue grama (Bouteloua gracilis) and hairy grama. Some of the other major grass

species were threeawns and green sprangletop (Leptochola dubia). Giant sacaton (Sporobolus wrightii) grew abundantly in bottomlands and flats subject to flooding.

Although the area was mainly dry, many herbaceous plants bloomed during the late summer months when the range received its main annual precipitation. Some of the more spectacular flowers found in the valleys were bladderpod (Lesquerella gordonii), spectaclepod (Dithyrea wislizenii), tufted evening primrose (Oenothera caespitosa), silverleaf nightshade (Solanum elaeagnifolium), Indian paintbrush (Castilleja confusa), bigelow aster (Aster bigelovii), several species of sunflowers (Helianthus spp.) and various locos (Astragalus spp.)

THE POPULATION

History of Introduction and Hunting

The aoudad is endemic to the Atlas massif of North Africa (Brentjes 1980). Fossil records of the species date back to the Pleistocene fauna in the Atlas massif (Vaufrey 1955 in Gray 1980). Remains of Ammotragus have also been found at Haua Fteah cave in the northern coast of Cyrenaican Libya dating back almost 85,000 years (McBurney 1967). Bate (1955) has mentioned the presence of aoudad remains from Quarternary deposits in Cyrenaica.

Live specimens were brought to the United States at the beginning of the twentieth century and maintained in zoos as an exhibition animal. As its numbers increased in captivity, surplus animals were harvested as food for large carnivores (Yoakum 1980). In the 1920s, surplus animals were procured by private land owners and released on the Hearst Ranch at San Simeon in California.

The first release of aoudads in New Mexico was in 1940 on the private game pasture of Joe McKnight, 6 km. south of Riverside. There, 3 males and 4 females, obtained from the St. Louis and San Diego zoos, were placed in a fenced enclosure (J. McKnight, pers. comm.). Despite efforts to contain them, the aoudad herd increased rapidly and some animals escaped. Two large escapes took place in

1965 (approximately 100 animals) and 1977 (approximately 50 animals). In addition, an average of 10-20 aoudads escaped from the pasture annually since their introduction. Today, the population has spread over 500 km^2 in the Hondo Valley and adjoining valleys. The group has extended its range from the Hondo Canyon to the foothills of the Capitan Mountains (Figure 1).

Hunting of free-ranging aoudads was started in 1967. A total of 379 animals of both sexes (69.66% males and 30.34% females) were reported by the New Mexico Game and Fish Department to have been harvested since the beginning of official hunting seasons until 1981 (Saiz 1981). The actual number of animals taken is believed to be higher since hunts conducted in 1980-81 on the South and McKnight ranches were not documented in the report. During that period 22 rams (T. Dickinson pers. comm.) were killed by hunters on the South Ranch and 17 ewes and rams (J. McKnight pers. comm.) were taken on the McKnight Ranch. Other animals were also taken on nearby ranches during the December 1981 season.

Other introductions in New Mexico include 57 aoudads released in the Canadian River gorge in 1950. Five years later 21 animals were released in Canyon Largo near Farmington. Both populations are believed to have thrived and expanded their range since their transplantation (Morrison 1980). Moreover, as a result of range expansion

aoudads have dispersed from the Hondo Valley and have colonized parts of the Guadalupe Mountains (Dickinson and Simpson 1980).

In the Palo Duro Canyon of the Texas Panhandle, aoudads released in 1957 and 1958 also have shown a tremendous increase in numbers. Recent estimates (Dvorak 1980) indicate that over 1500 animals inhabit the canyon rims.

Population Size and Density

The aoudad population in the Hondo Valley has only been studied through some aerial surveys intended to ascertain the density of the population in various localities in New Mexico. The attempt was made in this study to gather more-precise information on the size and structure of the Hondo population. The first few weeks were spent with familiarization with the area and in the establishment of techniques. From the preliminary surveys, it became evident that the main concentration of aoudad groups was on 96 km^2 of the South Ranch. Designated as the study area, that area's boundaries were demarcated on a topographic map and the tract divided into 37 approximately-equal square units. Using landmark features as guides, the location of each of these plots was determined. Population variance was determined by a preliminary investigation

and the number of plots required for a census survey were determined by the formula (Snedecor 1956):

$$n = \frac{1}{\frac{E^2}{t^2 s^2} + \frac{1}{N}}$$

where

n = sample size
N = total square kilometers being sampled
s = standard deviation
E = error allowed (arithmetic mean times designated fractional accuracy)
t = normal deviate at confidence limit level and degrees of freedom (from t table)

Each 2.56 km^2 sampling unit was surveyed by walking in a zig-zag pattern along ridgetops. Care was taken to visit overlooks throughout each plot. From ridge viewpoints, it seemed possible to sight all animals present on the plots. Following the preliminary sampling, foot-traverses over 12 of the 37 plots (Figure 2) were undertaken during August 1981 to establish a direct-count estimate (Seber 1973) of the aoudad population on the study area. On the 12 plots surveyed, 37 aoudad groups totalling 209 animals were observed. Based on the derived mean population density of 6.4 animals/km^2, the aoudad population for the entire 96 km^2 study area was projected (with 95% confidence limits) to be 615 ± 179.

An additional population survey was made in January-February 1982 using the single mark-recapture method (Seber 1973). At that time 13 aoudads were collared and 1002 animal-observations made at random throughout the study site. These data resulted in a population estimate of 560 (± 184 at 95% confidence limits) or 5.8 aoudads/km^2. (Replication of collared-animal sightings were known to have occurred but presumably were paralleled by similar replications of non-collared individuals).

Based on fecal pellet counts, Ogren (1965) estimated an average density of 2.37 aoudads per km^2 in the Canadian River gorge of northeastern New Mexico. Simpson et al. (1978) reported that in the Dry Creek branch of Palo Duro Canyon, Texas only about 50% of his marked radio-collared aoudads were counted during repeated helicopter surveys. After applying a correction factor, therefore, Gray (1980) estimated the mean density of aoudads in that canyon to be 2.2 animals per km^2. Confidence limits are not available for the works of Ogren and Gray but, if the differences are statistically significant, the density of aoudads in the Hondo Valley is much greater than in the two other areas.

Sex and Age Categories

Age and sex classes were differentiated on the basis of dimorphic behavioral characteristics and variation in

body, neckruff and chap length sizes.

Young-Juveniles (Figure 4). Young-juveniles were easily recognized by their small size and by horns shorter than ear length (under 10 cm.). Ages of this class ranged from birth to about 4 months. Members of this class were not separated by sex. Although Solbert (1980) stated that it is possible to sex lambs from urination postures, this criterion was not found to be reliable in the field.

Older-Juveniles (Figure 4). For these juveniles, horn length was longer than 10 cm. but less than 2x ear length. These animals ranged in age from about 4 to 8 months. At close range, the presence or absence of the penis was a useful sex indicator. Animals of this class could not be easily segregated by sex, however, when observation-distances ranged over 200 m.

Subadults (Figure 4). Aoudads are sexually mature before the start of their second year (Blunt 1963). Animals which had not attained adult body size but which had horn lengths ranging from 20 to 30 cm. were classified as subadults. Subadults ranged in age from 9 to about 15 months (Gray and Simpson 1980). They could be recognized by sex on most occasions by horn and body size. The horns of males were more massive at the base; the distance between the horn bases appeared to be greater in females. Males also had longer and more-abundant neck-ruff and chap hairs.

Young-juvenile

Older-juvenile

Sub-adult male

Adult female

Figure 4. Relative horn size of a young-juvenile, older-juvenile, sub-adult male and adult female. Drawn from slide transparencies.

They were somewhat larger than females, too, and were stockier in the forequarters.

Adult females (Figure 4). Adult females had horn lengths ranging in size from 30 to about 50 cm. They were easily distinguished from adult males by their smaller body size, narrower horns and shorter and less-dense neck-ruff and chap hairs. Since females with large horns possibly could be mistaken for Class I males, the presence or absence of the scrotum also was ascertained.

Adult males were divided into four classes as defined by Gray and Simpson (1980):

Class I (Figure 5). The horns of this youngest of adult male class were between 30 and 50 cm. long. Individuals ranged in age from 16 months to about 2.5 years.

Class II (Figure 5). Members of this category had horn lengths 50 to about 66 cm. and were approximately 2.5 to 4 years old.

Class III (Figure 5). These were the largest males observed on the Hondo Valley range. Their horn lengths varied from 66 to about 76 cm. in length. By age, they were 4 to about 6.5 years old.

Class IV (Figure 5). Males of this category are distinguished by horn length in excess of 76 cm. and are 6.5 years and older. No individuals in this category were observed during the present study.

Class I

Class II

Class III

Class IV

Figure 5. Relative horn size growth in four classes of adult aoudad males. Note heavy transverse bands indicating age. Drawn from slide transparencies.

Population Structure

Males started arriving on the female ranges, which also were the rutting grounds, in early August. This movement was initiated by Class I rams but was soon followed by the larger males. By the beginning of September, most adult males were present on the rutting grounds. Since most rams had departed from ranges occupied by females between December and July, population structure was best ascertained during the main September-November rutting season.

On the area studied, juveniles comprised the largest category in the aoudad population. They were followed by adult females, adult males and subadults (Table 1). In a hunted population during 1979 on the Dry Creek portion of Palo Duro Canyon, Texas, Gray (1980) found 26.4% juveniles, 3.7% subadults, 20.2% adult males and 49.9% adult females. Barrett (1980) determined that the Red Rock herd on the Hearst Ranch in California was comprised of 7.1% males, 5.9% subadults, 17.5% juveniles and 69.4% females in 1965. In all cases the proportion of subadults is low. Either there is high mortality among the juveniles or some animals of this age class may be mis-assigned to the adult age class. The second possibility is judged to be the more likely one though no supporting evidence was found in the present study.

From field observations of adult aoudads on the study

Table 1. Sex and age categories in a hunted population of aoudads sighted during the main rutting season (September-November). Hondo Valley, New Mexico.

Year	Adult males	Adult females	Subadults	Juveniles	Total Observations
1981	265 16.2%	550 33.7%	183 11.2%	634 38.9%	1632
1982	309 13.3%	829 35.6%	307 13.2%	885 37.9%	2330

area, the sex ratio was skewed toward females (X^2=30.41, p◄0.01). The sex ratio was 48 males:100 females in 1981 and 37:100 in 1982. The 42:100 average of these ratios is close to the 40:100 reported by Gray (1980) for Palo Duro Canyon aoudads in 1978-79. The unequal sex ratio in adult animals seems likely to be due both to trophy hunting and to the tendency for dispersal and range extension by males (Dickinson and Simpson 1980).

During April and May 1982, 385 juveniles were observed. Of these the sex of 67 males and 72 females was identified by the presence or absence of a penis. These determinations were made at close distance by means of a 20-45x spotting scope from a vehicular blind. The juvenile sex ratio was balanced with no significant inequality in the observed ratios (X^2=0.210, p►0.10).

From the age distribution of 278 females, ascertained by means of counting the annular horn rings of the animals in the field with a high powered spotting scope, a pyramid of age structure was constructed (Figure 6). Of these, 77.6% were under two years of age. Again, a large proportion of young animals in the population was indicated.

Natality

In their native North African habitat, aoudads are reported to lamb mainly in early spring (Asdell 1964).

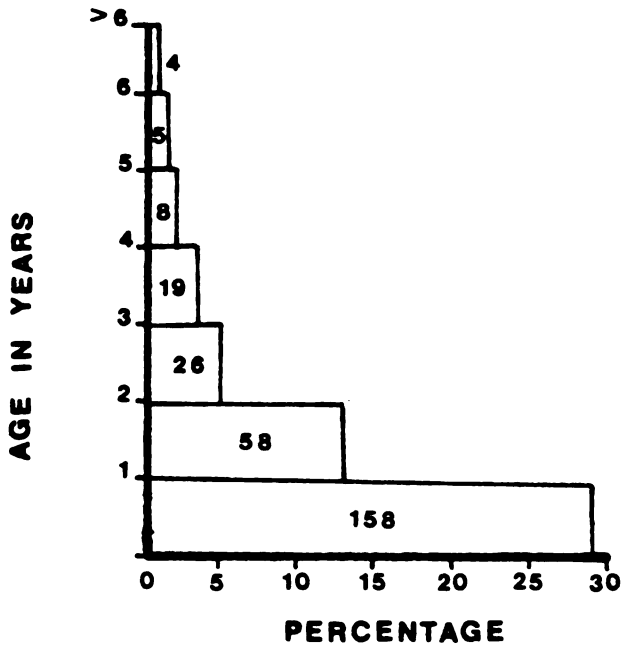

Figure 6. Age distribution of 278 female aoudads in Hondo Valley, New Mexico, April-May 1982. The numbers in the boxes indicate the total number of animals counted in each age category.

Gray (1980) noted that about 70% of neonates were observed in March and April in the Palo Duro Canyon. The gestation period lasts 22 to 23 weeks (Brown 1936, Labanov and Treus 1971).

On the South Ranch in 1982, four young which seemed to be only a few days old were observed with their mothers on 22 February. The main lambing period continued until mid-May (Table 2) with 85.8% of the year's young being born. Parturition slowed between June and August, with only 5 newborns observed during the summer months. In September, 17 neonates (9.2%) were observed, while one female gave birth to twins during the first week of October. The animals seemed to have two birth pulses but no animals were born during the coldest season (Table 2).

Ample forage was available for lactating females both in spring and fall. Estrus may be stimulated by external cues such as photoperiodism and temperature (Bissonnettee 1941, Hafez 1952, Sadleir 1969).

Aoudad neonates tended to remain close to their mothers during the first 5-6 weeks of life and were capable of following their mothers over the roughest terrain. From March to May, 549 young-juveniles were sighted, including 79 pairs of twins (Table 3). Thus twins comprised approximately 28% of the spring crop.

Table 2. Number of newborn aoudads seen. Hondo Valley, New Mexico, 1982.

Sampling Period	Frequency of births	Percentage
January	1	0.6
February	13	7.1
March	82	44.8
April	45	24.6
May	17	99.3
June	1	1.1
July	2	0.6
August	3	1.6
September	17	9.2
October	2	1.1
November	-	-
December	-	-
TOTAL	183	100.0

Table 3. Twinning ratios in young-juveniles observed during the spring lambing season, 1982, Hondo Valley, New Mexico.

Sampling period	Total Juveniles	Twin Pairs	Percentages born as twins
March	246	34	27.64
April	199	31	31.15
May	104	14	26.92
TOTAL	549	79	28.71

Dispersal

Originally introduced on the McKnight game pasture (Figure 2), the aoudad population has spread throughout the Hondo Valley with the main concentration being on the South Ranch in valleys adjacent to the fields along the Hondo River.

Onward movement among aoudads seems to be an innate behavioral trait. Dickinson and Simpson (1980) believed that dispersal of aoudads from an occupied range was initiated by rams, and only later followed by ewes and juveniles. The animals seemed to traverse long distances in random directions. They hypothesized that such dispersal enhanced the efficiency of colonization into suitable habitats and led to optimal range expansion.

From the Hondo Valley, the aoudad population has extended its range in different directions. To the south in the Guadalupe Mountains (Figure 1), the species has increased to over 550 animals (Yoakum 1980). Elsewhere as reported by ranchers aoudads have dispersed northward toward the Capitan Mountains. During a 1980 aerial survey, staff of the New Mexico Department of Game and Fish reported sighting an aoudad herd of 16 animals in the Malpais, almost 120 air km. northwest from the McKnight game pasture (Morrison, pers. comm.). During another survey, there also were reports of 5 aoudads southwest in the San

Andreas Mountains. Four of these animals, believed to have emigrated from the Guadalupe Mountains (Figure 1), were shot (Morrison 1980).

Distribution and Movements

On the South Ranch, the female segment of the population plus juveniles and subadults of both sexes, was divided into two sub-populations by a county road traversing Casey Canyon (Figure 2). Of the 10 collared females and juveniles, none was seen to travel from the eastern to the western side, nor did any of the four distinctively-recognizable females of the western section mingled with the eastern groups.

During the rutting season, adult males were seen to move frequently from one valley to another apparently in search of estrus females. Individually-recognizable males were seen to move within and between both segments of the female ranges. A Class II ram collared in the eastern Spring Valley on 20 October 1981, was observed in the Well Pasture of the western section a month later (Figure 2). On 13 January 1982, that animal was encountered again about 7 km. from the Well Pasture, 4 km. south of Spring Valley. Following the rut, he was seen in the range occupied by other adult males. Also in October 1982, a recognizable Class I ram with a blind left eye moved from Spring Valley to the Well Pasture. Two weeks later, he was observed in

Spring Valley again. Almost continual movements of rams during the rutting season seemed indicated.

In December, most adult males became segregated from the female bands. They remained in small groups in isolated valleys 2-4 km south of the female ranges until September. Since some births occurred in summer and autumn, however, some males must have visited female ranges occasionally during the spring months.

Major range segregation between rams and non-rams after the rut may serve to partition resources and to benefit the pregnant females and juveniles. While sexual segregation among the aoudads may have been a strategem which reduced intra-specific competition for food during a critical time of year, it was not possible to confirm that this result did ensue in the aoudads studied. Similar conditions also have been noted for Dall and Stone sheep (Ovis dalli)(Geist 1971), desert bighorn sheep (Ovis canadensis mexicana)(Lenarz 1979), Rocky Mountain bighorn sheep (Ovis canadensis canadensis)(Geist and Petocz 1977, Shank 1982) and for Marco Polo sheep (Ovis ammon poli) (Petocz et al. 1979). Segregation by sex among these and other Caprids, however, is still a poorly-understood behavioral trait.

SOCIAL BEHAVIOR

Introduction

The hypothesis suggesting a general relation between population control in animals and their social behavior was advanced by Wynne-Edwards (1959). The idea was later tested experimentally in the red grouse (Lagopus lagopus) and those studies indicated that the population density of these birds was indeed determined by their social interactions (Watson and Moss 1972, Wynne-Edwards 1978). Other researchers (Calhoun 1950, Southwick 1955, Wynne-Edwards 1962) have provided further evidence that social behavior, in particular aggressive behavior, takes an important part in regulating the size of animal populations.

By observing the behavior patterns of Stone, Dall and Rocky Mountain bighorn sheep, Geist (1971) formulated the hypothesis of population quality. According to Geist's hypothesis, animals from a high-quality population are socially more active, the greater level of activity being related to the high levels of forage-energy intake available to them. Shackleton (1973) tested this hypothesis in two populations of bighorn sheep and concluded that animals of both sexes from the high-quality Kootenay National Park population were not only more socially active but that

rams of differnt horn-size classes were more socially mature than similar individuals in the lower-quality Banff National Park population.

Methods

A behavioral pattern was considered to be any stereotyped, spatio-temporal sequence of movements and postures having constant and recognizable starting and end points (Shank 1972). Only patterns which had apparent social significance were recorded. An 'interaction' was defined as the behavior pattern(s) exhibited by one individual toward another. It was considered to have ended when the individual animals separated or entered into another activity. Since each animal was classified and the number of interactions tallied, comparative behavioral repertoire for the various sex-age classes could be assessed.

Each individual in a group was classified according to sex and age before the start of behavioral data collection. The sex-age composition of the group under study, the number of interactions and patterns per interaction, the sex-age class of the actor and object involved in an interaction were recorded in field note books.

Mother-Young Interactions

Female aoudad groups were observed from February onwards to detect the presence of newborns. Observation of such groups was continued daily until it was not possible to collect any further data. Disturbance of animals was avoided by maintaining maximum observation distances.

Behavioral data involving mothers and their young were collected on aspects of:

1. Suckling behavior
    a) Duration of suckle (recorded to nearest second)
    b) Time of suckle
    c) Method of initiation and termination of the bout
    d) Number of bunts per bout
2. Grazing behavior of young-juveniles
3. Play activity of juveniles
4. Group composition (sex-age classes and their numbers).

Data collection on suckling behavior started on 22 February 1982, when the first newborns were located, and continued until the end of September. Animals born through this period were studied at regular intervals.

A t-test was used to establish the statistical significance of differences between the mean of suckling durations for twins and that of single young-juveniles.

A logarithmic transformation was used to overcome the heterogeneity of variance of suckling durations (Little and Hills 1978).

Social Interactions

Data analysis of aoudad social behavior was based on Altmann's (1968) method in his study of rhesus monkeys (Macaca mulatta) as later modified by Shank (1972) in a study of feral goats (Capra hircus).

To assess the frequency of interactions among the different sex and age classes, Altmann's method called for the observability of each class to be calculated separately. Because of changes in social structure during the study period, the relative number of hours that aoudad groups were observed was used as a measure of animal-availability.

Interaction constants were derived by using the formula:

$$C_{i,j} = \frac{I_{i,j}}{(A_i)(A_j)(M)}$$

where $C_{i,j}$ is the interaction constant for patterns performed by animals of i^{th} class to members of j^{th} class; $I_{i,j}$ is the number of observed patterns performed by the i^{th} class to the j^{th} class. A_i and A_j are the aoudad-hours of observation for the respective classes while M is the total number of patterns performed by all sex-age classes during the total observation time.

Interaction indices were derived by using the formula:

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

The summations of interaction indices initiated and received by a particular sex-age category provide action and reception indices for each class.

Following Shank (1972) the deviation of the observed number of patterns performed from those expected on the basis of random interactions among all sex-age classes was derived from the formula:

$$E_{i,j} = \frac{A_i}{A} \cdot \frac{A_j}{A} \cdot M$$

where $E_{i,j}$ is the expected number of patterns performed by the i^{th} class toward the j^{th} class and A is the total aoudad hours of observability.

$R_{i,j}$, the relative deviation of patterns performed by the i^{th} class to the j^{th} class, was found by:

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

A $C_{i,j}$ matrix (Table 4) of these several values was constructed. In intra-class interactions where i=j there are N_i possible actors and N_i-1 possible receivers. Therefore the matrix has a built-in bias, however, along

the main diagonal (Altmann 1968). The effects of such a bias are considerable when the number of individuals in the class is small. Since a majority of the groups observed during the rutting season were large and contained more than one individual of each class, however, the effects of such a bias are believed not to be significant.

The interaction index gives the probability that a pattern was performed by one type of class to another randomly and is independent of the numbers of animals in the two classes. For example Class III rams initiated 310 while Class II began 306 interactions with adult females. It could be inferred that the two classes were equally involved in sexual interactions with females. Since the number of observed (availability) hours for Class II rams was almost twice that of Class III males, the derived index values of .0877 and .1888 (Table 4) reveal that involvment in this form of behavior is quite unequal.

Correlation coefficients were calculated to enable intra-specific comparisons of behavioral patterns and the degree of association between animals of various age classes. To standardize results, the number of each pattern observed was transformed into a number per 100 interactions of all types. The t-test with 2 degrees of freedom (Bailey 1981) was used to check if the correlation coefficients were significantly different from zero.

Table 4. Matrix of interaction indices, action indices and reception indices for total behavior among the various sex-age classes.

		RECIPIENT							
		Juvenile	Subadult female	Subadult male	Adult female	Class I male	Class II male	Class III male	Action Index
INITIATOR	Juvenile	.0018	.0001	.0000	.0002	.0000	.0000	.0000	.0021
	Subadult female	.0013	.0013	.0000	.0001	.0000	.0000	.0000	.0027
	Subadult male	.0034	.0211	.0155	.0038	.0000	.0000	.0000	.0438
	Adult female	.0006	.0003	.0011	.0018	.0001	.0002	.0002	.0043
	Class I male	.0311	.0200	.0039	.0255	.0122	.0000	.0000	.0927
	Class II male	.0189	.0555	.0211	.0877	.0588	.0477	.0070	.2967
	Class III male	.0144	.1111	.0233	.1888	.1033	.1033	.0155	.5597
	Reception Index	.0715	.2094	.0649	.3079	.1744	.1512	.0227	

Investigations of social preferences among the different sex-age classes were made by Chi-square analysis (Bailey 1981). The percentages of animals available and present in each sex-age category was calculated from group composition data. These were then compared to yield a preference index (Geist 1971).

Results

Mother-Young Behavior

Three hundred and ninety suckling attempts by young juveniles of different ages were observed during the 1982 lambing season. 28.6% of suckling attempts were refused by females. The average suckling duration for young of all age groups was 32.2 (± 23.2) seconds. Suckling endured from 4-150 seconds at each bout, with the majority of bouts (86.8%) lasting for 6-45 seconds (Figure 7). As the animals grew older, the duration of their suckling decreased. A mean of 51.7 (± 35.5) seconds was recorded for week-old juveniles but 17.8 (± 5.44) for 12-week animals (Table 5).

The duration of an average suckle dropped until the fourth week of life. After that, it levelled off (Figure 8). A suckling bout for week-old juveniles was rather prolonged with 30% of the suckles observed at this age lasting over 60 seconds. The longest was 150 seconds and was terminated by the juvenile.

Table 5. Suckling durations and average bunts per suckling bout observed among young-juveniles, Hondo Valley, New Mexico, February to September 1982.

Estimated age of juvenile in weeks	Number of bouts observed	Mean suckling duration (seconds) with standard deviations	Mean number of bunts/ suckling bout with standard deviations
1	50	51.74 (+35.58)	2.3 (±1.21)
2	58	36.92 (+20.11)	6.0 (±5.15)
3	24	29.08 (±11.46)	5.1 (±3.57)
4	15	24.26 (± 9.19)	4.5 (±1.71)
6	20	23.15 (± 9.40)	4.6 (±1.22)
8	24	22.87 (±14.82)	4.0 (±1.0)
10	25	19.76 (± 5.23)	3.8 (±1.53)
12	23	17.86 (± 5.44)	3.6 (±2.31)

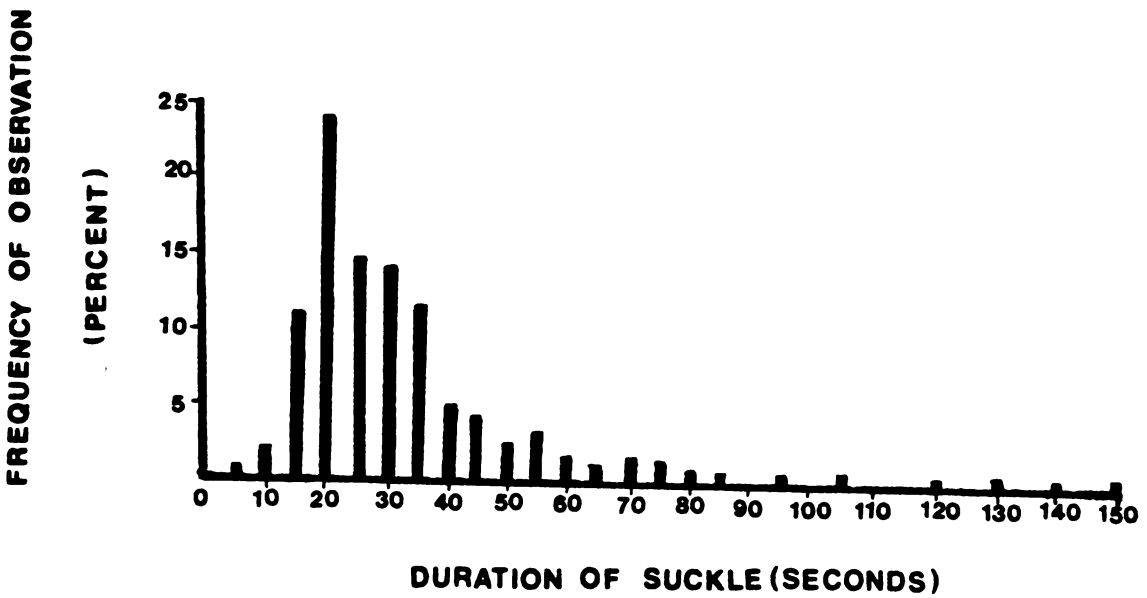

Figure 7. Frequency distribution of suckling durations, Hondo Valley, New Mexico.

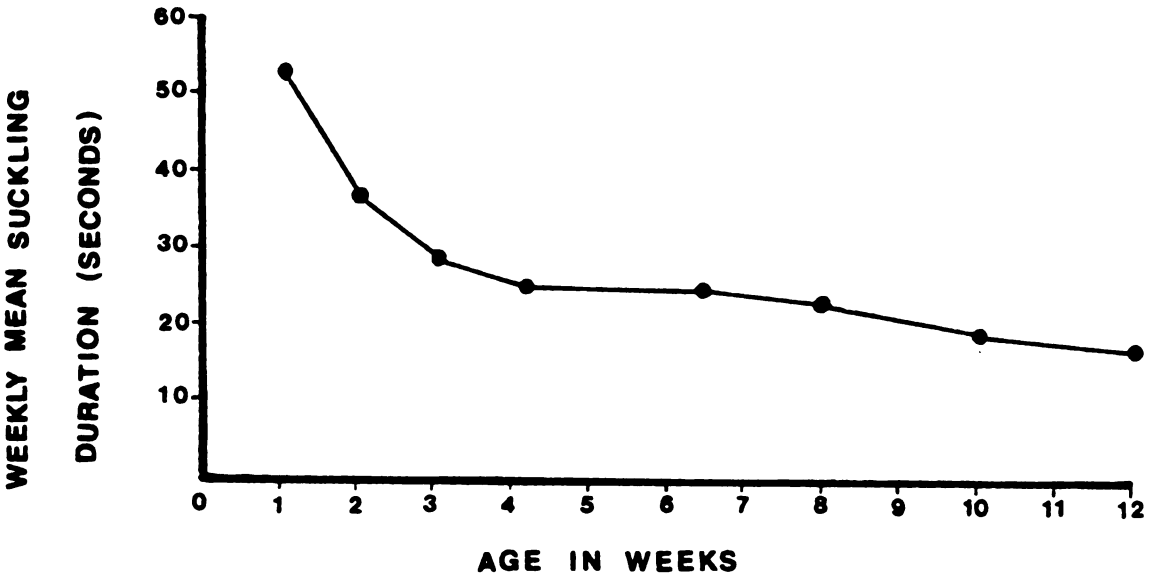

Figure 8 . Mean suckling duration as related to the age of young-juveniles.

All of the suckles terminated voluntarily were observed among neonate young (Table 6). Of the 111 suckles refused by females, neonates were involved only 26.1% of the time. Most of the refused suckles were those in which the juveniles attempted to suckle a strange female or tried to suckle their mother shortly after a successful attempt.

Suckling durations for twin and single animals were not significantly different ($t = 0.37$, $p \blacktriangleright 0.025$). Twins from different age groups suckled for the same length of time as single juveniles of their age category.

Although bunting was observed among all age groups, few one-week old juveniles were seen to bunt. Bunting was more frequent at the start and toward the end of a suckling bout. No correlation existed between the number of bunts and the duration of suckles ($r = 0.22$, $t_o = 1.59$, $p \blacktriangleright 0.05$).

Foraging Behavior of Young-Juveniles

Sustained vegetative foraging by juveniles did not start until the fifth week of life. Up to the second week, the animals were entirely dependent on their mothers's milk. During the third week of life juveniles were witnessed to nibble on vegetation for a few seconds at a time. They did not engage in foraging for long periods of time, however, even when they closely followed their mothers. Foraging for a sustained period was started only when the young

Table 6. Frequency and terminations of suckles by young-juveniles of various ages, Hondo Valley, New Mexico, February to September 1982.

Age in weeks	Total number of suckles observed	Number of suckles terminated by the young-juveniles	Percentages of suckles terminated by young-juveniles
1	50	7	14.0
2	58	3	5.17
3	24	1	4.16
4	15	1	6.66
6	20	-	-
8	24	-	-
10	25	-	-
12	23	-	-

juveniles were about six week old. At this age, they browsed on mountain mahogany and occasional grasses. Older animals were observed nibbling on prickly-pear cactus pads. No animals were seen to graze immediately following a successful suckling attempt. After nursing, young-juveniles either stayed by the mothers' side or engaged in play activity with their peers.

Play Activity

In the absence of an adequate definition of play behavior among wild mammals (Beach 1945, Hinde 1966, Espmark 1969), play was considered to be those behavioral patterns which had no evident purpose except pleasure and, perhaps, learning. Behavioral patterns performed by the young while playing often were similar to those of adults but frequently lacked portions of the complete pattern.

While play activity invariably was initiated by a young or older juvenile, adult animals participated 25.9% of the time. The average duration of play bouts was 6.6 ($\pm$ 4.7) minutes and ranged from 2 to 20 minutes. Sub-adults of both sexes as well as adult females frequently participated in play bouts initiated by juveniles. On three occasions, an entire female group was seen to participate in such activity. No significant differences ($t = 1.14$, $p \blacktriangleright 0.01$) occurred in the duration of play bouts with adult participation and those in which juveniles only took part.

Five different kinds of play behavior were recognized among the 54 observations which were classified as play or play-related:

Play-fighting: Play patterns which involved aggressive encounters such as abdomen lifting, butting, horning, sparring, neck-fighting and wrestling were categorized as play-fighting. Contests of this type were of short duration and often were followed by gamboling, lone-rushing and chasing.

Gamboling: The animals abruptly engaged in frolicking movements by leaping vertically into the air or on rocks. The bounds were accompanied by a shaking of the head and a kicking of legs in an irregular manner. Gamboling was usually followed by lone-rushing or chasing.

Lone-rushing: This behavior was featured by the fast running of a lone juvenile, either away from or toward its mother. If the former, the juvenile usually then circled around and among other members of the group before returning to the mother.

Chasing: This pattern, commonly initiated by a juvenile or a pair of juveniles, was usually joined by mothers and at least some subadult members of the group. Chasing started when a juvenile would run away from its play group. Once 50-70 m. away from the group, the young one would turn around and run back to the group.

Sexual-play: Characterized by a mounting or evident intent to mount another juvenile, the patterns used by the young

animals were overt and lacked the full courtship sequence seen in adults. Mountings were of short duration and were followed by another kind of play once the pair disengaged.

Adult Social Behavior

A total of 22 social patterns (each given a symbol) was recognized in the aoudad population. These fell into three categories: 1) sexual 2) aggressive and 3) contact.

Sexual Displays

Chase (Ch): A sexually-aroused adult male runs after a fleeing female which tried to avoid him.

Headshake (Hs): Performed after the male has approached a female and stands beside or behind her. The male bobs his head with a sudden jerk. The head-shake is occasionally accompanied by the tongue flick.

Lipcurl (Lp) Figure 9: Performed after the male licks the expelled urine of a female, the female's vulva or her legs or urine on the ground. After nuzzling the urine or the females hindquarters, the male opens his mouth slightly, retracts his lips, lifts his head and exposes the palate. At the end of the lipcurl, the male licks his lips and returns to a normal stance. Females also performed the lipcurl after another female urinated.

Crouch (Cr) Figure 10: Performed by males of all age classes except juveniles, the male crouches at the female with his

hindquarters close to the ground. The penis is unsheathed, erect and flicked against the belly. The crouch is often accompanied by tongue-flicking.

Tongue-flick (Tf): The male protrudes his tongue and flicks it while simultaneously producing a deep guttural sound.

Low-stretch (Ls) Figure 11: In this posture, the male keeps his head low with the neck extended as he moves with quick steps toward the female or subordinate male. The low-stretch is primarily displayed by adult rams.

Twist (Tw) Figure 12: A male approaches the female with his neck stretched low. While dipping the head low, he rotates his body, flicks with the tongue and growls loudly. Contact is sometimes made by pushing the muzzle into the side of the partner.

Rear sniff (Rs) Figure 13: After approaching a female in low-stretch, twist or normal posture the male sniffs and nuzzles the female's rear.

Mount (Mt): In the mounting posture, the animal rests its two front feet on the back of the receiver. The body is erect and the head held high.

Stand (St) Figure 14: An adult male stretches his head and neck forward, the head is tilted so low as to be on a plane with the back. Males often stand in this posture for long periods of time in front of a bedded or standing female.

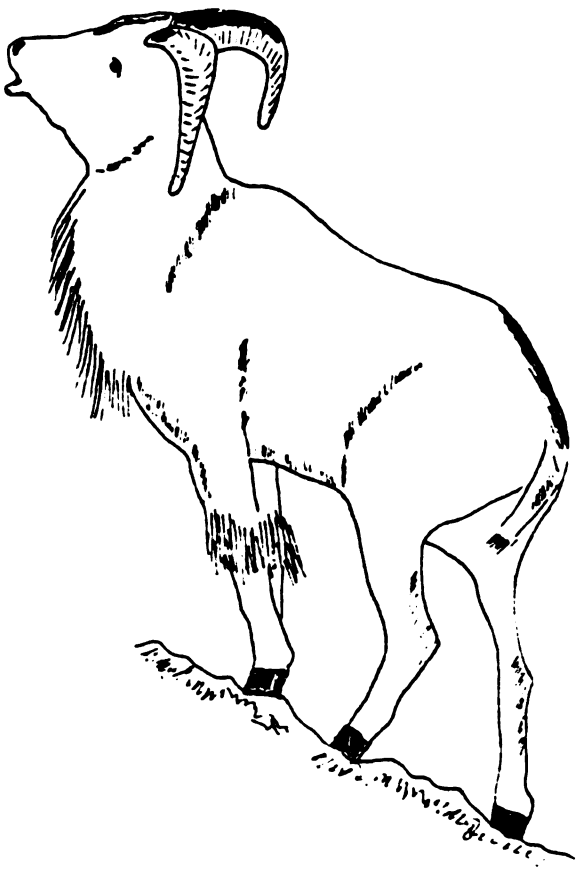

Figure 9. A Class I male lipcurling after rear-sniffing a female.

Figure 10. A Class III male crouching before a female. When crouching, the penis is unsheathed and flicked against the belly.

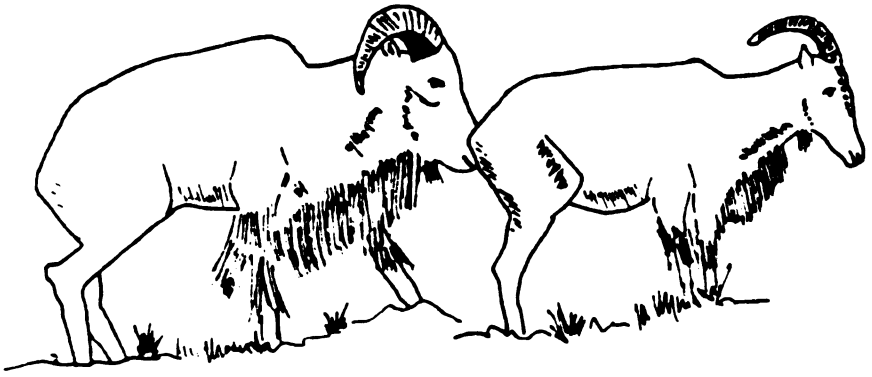

Figure 11. A Class III male approaching a female in low-stretch.

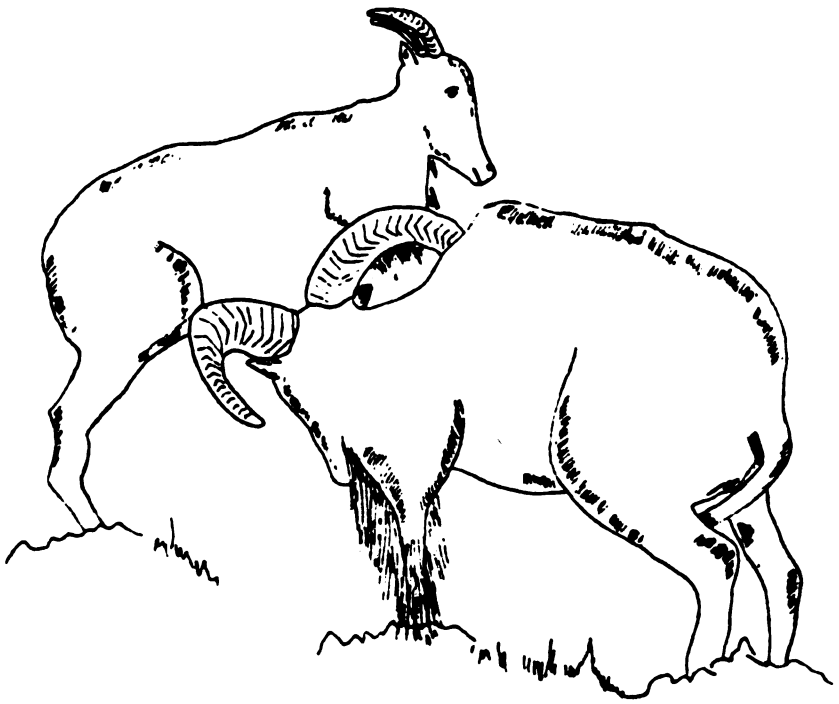

Figure 12. A Class III male twisting at a sub-adult female.

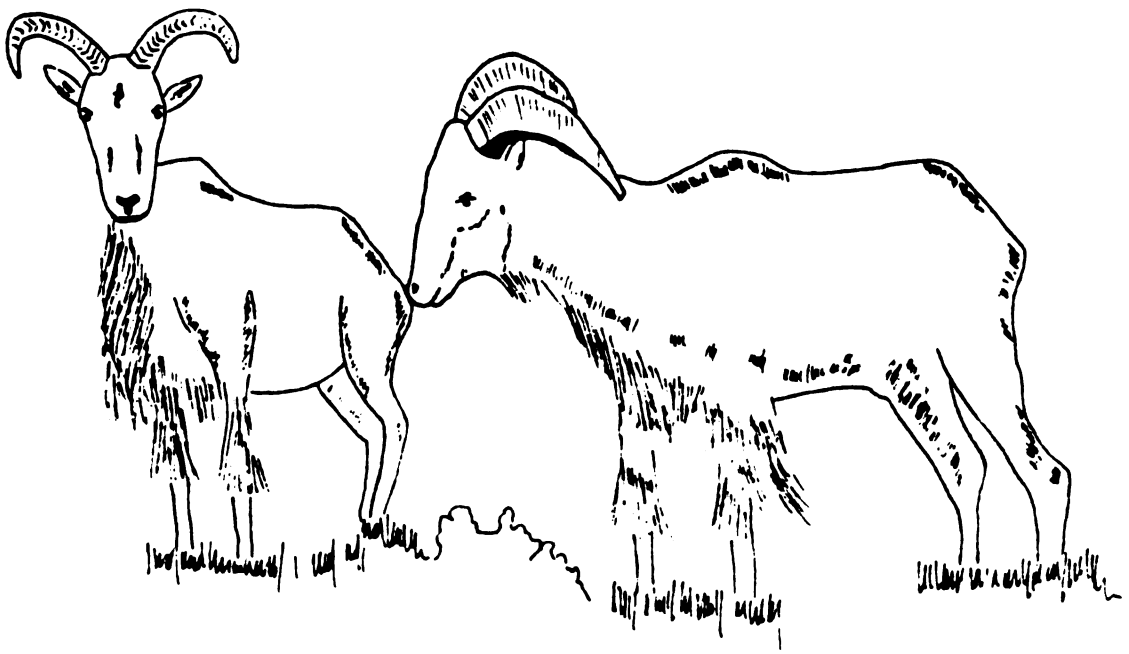

Figure 13. A Class III male rear-sniffing an adult female.

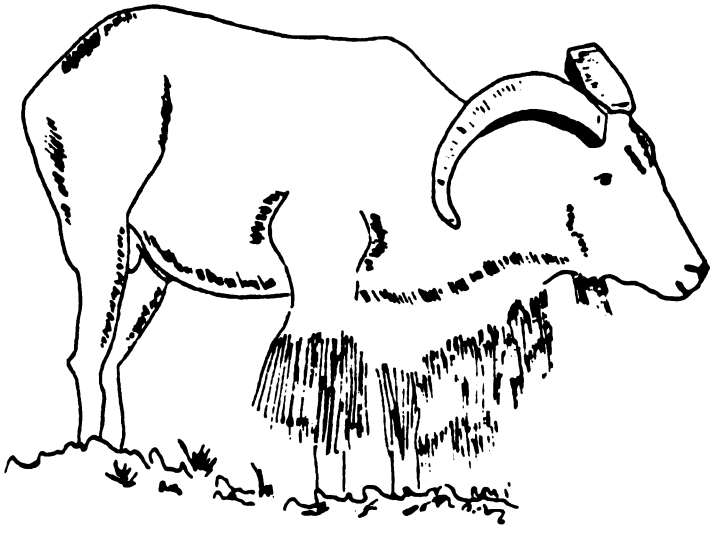

Figure 14. A Class III male in standing display. In this posture the head is held low and the neck stretched forward.

Aggressive Displays

With the exception of abdomen lifting which was noticed only among lambs, all other displays were performed by members of all sex and age classes:

Abdomen-lift: Performed by young-juveniles while playing or displaying agonistic patterns. The actor ducks its head under the abdomen of the partner and tries to lift the opponent off the ground.

Spar (Sp) Figure 15: The opponents stand opposite each other and make contact by clashing their horns. After the clash both animals retreat a few steps backward and bob their heads several times. They then move toward each other to deliver another blow.

Butt (Bt) Figure 16: The actor lowers its head and delivers a blow and push with the horns. The actor continues to push the opponent once contact is made.

Hook (Hk): Contact is made with the tip of one or both horns. The blow is directed by twisting the neck toward the opponent and swinging the horns is a sideway motion.

Horn (H): Contact with the horn tip(s) is made while the head is held low but without further pushing the opponent.

Horn Threat (Ht): A movement is made as if to butt but no contact is made. The pattern only involves lowering the horns and showing them to the opponent.

Neck fight (Nf): The actor puts its chin and throat over the neck of an opponent and tries to push it to the ground.

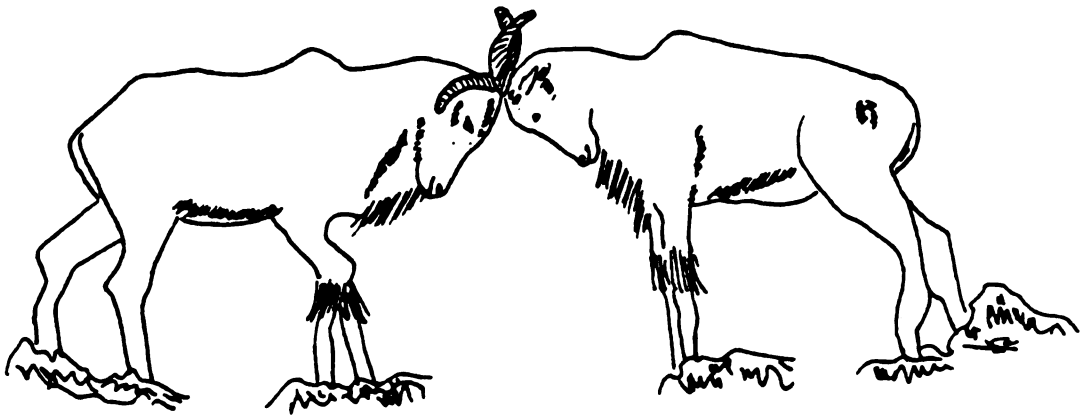

Figure 15. Two sub-adult males sparring.

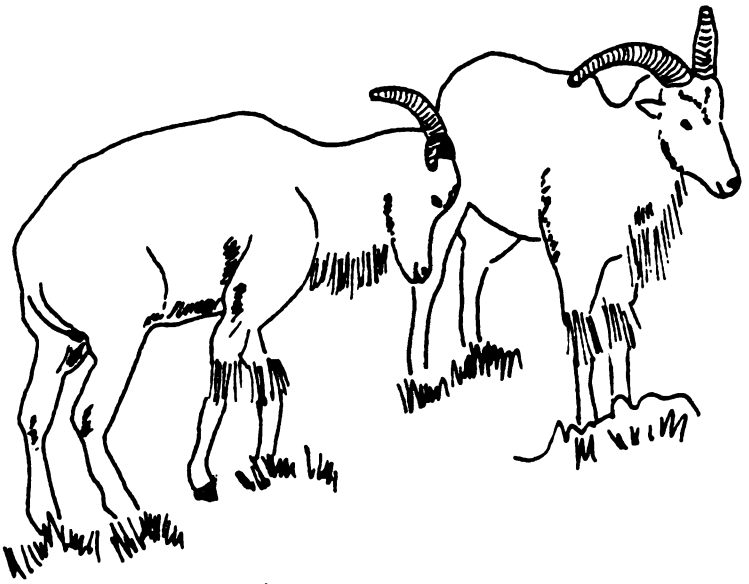

Figure 16. An adult female butting another female.

Wrestle (Wr) Figure 17: The opponents stand head to tail while the actor puts one horn around the flank of the opponent and tries to push it to the ground by applying a downward thrust with the neck. Once the opponent is wrestled down, the victor holds it firmly against the ground by resting his entire weight on him.

Rush (Ru) Figure 18: The actor runs a few steps toward the opponent with the head lowered and threatens with horns without making contact. The rush tends to intimidate the opponent without the necessity of physical contact.

Horn-lock (Hl) Figure 19: Occurs after two males engage in a prolonged fight. The animals stand parallel to each other head-to-head. The actor extends his horn into the curl of the horn of the partner and the two attempt to shove and push each other.

Broadside (B): A male stands in front of an opponent with erect body as if threatening to engage in an aggressive encounter.

Contact

Rubbing (Rb) Figure 20: The actor rubs his horns on the body or flank of the partner. This is an appeasement posture mainly initiated by a subordinate ram toward a more dominant individual.

Group Clash

This activity involves a number of sexual and aggressive

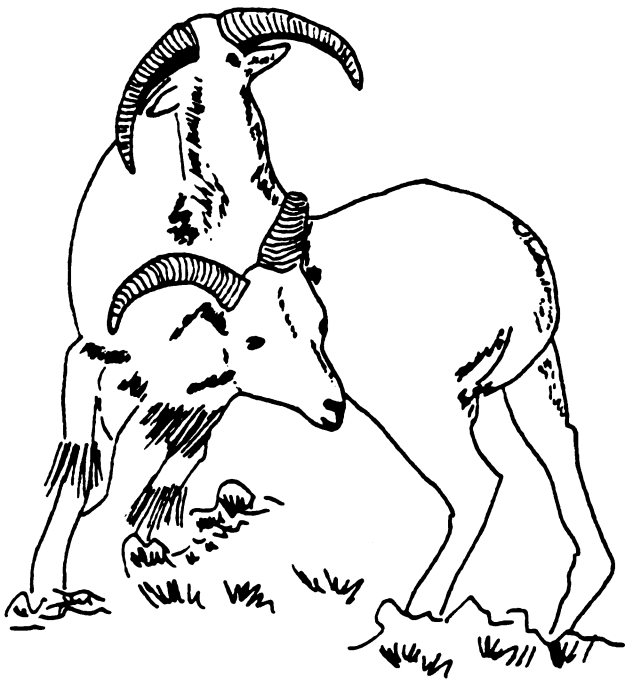

Figure 17. Sub-adult males wrestling. By putting their horn around the flank of the opponent the animals apply downward thrust to bring the rival to the ground.

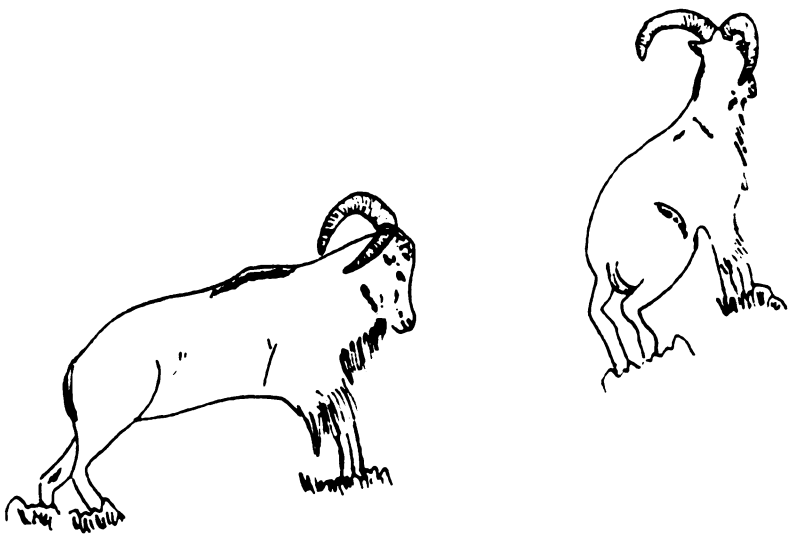

Figure 18. A dominant male rushing toward his opponent in a threatening posture to intimidate the subordinate.

Figure 19. Class III males engaged in a horn-lock combat.

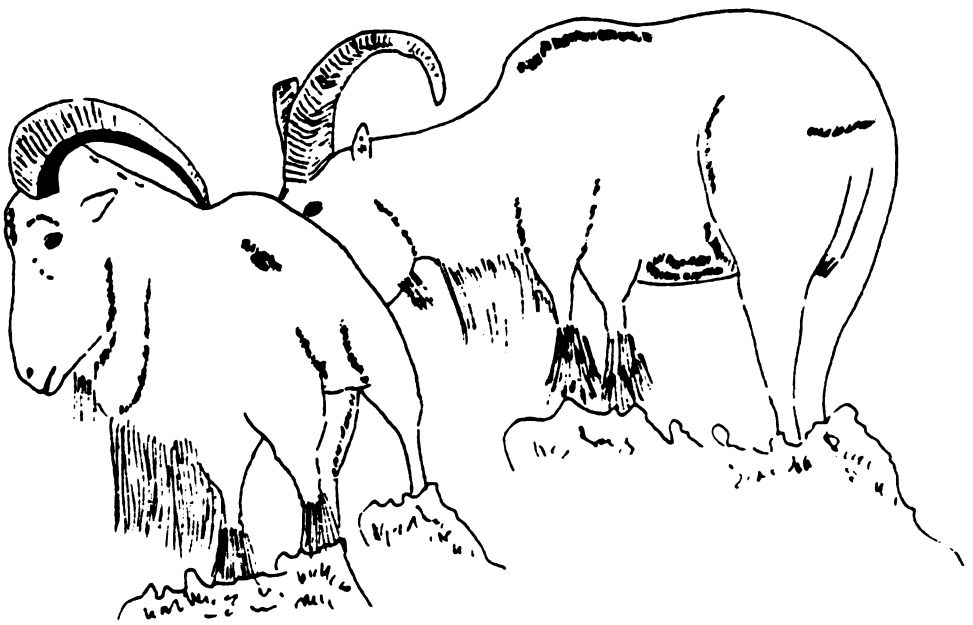

Figure 20. A subordinate male rubbing his face on the back of the dominant in appeasement.

patterns used simultaneously by a large number of animals. An interaction in which almost all members of the group participate, usually starts when one individual mounts another. Social restraints imposed by the dominant males evidently become ineffective on occasion. When this occurs, a disorganized series of intensive but random sexual and agonistic encounters occurs between many or all members of the group. The activity is too intense to permit documentation of the numbers and kinds of patterns taking place.

Total Behavioral Aspects

A total of 1596 interactions involving 3472 social behavior patterns was recorded during the 1982 rutting season. In addition, 415 interactions with 978 patterns were observed during the non-rutting season mainly among female herds.

Diagrams of rutting-season frequencies of observed behavioral expressions (Figure 21) and deviations from expected behaviors (Figure 22) indicate the complexity of aoudad social interactions. Comparisons of total observed and expected values yielded a X^2 value of 32,549.6 with 36 degrees of freedom. This value is highly significant beyond the 0.001 level, indicating that interactions did not take place randomly.

Social partners were chosen by the dominant males. The order of preference was controlled by the position of the animal in the social hierarchy. Dominance within both

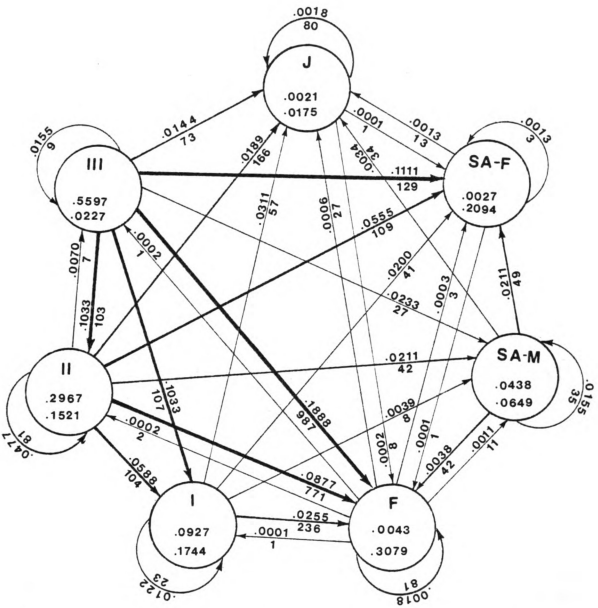

Figure 21. Sociogram of interactions among aoudad groups during the rutting season (September to November, 1982), Hondo Valley, New Mexico. The upper figure on the lines represents the interaction index while the lower figure is the number of times that a pattern was observed. Within the circles, the upper figure is the action index while the lower one is the reception index. J=juvenile, SA-F=sub-adult female, SA-M=sub-adult male, F=adult female, I=Class I male, II=Class II male, III=Class III male.

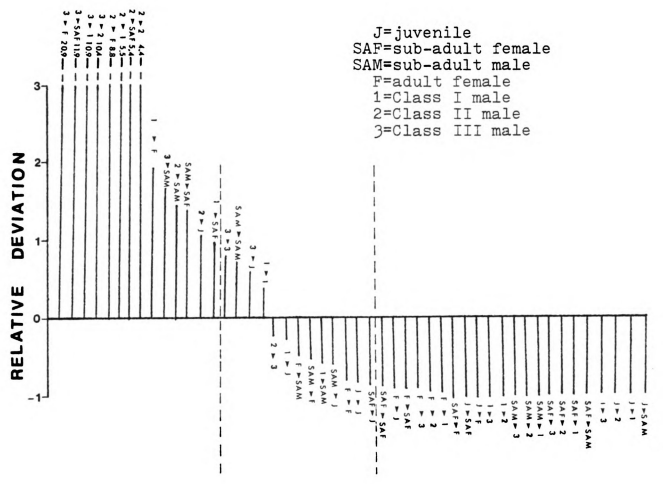

Figure 22. Relative deviation of observed social patterns from those expected during the rutting season (September to November 1982) among the different sex-age classes of aoudads in the Hondo Valley, New Mexico, as based on a matrix (Table 4) with 36 degrees of freedom. Positive values show preferences for social interactions, while negative values represent social avoidance. Interactions outside the dashed lines show the most deviant values.

sexes between the various age classes apparently was determined by horn size, with the largest rams pairing with females most frequently.

Attractions and repulsions seemed to exist in procedures leading to the selection of a partner (Figure 22). Most interactions were between large males and adult females and between males of equal horn size or subordinate males. Juveniles, subadults and females tended to avoid interacting with large males.

During the rutting season, adult males were most active in initiating behavioral patterns toward prospective partners (Figure 21). Although dominant males frequently interacted with females, juveniles and with sub-adult males, few interactions were observed between males of the same size class. Significant interactions between animals of equal size were noticeable only among juveniles and females.

Aggressive Behavior

Dominant rams primarily used horn displays when interacting with subordinate males. While courting a female, dominant rams displayed agonistic patterns toward subordinates mainly through non-contact patterns such as horn threats and rush associations. Together, these displays comprised 90.29% of the behavioral patterns used by dominants toward subordinates (Table 7). Such intention-movements evidently enabled dominants to intimidate subordinates without making physical contact.

Table 7. Percentages of agonistic patterns performed by dominant rams toward subordinates and by adult females toward females of equal or subordinate horn size, Hondo Valley, New Mexico, 1982.

Pattern type	Dominant ram to subordinate	Adult female to subordinate
Butt	2.62	7.52
Displace	0.79	3.0
Horn	0.53	2.25
Hook	2.36	6.78
Horn-lock	0.00	8.27
Horn-threat	59.05	13.53
Neck-fight	1.05	0.00
Rush	31.24	6.01
Spar	2.36	52.64
Wrestle	0.00	0.00
	100.00	100.00

Subordinates of different class sizes were treated equally by Class III males. The correlation coefficient for interactions of Class III males with Class II and I males ($r=0.997$, $t_o=36.43$, $p<0.001$, Table 8) does not differs significantly from unity. This indicates that Class III males act equally aggressively to Class I as they do to Class II males when courting a female. Since the value of r is close to unity and it differs significantly from zero, the aggressive behavior of Class II to Class I males can be inferred as being equally severe. In the absence of Class III males, Class II males treated subordinates in similar fashion (Table 9). Thus no significant differences were observed in the treatment of subordinates by dominant rams of either Class III or Class II (Table 10).

The agonistic patterns described above for males do not include those patterns displayed by rams during actual combat. Only four fights between rams of equal horn size were observed during the study period. In these fights, initial sparring between the rival animals prevailed, accounting for 79 % of the patterns performed. Horn-locking (11.1%) and wrestling (3.1%) were predominant among the other patterns displayed.

Excerpts from field notes describe a dominance fight between two Class III males observed on 6 October 1981: Six males appear as a group from behind cactus thickets. Behaving aggressively, members of the group display

Table 8. Numbers of aggressive behavior patterns directed toward subordinate males by Class III males when courting a female (expressed as numbers per 100 interactions) during the rutting season 1982, Hondo Valley, New Mexico.

Pattern type	Bt	D	H	Hk	Hl	Ht	Nf	Ru	Sp	Wr
Class III to II (N=105)	5	3	0	3	0	60	0	32	0	1
Class III to I (N=89)	3	0	2	1	0	74	0	41	1	0

$r=0.997$ $t_o=36.43$ $p<0.001$

Note: Bt=butt, D=displace, H=horn, Hk=hook, Hl=horn-lock Ht=horn-threat, Nf=neck-fight, Ru=rush, Sp=spar, Wr=wrestle
N= interactions, each often with several patterns.

Table 9. Numbers of aggressive behavior patterns directed toward subordinate males by Class II males when courting a female (expressed as numbers per 100 interactions) during the rutting season 1982, Hondo Valley, New Mexico.

Pattern type	Bt	D	H	Hk	Hl	Ht	Nf	Ru	Sp	Wr
Class II to I (N=25)	0	0	0	4	0	52	4	36	8	0
Class II to SA-M (n=61)	2	0	0	2	0	27	0	10	0	0

$r=0.947$ $t_o=8.34$ $p<0.001$

Table 10. Numbers of aggressive behavior patterns directed toward Class I males by Class III males when courting a female as compared with agonistic behavior of Class II to Class I males, (expressed as numbers per 100 interactions) during the rutting season 1982, Hondo Valley, New Mexico.

Pattern type	Bt	D	H	Hk	Hl	Ht	Nf	Ru	Sp	Wr
Class III to I (N=89)	3	0	2	1	0	74	0	41	1	0
Class II to I (N=25)	0	0	0	4	0	52	4	36	8	0

$r=0.982$ $t_o=14.71$ $p<0.001$

agonistic patterns as they move toward a mixed herd which is feeding on the slope a few meters downhill. After sparring and locking horns, two Class III males detach themselves from the smaller members of the group and challenge one another by horn-threats. The two rams move apart and when about 10 m. from each other, charge toward one another ending in a full-force head-on collision. Moving back and charging again, the rivals clash 35 times in 7 minutes. The sparring is occasionally interrupted by brief neck-fights. Unable to subdue each other by sparring, the rams lock horns and shoulder-push one another for 15 minutes. Eventually, they unlock horns and move into a head to tail position. They try to wrestle one another down by placing one horn across the other's flank. After continuously wrestling for over 30 minutes, one of the rams is brought to the ground. The victor holds his rival down by pressing his body weight over him. Struggling for breath, the loser finally manages to free himself and immediately abandons the vicinity, running down to the valley floor. The victor chases the fleeing male briefly but returns to the females as other males try to court them.

Unlike other members of the Caprini tribe, sexual dimorphism is not pronounced in the aoudad. The females also grow large horns, which in some individuals measure 50 cm. in length. Because of their large horn size, females were able to deliver or receive forceful blows with their well-armoured heads. Due to this characteristic, females

often behaved aggressively toward their peers (Katz 1949, Haas 1959). Probably as a result of their large horn size, the behavior of adult females toward females of their own or subordinate horn size significantly resembled that of males in dominance fights (Table 12). Sparring (52.6%) was the most commonly used behavior pattern (Table 7), followed by horn-locking (8.3%) and butting (7.5%). Adult females of equal or smaller horn size frequently interacted with each other, accounting for 48.7% of all interactions directed by females.

Sexual Behavior

Sexual behavior was primarily dominated by Class III and Class II males. These larger males performed 76.8% of all the sexual interactions directed toward females of all age classes. Patterns exhibited by the rams toward females were almost entirely related to sexual behavior and were devoid of aggressive displays (Table 12). The low-stretch, rear-sniff and twist were the most commonly used behaviors shown by rams while courting females (Table 12).

Subadult females were not courted at the beginning of the rutting season in September. The majority of sexual interactions (95.1%) between adult males and subadult females took place after mid-October. It is believed that during the early stages of the rut, in the presence of estrus

Table 11. Numbers of behavior patterns directed toward females of equal size and subordinates by adult females as compared to the behavior of males in dominance combats, (expressed as numbers per 100 interactions), Hondo Valley, New Mexico.

Pattern type	Bt	D	H	Hk	Hl	Ht	Nf	Ru	Sp	Wr
Class II to II (N=81)	10	0	0	30	90	30	0	10	640	0
F to F or Sub. (N=80)	12	5	4	11	14	22	0	10	87	0

$r=0.977$ $t_o=12.96$ $p<0.001$

Table 12. Percentages of major sexual patterns performed by aoudad males in social interactions with adult females, sub-adult females and juveniles, Hondo Valley, New Mexico.

Pattern type	Males/adult F	Male/SA-F	Male/Juvenile
Chase	1.00	0.72	0.00
Crouch	11.33	10.83	10.70
Head-shake	11.08	9.75	14.02
Lipcurl	7.32	10.83	7.38
Low-stretch	19.52	19.13	26.57
Mount	3.16	0.36	0.00
Rear-sniff	16.90	29.96	15.13
Stand	1.20	0.36	0.00
Tongue-flick	8.67	5.42	7.75
Twist	19.82	12.64	18.45
	100.00	100.00	100.00

Note: For number of patterns initiated by males refer to Figure 21.

and pro-estrus females, males were more inclined to seek adult females for mating. As the majority of the adult females were bred, the male's interest turned to subadult females. This was evident from the "rape-chases" of subadult females by the rams in October. In these chases, a group of males persistently followed a female. With each individual male striving to mount the female, interactions between members of the male band were often intense. The dominant ram was constantly engaged in chasing away other males. While doing so, the smaller Class I and subadult males took advantage of the situation and attempted to mount the female.

The longest "rape-chase" of a subadult female was observed during the last week of October, 1981. A band of 8 males persistently chased a subadult female for over 36 hours. During the second day of the ordeal, the female seemed excessively tired. Her movements were lethargic and she constantly bedded down, resting at intervals of 5 to 10 minutes, while the rams encircled her. By the third day, neither the female nor the rams could be found in the area.

Subadults showed signs of maturity during the first year of life. A subadult female with deformed horns was successfully bred in fall of 1981 and was seen being followed and suckled by a lamb in May of 1982. A one-year old female

which died in the netting operation of November of 1981 was carrying a 50-60 day old fetus.

Behavior of Males Toward Females

The sex of juveniles could not be determined from the distances involved while observing sexual behavior. Hence, male sexual behaviors directed toward juveniles could not be assessed with certainty. Aoudad males, however, treated non-estrus adult and subadult females alike. Class III and II males behaved similarly toward adult and subadult females (Tables 13 and 14).

Females in estrus were recognized when several males chased and courted a female persistently, Males courting a female in estrus performed more patterns toward that female and interacted frequently with it. Continuous twisting was followed by crouching and mounting by the ram. In one incident, a Class III ram was observed to mount or try to mount a female 22 times during 3 hours of observation. Dominant males vigorously defended an estrus female by horn-threats and by rushing at the subordinate rams. Subordinates responded by elusively avoiding contact with the dominant.

In the presence of the larger rams the behavior of Class I rams seemed to be supressed by the more dominant males. During the spring and summer months, however,

Table 13. Numbers of behavior patterns directed toward females by Class III males during the rutting season, 1982 (expressed as numbers per 100 interactions) Hondo Valley, New Mexico.

Pattern type	Ch	Cr	Hs	Lp	Ls	Mt	Rs	St	Tf	Tw
Class III to F (N=310)	4	39	46	21	62	9	45	5	22	65
Class III to SA-F (n=56)	2	28	34	16	30	0	66	2	9	43

$r=0.804$ $t=3.82$ $p<0.01$

Note: Ch=chase, Cr=crouch, Hs=head-shake, Lp=lipcurl, Ls=low-stretch, Mt=mount, Rs=rear-sniff, St=stand, Tf=tongue-flick, Tw=twist.

Table 14. Numbers of behavior patterns directed toward females by Class II males during the rutting season, 1982 (expressed as numbers per 100 interactions) Hondo Valley, New Mexico.

Pattern type	Ch	Cr	Hs	Lp	Ls	Mt	Rs	St	Tf	Tw
Class II to F (N=306)	2	27	20	18	48	6	41	2	34	54
Class II to SA-F (N=61)	2	15	6	23	46	2	59	0	16	10

$r=.639$ $t_o=2.34$ $p<0.05$

smaller males often were the dominant rams in mixed groups. In such a group, dominant Class I males displayed overt patterns and showed lack of refined sexual behavior. Spontaneous mounting of anestrous females without prior courtship and frequent sexual displays were common in these rams (Table 15).

Social Preferences

Since interactions between the various sex-age classes did not occur stochastically, animals must have shown preferences toward members of certain classes while avoiding individuals of other classes. Class III rams interacted with all age classes but displayed to Class I and II males and to adult females more frequently than would be expected on the basis of the availability of animals in these categories. Conversly, they participated in fewer than expected interactions with rams of their own size class or with subadults of either sex or juveniles. Class III males, for example, chose Class II males 2.38 times as often as would be expected by chance (Table 16, Figure 23). Since the difference is highly significant ($X^2=84.57$, $p<0.001$) it can be concluded that Class III rams sought out subordinate males for behavioral displays while avoiding males of their own class category ($X^2=17.45$, $p<0.001$, Table 16).

Table 15. Numbers of overt patterns displayed by Class I males (as dominant males, top row and subordinate males, bottom row), (expressed as numbers per 100 interactions) Hondo Valley, New Mexico.

Pattern type	Ch	Cr	Hs	Lp	Ls	Mt	Rs	St	Tf	Tw
Class I to F (N=27)	18	17	37	41	11	96	71	21	155	88
Class I to F (N=127)	2	17	13	21	38	14	56	0	0	23

$r=-0.101$ $t_o=-0.28$ $p \blacktriangleright 0.05$

Table 16. Preference index calculation for aoudads, Hondo Valley, New Mexico, 1982.

Class III Males

	III	II	I	F	SA-M	SA-F	J
Percent per class present	5.16	6.92	6.81	34.56	7.12	7.30	32.13
No. of interactions observed	9	105	89	310	27	58	43
No. of interactions expected	33	44	44	221	45	47	205
Preference index	0.27	2.38	2.02	1.40	0.6	1.23	0.21
X^2 values	17.45	84.57	46.02	35.84	7.2	2.57	128.0
p	0.001	0.001	0.001	0.001	0.01	NS	0.001

Class II Males

	III	II	I	F	SA-M	SA-F	J
Percent per class present	4.15	6.98	6.83	33.0	7.73	7.48	33.83
No. of interactions observed	7	11	25	306	42	61	83
No. of interactions present	22	37	36	176	41	40	180
Preference index	0.32	0.30	0.69	1.74	1.02	1.52	0.46
X^2 values	10.23	18.27	3.36	96.02	0.02	11.02	52.27
p	0.01	0.001	NS	0.001	NS	0.001	0.001

Class I Males

	III	II	I	F	SA-M	SA-F	J
Percent per class present	3.93	6.60	7.35	32.33	7.52	7.68	34.59
No. of interactions observed	0	0	5	127	3	25	29
No. of interactions expected	7	12	14	61	14	14	65
Preference index	0	0	0,35	2.08	0.21	1.78	0.45
X^2 values	7	12	5.78	71.40	8.64	8.64	19.93
p	0.01	0.001	0.05	0.001	0.01	0.01	0.001

Table 16 Continued. Preference index calculation for aoudads, Hondo Valley, New Mexico, 1982.

Sub-adult Males

	III	II	I	P	SA-M	SA-P	J
Percent per class present	3.85	6.51	6.75	32.29	7.95	7.45	35.18
No. of interactions observed	0	0	0	34	10	18	19
No. of interactions expected	3	5	5	26	6	6	28
Preference index	0	0	0	1.31	1.66	3.0	0.68
X^2 values	3	5	5	2.46	2.66	24.0	2.89
p	NS	0.05	0.05	NS	NS	0.001	NS

Adult Females

	III	II	I	P	SA-M	SA-P	J
Percent per class present	4.05	6.42	6.72	32.62	7.56	7.48	35.14
No. of interactions observed	0	2	1	42	11	3	27
No. of interactions expected	3	5	6	28	6	6	30
Preference index	0	0.4	0.16	1.5	1.83	0.5	0.90
X^2 values	3	4.5	4.16	7.0	4.16	1.5	0.30
p	NS	0.05	0.05	0.01	0.05	NS	NS

Sub-adult Females

	III	II	I	P	SA-M	SA-P	J
Percent per class present	3.95	6.40	6.88	32.46	7.5	7.82	34.97
No. of interactions observed	0	0	0	1	0	3	7
No. of interactions expected	0.4	0.7	0.76	4	0.8	0.86	4
Preference index	0	0	0	0.25	0	3.48	1.75
X^2 values	0.4	0.7	0.76	2.25	0.8	5.32	2.25
p	NS	NS	NS	NS	NS	o.05	NS

Table 16 Continued. Preference index calculation for aoudads, Hondo Valley, New Mexico, 1982.

Juveniles

	III	II	I	F	SA-M	SA-F	J
Percent per class present	4.05	6.42	6.72	32.62	7.56	7.48	35.14
No. of interactions observed	0	0	0	8	0	1	44
No. of interactions expected	2	3	3	17	4	4	18
Preference index	0	0	0	0.47	0	0.25	2.44
X^2 values	2	3	3	4.76	4	2.25	37.55
p	NS	NS	NS	0.05	0.05	0.05	0.001

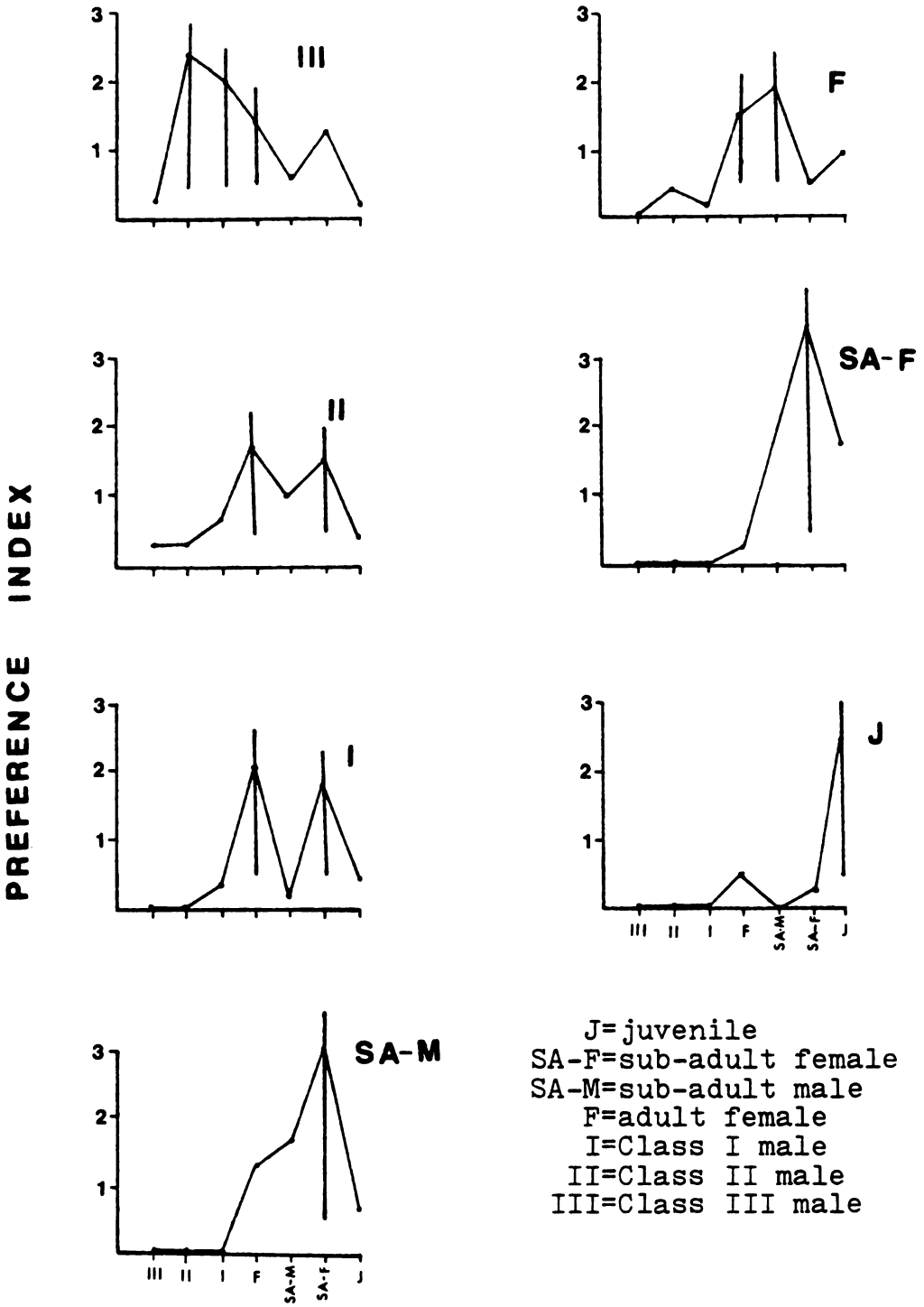

Figure 23. Social preferences of aoudads based on numbers of interactions between various sex-age classes, Hondo Valley, New Mexico. Heavy vertical bars indicate the classes in which significant preference was observed.

Class II rams, on the other hand, behaved differently (Table 16). Males of this class avoided males of all other categories, displaying preferentially toward adult and subadult females. Class I males (Table 16) also entirely avoided the larger rams and like the Class II rams, were more inclined toward interactions with adult and subadult females (Figure 23). The behavior of subadult males in choosing partners during behavioral interactions also resembled that of Class I rams in avoiding the larger males. The majority of their interactions were also directed toward adult and subadult females (Table 16).

In contrast to males (Figure 23) females and subadult females and juveniles (Table 16) were observed to be frequently interacting with members of their own class. Social patterns exhibited by females toward members of their own class were dominated (Table 7) by aggressive behavior. On two occasions, a female lipcurled as another female was urinating. Females were observed to mount other females during group clashes, yet because of the intensity of activity, it was not possible to document the full sequences of their behavior during such interactions.

In contrast to adult females, juveniles of both sexes directed both sexual and aggressive patterns toward other members of their class throughout the study period and occasionally also rear-sniffed. Subadult females, on the

other hand participated in only 11 interactions and showed significant preference only toward members of their own age class.

Discussion

Mother Young Behavior

It has been noted (Klein 1954, Geist 1971) that different populations of an ungulate species show varying developmental and reproductive characteristics. Studies of mountain sheep by Geist (1971) showed that differences between two populations were not only confined to physical characteristics but also to behavior. The frequency and duration of suckles, foraging at an early age and play behavior have been used as characteristics to postulate population quality (Geist 1971, Shackleton 1973, Horejsi 1975). In his study of Rocky Mountain bighorn sheep in Banff and Kootenay National Parks, Alberta, Shackleton (1973) found that females from a well-nourished Kootenay population permitted their young to suckle for longer periods and terminated fewer suckles than did females from a poorly-nourished Banff population. In a comparative study of Stone sheep (Ovis dalli stonei) in the Cassiar Mountains of northern British Columbia and of Rocky Mountain bighorns of the Banff National Park, Geist (1971) observed longer suckles in the Stone sheep lambs. Stone lambs were also more agile than the bighorns, suggesting that they were better nourished.

Geist concluded that differences in the vigor of lamb behavior in the two populations could have been due to differences in nutritional levels.

Suckling bouts among aoudads seemed to be of long duration ($\bar{x}$ = 32.3 seconds). Especially during the first two weeks of life, 30% of the suckles lasted over 60 seconds. Voluntary termination of suckling bouts by neonates also was indicative of high levels of milk production during the first few weeks after birth and a possible rapid growth of the young.

Domestic ewes nursing twin lambs produce more milk than is produced by females nursing a single lamb (Wallace 1948, Alexander and Davies 1959, Donly and Murno 1962). In aoudads the lack of differences in the duration and frequency of suckling bouts between single and twin lambs would seem to indicate that twins received the same amount of milk as single lambs.

Many of the refused suckles were attempted on strange mothers. Reaction of a female to a strange juvenile was often violent, with the female usually threatening the juvenile with her horns. Unsuccessful suckling attempts by strange individuals has also been noted among domestic goats (Capra hircus) (Klopfer and Klopfer 1969), roe deer (Capreolus capreolus)(Espmark 1969), bighorn sheep (Geist 1971) and Marco Polo sheep (Habibi, pers. obser.). Although

it was not possible to identify a strange young on every occasion, it is likely that a large number of the refused attempts involved strangers. From the evolutionary standpoint, a nursing mother would jeopardise the survival of her own young by allowing a strange young to suckle (Shackelton 1973).

Some females were observed to be suckled by both a young and an older juvenile, evidently of a previous birth. Attempts by older juveniles to join young juveniles in the suckling bouts were mostly terminated by the animals' mother.

According to Geist (1971), the play behavior of lambs reflects the energy levels of foods available to them. Growth data from snow sheep (Ovis nivicola) (Cherniavski 1962) showed that fresh vegetative growth contributed to the nutrition of the mother's milk. A high level of such energy may well be expressed by the vigor of play as well by the rate of body growth. Lambs which are well-fed also must have more time to engage in play than those which have to supplement low milk intake by grazing and ruminating. Shackleton (1973) observed that the well-fed Kootenay lambs spent more time in play than did the Banff lambs. Similar observations also were made by Geist (1971) for the more active Stone lambs as compared to the more-lethargic bighorn lambs.

Aoudad young in the Hondo Valley were observed to engage in play activity which was frequent and which lasted for long periods. The long suckling durations, few refusals

by adults, the low level of foraging among neonates and the high levels of play with frequent participation by adult animals indicate a vigorous and healthy population.

Social Behavior

The social hierarchy of the aoudad resembles that of other species of the Caprini tribe. Evidently throughout this group, the largest horn-size males participate in a high percentage of courtship and mating activities with females (Katz 1949, Geist 1971, Shank 1972, Grubb 1974, Nievergelt 1974, Schaller and Mirza 1974, Schaller 1977). The larger rams establish dominance and higher rank status by challenging, during the early stages of the rut, any subordinates that try to court the females. A system of linear hierarchy based on horn size is established (Geist 1966 a, 1966 b) with the large-horned males enjoying reproductive advantage. By participating in the majority of interactions with estrus females, males high in the social hierarchy apparently cause conception in most of the females and are thus the main contributors to the population gene pool.

Male non-aggressive behavior toward females is essential in sexual behavior since aggressive encounters with females could result in the latter's withdrawal rather than in the desired contact (Buechner and Schloeth 1965, Geist 1971, Shank 1972). As a result, only four agonistic patterns were

directed by males toward females. Aggressive patterns, although lacking the intensity seen among adult animals, were commonly displayed by juveniles toward one another. This behavior was expressed in the form of play fighting between rivals and may assist in the establishment of dominance relationships between siblings (Dzieciolowski 1969, Lumina 1972).

Large rams (Class III) not only engaged in more sexual interactions with females but also displayed more sexual patterns per sexual interaction. There was a positive correlation between horn size and sexual activity (Figure 24). Males with the largest horns exhibited the greatest sexual activity toward the females. It can be concluded that the level of sexual activity in male aoudads is proportional to horn size.

Males of the largest horn size were the most mature and undertook a longer courtship before mounting the female. As a result, the largest rams in a group spent most of their time engaged in sexual activity with females. The cnly exception to the system of linear dominance based on horn size was the activity of subadult males toward subadult females. Although participating in only 11% of the sexual interactions exhibited by males of all age classes, subadult males initiated short overt sexual patterns toward females of their own class.

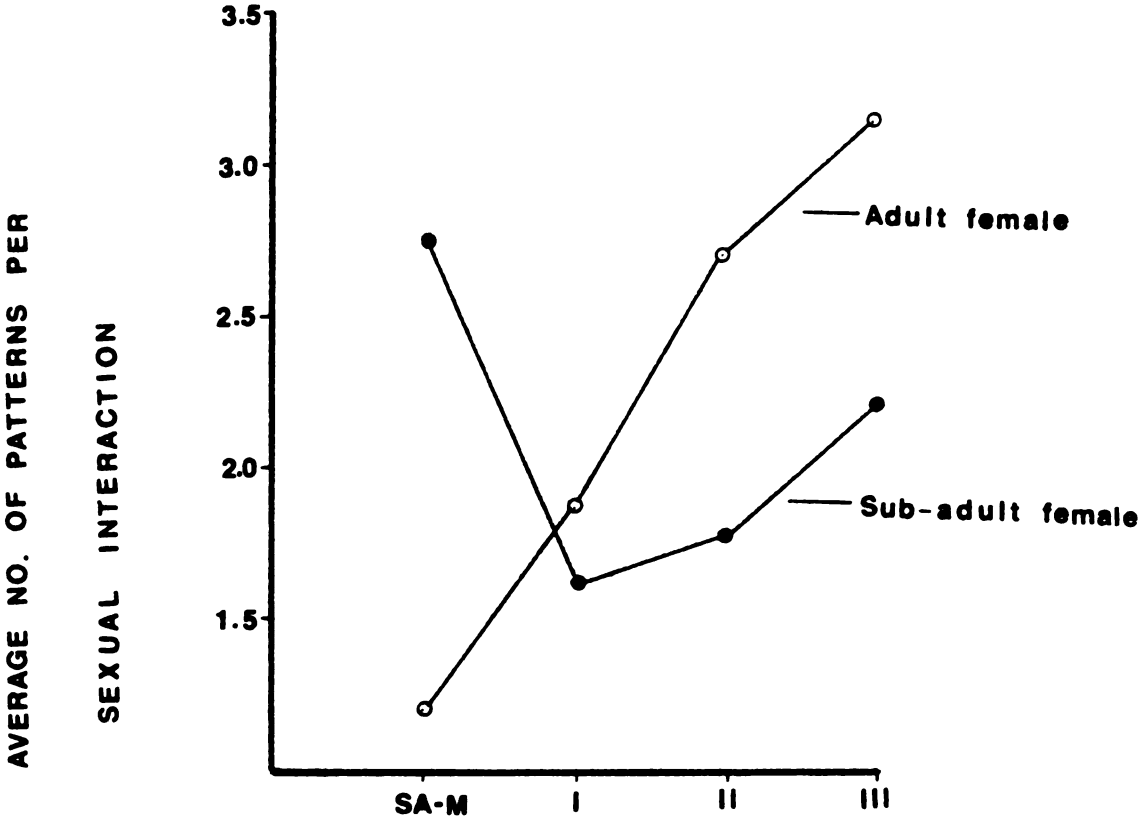

Figure 24. Average number of sexual patterns displayed by males of the several age classes, during the rutting season, 1982, Hondo Valley, New Mexico.

Class II males, averaging 4 years of age, displayed prolonged sexual behavior patterns toward females. In the absence of Class III rams, the Class II males behaved as social equivalents of the larger rams indicating their nearly full growth and approaching physiological and social maturity. Fast growth is characteristic of an expanding and colonizing population (Geist 1971). Such behavioral traits among the aoudad may be indicative of a vigorous population.

Although the animals constantly engaged in aggressive encounters, such combats were not seen to result in serious injuries. After delivering several blows, the pair maintained close body contact in the form of neck-fighting, wrestling or locking their horns. Body contact has apparently been adopted as a defensive behavior in order to diminish wounding blows from the antagonist's sharp horns (Geist 1966 a, Walther 1974).

Sexual dimorphism among the aoudad is not as pronounced as in true sheep (Schaller 1977). Females attain almost 75% of their adult horn size during the first year. Using their horns as weapons, females become more aggressive as they grow in horn and body size. Although females did not engage in ritualized fights to gain dominance within the group, the aggressive displays employed by dominant females against subordinates were similar to those exhibited by rams

in combat with other males. The high level of aggressiveness displayed by adult females seemed to reflect their desire to maintain a high social status within the female group.

At this point in the development of aoudad ethology, the selective advantage of high levels of aggressiveness among females can only be speculated. Agonistic displays by the females may serve to possess more-dominant and hence more-healthy mates. Also it may help to secure better foods and bedding sites and to assist in protection of young from harrasement by other members of the group (Schaller 1977).

The majority of behavioral patterns seen in aoudads are rather widespread in the Caprini tribe (Table 17). Most of the patterns observed have also been reported for the mountain goat (Oreamnos americanus) (Geist 1964), Nilgiri tahr (Hemitragus hylocrius)(Schaller 1970), bighorn and Dall sheep (Geist 1971), markhor (Capra falconeri)(Schaller and Mirza 1974), feral goat (Shank 1972), urial sheep (Ovis orientalis)(Schaller and Mirza 1974), feral Soay sheep (Ovis aries)(Grubb 1974), wild goat (Capra aegagrus)(Schaller and Laurie 1974), Himalayan tahr (Hemitragus jemlahicus)(Schaller 1977) and Asiatic ibex (Capra ibex) and Marco Polo sheep (pers. obser.)

A comparison of individual courtship and aggressive patterns employed by the aoudads and other Caprids shows

Table 17. Behavioral patterns used by aoudads and other members of the Caprini tribe.

		Ovis				Capra						
	Aoudad	Mouflon	Urial sheep	Bighorn sheep	Soay sheep	Markhor	Wild goat	Asiatic ibex	Feral goat	Tahr	Bahral	Mountain goat
Aggressive												
Abdomen-lift	*	-	-	-	-	-	-	-	*	-	-	-
Broadside	*	-	-	-	-	x	x	-	x	x	-	x
Butt	x	x	x	x	x	x	x	x	x	x	x	x
Hook	x	-	-	-	-	-	-	-	-	x	-	x
Horn	x	x	x	x	x	x	x	x	x	x	x	x
Horn-lock	x	x	*	*	-	-	-	-	-	-	-	-
Horn-threat	x	x	x	x	x	x	x	x	x	x	x	x
Huddle	x	x	x	x	?	-	-	-	-	-	x	-
Jump	-	x	x	x	?	x	x	x	x	x	x	x
Neck-fight	x	x	-	*	-	-	-	-	*	*	x	-
Parallel-walk	x	x	x	x	-	-	-	x	*	-	x	x
Rush	x	x	x	x	x	x	x	x	x	x	x	x
Clash	x	x	x	x	x	x	x	x	x	x	x	-
Shoulder-push	x	x	*	x	x	*	*	*	x	x	x	x
Sexual												
Crouch	x	-	-	-	-	-	-	-	-	-	-	-
Headshake	x	x	-	x	x	x	x	x	x	-	-	-
Kick	-	x	x	x	x	x	x	x	x	x	x	x
Lipcurl	x	x	x	x	x	x	x	x	x	x	x	x
Low-stretch	x	x	x	x	x	x	x	x	x	x	x	x
Penis-mouthing	x	-	-	-	-	x	x	x	x	x	x	-
Rear-sniff	x	x	x	x	x	x	x	x	x	x	x	x
Urine-spraying	-	-	-	-	-	x	x	x	x	x	-	-
Stand	x	-	-	-	-	-	-	-	-	-	-	-
Tongue-flick	x	x	x	x	x	x	x	x	x	x	x	x
Twist	x	x	x	x	x	x	x	x	x	*	-	x

x = trait observed
* = rare or found only in young
? = observation not clear
- = trait not observed or absent

differences in the execution of the various patterns. Unlike wild goats (Schaller and Laurie 1974), aoudads do not raise the tail when sexually aroused. Instead, the tail is folded under the hindquarters and between the legs (Figure 9 and 12). Tail-raising was observed when aoudads were alarmed but, in contrast to goats, the tails were raised only to the horizontal position. In the alarm posture they snorted loudly by expelling air through the nostrils. Such snorting is also common in the mouflon (Ovis ammon musimon) (Pfeffer 1967), mountain goat and feral goat (Rudge 1979, Shank 1972).

Regardless of age, rear-sniffing is common among male aoudads. On three occasions females also were observed to rear-sniff both female and male partners. Mimicry of male behavior by females in estrus has been noted by Geist (1968) among mountain goats and bighorn sheep. Sniffing of perineal areas by males stimulated female aoudads to urinate. In contrast to the wild goat which often waits until the female has urinated before sniffing the urine (Schaller and Laurie 1974), aoudad males let the females urinate directly on their lips, a behavior also noted among mountain sheep (Geist 1971). While lip-curling, aoudads waved their heads from side to side in a fashion similar to that of the Asiatic ibex and the markhor (Schaller and Laurie 1974).

The front-kick commonly used by Capra and Ovis during

sexual displays (Geist 1971, Shank 1972, Shackleton 1973, Walther 1974, Schaller 1977) and also by mountain goats (Geist 1964) was not noted among the aoudads nor has it been reported in the literature (Katz 1949, Haas 1959).

The spraying of forelegs and head with urine (Shank 1972, Schaller and Laurie 1974) as seen among goats was not present in aoudads. Like goats, however, the male aoudad sometimes nuzzled its penis and inserted it in the mouth (Katz 1949). Spontaneous ejaculation was observed on two occasions.

In courting females, aoudad males frequently low-stretched and twisted. These patterns, though, did not seem to be as extended as in bighorn sheep (Geist 1971). They were of short duration and ended abruptly as the male approached the female closely. The crouch (Figure 15) which followed after low-stretching and twisting was a prevalent display among the aoudads which is absent among other species in the Caprini tribe.

Agonistic behavior of the aoudad is also of interest when compared to other Caprids, and shows some distinct differences from those animals. Before clashing, aoudads run on all fours and clash without raising their forelegs. This form of head-on charge is similar to that of primitive Ovis species (Pfeffer 1967, Hafez and Scott 1969) and is in sharp contrast to the bipedal clash of other members

of the Caprini tribe (Nievergelt 1967, Roberts 1969, Schaller 1970, Geist 1971, Walther 1974).

Wrestling is common in aoudads after an initial sharp body contact. This behavior is lacking in both sheep and goats and evidently is peculiar to the aoudad among Caprids. Neck-fighting, homologous to the head-wrestling described by Shank (1972) for the feral goat, is performed by markhor (Roberts 1969) and mouflon (Pfeffer 1967) as well as by aoudads. Although young mountain sheep head-wrestle during play (Shackleton in Shank 1972), the pattern is only seen in a very rudimentary form in adult bighorns (Geist 1971). Similarly, shoulder-pushing which is used by aoudads, tahr, and mouflon has not been described among true goats.

Among the Caprids, the most primitive species, the Himalayan tahr, has the shortest horns. Horn size increases in length and mass among the most highly-evolved goats and sheep (Geist 1971). Perhaps as a result of differences in horn size and shape, two different modes of combat, ramming and wrestling have arisen (Geist 1966 a). The supracervical horns of primitive Caprids enable them to engage in wrestling and pushing contests by swinging one horn around the flank of the opponent. In contrast, those species which have evolved heavy skulls and horns ram one another head-to-head and then disengage after clashing at full speed.

In aggressive behavior, the aoudad displays patterns which are similar to that of the mouflon (Table 17).

Aoudads run, and clash on all four feet, withdrawing from the head-to-head combat after each clash, moving backward a few steps and then charging at each other again. Neck-fighting and shoulder-pushing also resemble that of mouflon (Pfeffer 1967). These patterns, characteristic of primitive Caprids (Hafez and Scott 1969, Walther 1974) are commonly used by both aoudads and mouflons. In the Rocky Mountain bighorn sheep, however, these two patterns occur only in a rudimentary form (Geist 1971).

Two sexual patterns, the crouch and the stand, evidently are unique to Ammotragus. Walther (1974) notes that during courtship displays, the male tries to establish superiority and detect whether the female is ready to accept a close approach without withdrawing. The crouch, a highly-ritualized behavior pattern of the ram is displayed by him for an extended period prior to mounting. The crouch and stand seems to act to concentrate the female's attention and to lead to sexual arousal. Display threats such as the front-kick are used by all other members of the Caprini tribe in their courtship of females. Aoudad males do not perform such aggressive displays during courtship. Specialized patterns, such as the crouch and stand, probably have been developed in lieu of sexual contact displays. In other sexual behaviors, the aoudad displays patterns which are common to both Capra and Ovis, with the exception of penis-mouthing which has only been observed among Capra.

Little is known about the evolutionary origins of the aoudad. Based on its anatomy, the species shows mixed affinities. The behavioral repertoire of the aoudad also does not clearly demarcate the genus to which it is most closely related. In both qualitative and quantitative aspects the total social behavior patterns of the aoudad differ little from those of goats and sheep. They include forms of displays which are common to both groups. In accordance with Schaller and Mirza (1974), it may be best to conclude that the behavioral characteristics of the aoudad place it in an intermediate position between Capra and Ovis.

MANAGEMENT RECOMMENDATIONS

Among the wild ungulates introduced into the United States none may have been as successful as the aoudad. The species has thrived and extended its range considerably during the past four decades. It is estimated that from a collective total of 400 animals released into various areas of the southwest since the early 1940s, the aoudad population had increased to almost 6,500 by 1980 (Simpson and Krysl 1981). This conservative figure does not include over 2,000 animals which have been harvested since legal hunting began in the mid 1950s.

The aoudad appears to exhibit plasticity in its selection of various habitats. Records show that the aoudad has dispersed widely in New Mexico and has colonized suitable habitats throughout the state. It has become successfully established in vegetative types ranging from creosote-bush lowland deserts to pinyon-juniper vegetation typical of dry mountain foothills (Simpson and Krysl 1981). The rapid dispersal of the species confirms its reproductive and survival capabilities in its new habitat.

It is believed that the population may increase in future years in the Hondo Valley and cause management problems there. To continue the harvesting of trophy

animals on a sustained basis and to prevent the population from further expanding and degrading range conditions, the following recommendations are made:

1) A careful monitoring of trophy quality should be undertaken to detect trends in the sizes of rams harvested. At present, 15-20 rams are harvested annually in the Hondo Valley. Most rams shot are Class II males. Of the 20 trophy rams legally harvested during the 1982 hunting season, only three were Class III rams. Most of the hunting pressure was concentrated on the medium size Class II rams. Due to their low numbers, trophy quality males are likely to decline if current harvesting practices are continued for an extended period. In case of a decline in horn size, trophy hunting might be discontinued for a short time to allow the numbers of mature rams to increase.

2) To reduce the number of females and to take advantage of an unexploited resource, the female sector of the population should be cropped at a maximum sustainable rate. Population structure on the study area revealed a high proportion of females. A large percentage of females in a population causes maximization of the reproductive rate and thus an increased rate of population growth. Such an increase in numbers eventually will result in range overuse and/or the dispersal of animals into unoccupied areas.

3) To reduce the number of domestic stock utilizing

pastures close to the Hondo River. Although the present level of about 21 hectares per animal unit on the South Ranch seems to be compatable with the preservation of good range conditions, heavy use of agricultural fields, especially by the female segment of the aoudad population, was noted throughout the year. Heavy utilization of pastures near the river has caused deteriorating vegetative conditions and resulted in erosion of the topsoil. Those landscapes are now marked by shallow gullies.

4) Dietary studies are recommended to reveal the degree of competition for food resources by aoudads, mule deer and domestic sheep. These procedures are necessary to detect the conditions under which one or more species is at a competitive disadvantage and to indicate if further management procedures need to be undertaken.

Some plant species appeared to be eaten by all three species, yet the degree of competitive range use by these sympatric species is not well known. If competition for preferred forage plants is severe, it could result in the rapid deterioration of range conditions. Interspecific competition possibly also occurs with the desert bighorn sheep where aoudads overlap their range. Of 49 desert bighorn food plants evaluated, 37 have been recorded also to be eaten by aoudads (Simpson et al. 1978).

5) Until the results of interspecific competition with native ungulates are known, efforts should be made (probably

by intensive hunting of all sex and age categories) to stop the spread of aoudads from spreading beyond its present range.

Reports of aoudad movements indicate that the species has dispersed widely in eastern New Mexico and has probably colonized all suitable areas in that part of the state (Simpson and Krysl 1981). The westward extension of its range into the San Andreas mountains is threatening the already beleaguered desert bighorn sheep population there. The extensive westward range expansion by aoudads and its arrival close to the continental divide in New Mexico means that in future years the species could extend its range into Arizona where it is likely also to infiltrate existing bighorn habitats.

SUMMARY

The population characteristics and social behavior of the aoudad (Ammotragus lervia) were studied between July 1981 and December 1982 in the Hondo Valley, New Mexico.

A population estimate by direct count was made on 12 randomly-selected plots. It yielded a mean density of 6.4 animals/km^2, indicating a total of 615 (± 179) animals on the entire 96 km^2 study area. A Lincoln-Petersen estimate based on sightings and involving 76.9% of marked animals gave a similar population estimate of 560 (± 184).

Population structure was estimated during the rutting season when members of all sex-age classes were present on ranges occupied by females throughout the year. A Chi-square test showed no significant difference from unity in juvenile sex ratios. The sex ratio in adult animals, however, was skewed toward females. Ratios tallied during the two respective years were 16.2-13.2% adult males, 33.7-35.6% adult females, 11.2-13.1% subadults and 38.8-37.9% juveniles.

Parturition took place mainly between March and May in 1982, when 85.5% of the recorded births occurred. Some females gave birth through the summer and fall but virtually none took place during winter.

The average suckling duration for young juveniles of all ages was 32.2 (± 23.2) seconds. Suckling endured

4-150 seconds at each bout, with the majority 86.8% of bouts lasting 6-45 seconds. Thirty percent of suckles observed among one week old juveniles lasted over 60 seconds. As the young grew older, the duration of their suckles dropped until the fourth week of life when it levelled off. Suckling durations for twins and single animals were not significantly different.

Aoudad young in the Hondo Valley engaged in play activity which was both frequent and long-lasting. Play behavior of five different kinds i.e. play-fighting, gamboling, lone-rushing, chasing and sexual-play, were recognized. While play activity invariably was initiated by a juvenile, adult animals participated 25.9% of the time.

The long suckling durations, few refusals by mothers, low levels of foraging among neonates and high levels of play with frequent participation by adult animals are all features which seem to indicate a vigorous and healthy population.

Frequencies of behavioral interactions between members of the various sex-age groups indicated that the order of social preference was controlled by the positions of the animals in the social hierarchy. Social partners were chosen by dominant males. With an established position in the social hierarchy, each animal showed preferences for members of certain classes and avoided individuals of other classes. Dominance was determined by horn size with rams

with the largest horns pairing most frequently with females during courtship. In the presence of a larger ram, the behavior of subordinate males seemed to be supressed.

Agonistic patterns used by dominant rams toward subordinates primarily involved horn displays. Such intention-movements evidently enabled dominants to intimidate subordinates without making physical contact. Also displaying their large horns, females sometimes behaved aggressively toward their partners. Probably as a result of the lack of pronounced sexual dimorphism, the behavior of females toward their subordinates resembled that between males in dominance fights.

The majority of behavior patterns seen among the aoudads also are widespread in the Caprini tribe. Individual courtship and aggressive patterns, however, showed differences in the execution of various patterns. In both qualitative and quantitative aspects, the total social behavior patterns of Ammotragus differ from those of Capra and Ovis but include forms common to both groups. The behavioral repertoire of the aoudad does not clearly demarcate the genus to which it is most closely related. Based on its behavioral characteristics, it seems to occupy an intermediate position between the two groups.

LITERATURE CITED

Alexander, G. and H.G. Davies 1959. Relationship of milk production to number of lambs born and suckled. Aust. J. Agric. Res. 10:720-724.

Altmann, S.A. 1968. Sociobiology of the rhesus monkeys. The basic communication network. Behavior. 32:17-32.

Bailey, T.T.N. 1981. Statistical methods in biology. John Wiley and Sons, New York.

Barrett, H.R. 1980. History of the Hearst Ranch Barbary sheep herd. Pages 46-51 in C.D. Simpson, ed. Proc. Barbary sheep ecology and management symp. Texas Tech Univ. Press, Lubbock.

Bate, D.M.A. 1955. Vertebrate faunas of Quartenary deposits in Cyrenacia. Pages 274-291 in P.B.M. McBurney and R.W. Hey eds. Prehistory and Pleistocene geology in Cyrenacia. Cambridge Univ. Press, Cambridge.

Beach, A.E. 1945. Current concepts of play in animals. Amer. Nat. 79:523-540.

Bissonnette, T.H. 1941. Experimental modification of breeding cycles. Physiol. Zool. 18:229.

Brentjes, B. 1980. The Barbary sheep in ancient North Africa. Pages 25-26 in C.D. Simpson ed. Proc. Barbary sheep ecology and management symp. Texas Tech Univ. Press, Lubbock.

Brown, C.E. 1936. Rearing wild animals in captivity, and gestation periods. J. Mammal. 17:110-113.

Buechner, H.K. and R. Schloeth. 1965. Ceremonial mating in Uganda kob (Adenota kob thomasi). Z. Tierpsychol. 22:209-225.

Calhoun, J.B. 1950. The study of wild animals under controlled conditions. Annal. N.Y. Acad. Sci. 51:1113-1122.

Cherniavski, F.B. 1962. On the reproductive and growth of the snow sheep (Ovis nivicola). Zoologicheskii Zhurnall. 51:1556-1566.

Dickinson, T.G. and C.D. Simpson. 1980. Dispersal and establishment of Barbary sheep in southeastern New Mexico. Pages 33-45 in C.D. Simpson ed. Proc. Barbary sheep ecology and management symp. Texas Tech Univ. Press, Lubbock.

Donly, M.J. and J. Murno. 1962. The effects of suckling, management and season on sheep milk production as estimated by lamb growth. Anim. Prod. 41: 215-270.

Dvorak, D.F. 1980. A brief history and status of aoudad sheep in Palo Duro Canyon, Texas. Page 23 in C.D. Simpson ed. Proc. Barbary sheep ecology and management symp. Texas Tech Univ. Press, Lubbock.

Dzieciolowski, R. 1969. Growth and development of red deer calves in captivity. Acta Theoriol. 14:141-151.

Espmark, V. 1969. Mother-young relationship and development of behavior in roe deer. Viltrevy. 6:461-530.

Geist, V. 1964. On the rutting behavior of mountain goat. J. Mammal. 45:551-568.

_____ 1966 a. Evolution of horn like organs. Behavior. 27:175-214.

_____ 1966 b. The evolutionary significance of mountain sheep horns. Evolution. 20:558-566.

_____ 1968. On the inter-relation of external appearance, social behavior and social structure of mountain sheep. Z. Tierpsychol 25:199-215.

_____ 1971. Mountain sheep. A study in behavior and evolution. The Univ. of Chicago Press, Chicago.

_____ and R.G. Petocz. 1977. Bighorn sheep in winter: do rams maximize reproductive fitness by spatial and habitat segregation from ewes? Can. J. Zool. 55:1802-1810.

Gray, G.G. 1980. Aspects of Barbary sheep (Ammotragus lervia) biology in the Palo Duro Canyon, Texas. Ph.D. Thesis. Texas Tech Univ., Lubbock.

_____ and C.D. Simpson. 1980. Identification of Barbary sheep sex and age classes in the field. Pages 63-65 in C.D. Simpson ed. Proc. Barbary sheep ecology and management symp. Texas Tech Univ. Press, Lubbock.

Grubb, P. 1974. Mating activity and social significance of rams in a feral sheep community. Pages 467-476 in V. Geist and F. Walther eds. The behavior of ungulates in relation to management. IUCN Publ. No. 24, Morges.

Haas, G. 1959. Untersuchungen über angeborene Verhaltensweisen Verhaltensweisen bei Mähnenspringern (Ammotragus lervia Pallas). Z. Tierpsychol. 16:218-242.

Hafez E.S.E. 1952. Studies on the breeding season and reproduction of the ewe. J. Agric. Sci. 42:189-265.

_____ and J.P. Scott. 1969. The behavior of sheep and goats. In E.S.E. Hafez ed. The behavior of farm animals. Bailliere, Tyndell and Cox, London.

Hall, F.R. 1964. Chemistry of water of a section of the eastern flank of the Sacramento Mountains, Lincoln and Otero Counties, New Mexico. New Mexico Geological Society. 15th Field Conference, 161-166.

Hamdy, A.R. and T. Schmidt. 1972. Aggressive and social behavior among the Barbary sheep or aoudads (Ammotragus lervia) of the herd of the Egyptian Zoo in Cairo. Bull. Fac. Sci. Cairo Univ. 42:277-283.

Hinde, A.R. 1960. Animal behavior. McGraw Hill Inc., New York.

Horejsi, B.L. 1975. Suckling and feeding behavior in relation to lamb survival in bighorn sheep. Ph.D. Thesis. Univ, of Calgary.

Katz, I. 1949. Behavioral interactions in a herd of Barbary sheep (Ammotragus lervia). Zoologica 34: 9-18.

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

Klopfer, P.H. and M.S. Klopfer. 1968. Maternal "imprinting" in goats: fostering of alien young. Z. Tierpsychol. 25:862-866.

Labanov, V. and V.D. Treus. 1971. Reproduction of Ammotragus lervia at the Askamiya-Nova Zoo. Vest. Zool. 5:23-26.

Lenarz, S.M. 1979. Social structure and reproductive strategy in desert bighorn sheep (Ovis canadensis mexicana). J. Mammal. 60:671-678.

Little, M.T. and F.J. Hills. 1968. Agricultural experimentation. Design and analysis. John Wiley and Sons, New York.

Lumina, A.R. 1972. The relationship between dominance and play behavior in American buffalo (Bison bison) Z. Tierpsychol. 30:416-419.

Martin, C.W. 1964. Some aspects of the natural history of the Capitan and Jicarilla mountains and Sierra Blanca region of New Mexico. New Mexico Geological Society, 15th Annual Conference. 171-176.

McBurney, C.B.M. 1967. The Haua Fteah (Cyrenica) and the Stone Age of the southeastern Mediterranean. Cambridge Univ. Press, Cambridge.

Morrison, B.L. 1980. History and status of Barbary sheep in New Mexico. Page 15 in C.D. Simpson ed. Proc. Barbary sheep ecology and management symp. Texas Tech Univ. Press, Lubbock.

Nievergelt, B. 1967. Die Zusammensetzung der Gruppen beim Alpensteinbock. Z. Säugetierk. 82:129-144.

_____ 1974. A comparison of rutting behavior and grouping in the Ethiopian and Alpine ibex. Pages 324-340 in V. Geist and F. Walther eds. The behavior of ungulates in relation to management. IUCN Publ. No. 24, Morges.

Ogren, H.A. 1965. Barbary sheep. Bull. No. 13. New Mexico Dept. of Game and Fish. Santa Fe.

Petocz, R.G., K. Habibi, A. Jamil and A. Wasey. 1978. Report on the Afghan Pamir. Biology of the Marco Polo sheep (Ovis ammon poli). Field document No. 6 FO/AFG/74/016.

Pfeffer, R. 1967. Le mouflon de Corse (Ovis ammon musimon). Mammalia. 31. Supplement.

Roberts, T. 1969. A note on Capra falconeri (Wagner 1839). Z. Säugetierk. 34:238-249.

Rudge, M.R. 1970. Mother and kid behavior in feral goats. Z. Tierpsychol. 27:687-692.

Sadlier, R.M.F.S. 1967. The ecology of reproduction in wild and domestic mammals. Mathew Co. Ltd., London.

Saiz, B.R. 1980. Barbary sheep harvest and population trend information. Proj. No. 4 W-93-12-23. Performance report, New Mexico Dept. of Game and Fish, Mimeo.

Schaller, G.B. 1970. Observations on the Nilgiri tahr (Hemitragus hylocrius, Ogilby 1838). J. Bomb. Nat. Hist. Soc. 67:365-389.

_____ 1977. Mountain monarchs. Wild sheep and goats of the Himalaya. The Univ. of Chicago Press, Chicago.

_____ and A. Laurie. 1974. Courtship behavior of the wild goat. Z. Säugetierk. 39:115-127.

_____ and Z.B. Mirza. 1971. On the behavior of Kashmir markhor (Capra falconeri cashmirensis). Mammalia. 35:548-566.

_____ and _____ 1974. On the behavior of Punjab urial (Ovis orientalis punjabensis). Pages 306-323 in V. Geist and F. Walther eds. The behavior of ungulates in relation to management. IUCN Publ. No. 24, Morges.

Seber, G.A.F. 1973. The estimation of animal abundance and related parameters. Griffin, London.

Shackleton, D.M. 1973. Population quality and bighorn sheep (Ovis canadensis canadensis). Ph.D. Thesis, Univ. of Calgary.

Shank, C.C. 1972. Some aspects of social behavior in a population of feral goats (Capra hircus). Z. Tierpsychol. 30:488-528.

_____ 1982. Age-sex differences in the diets of wintering Rocky Mountain bighorn sheep. Ecology. 63:627-633.

Simpson, C.D. and L.J. Krysl, D.B. Hampy and G.G. Gray. 1978. The Barbary sheep: a threat to desert bighorn survival. Desert Bighorn Council Trans. 22:26-31.

_____ and _____ 1981. Status and distribution of Barbary sheep in the southwest United States. Desert Bighorn Council Trans. 25:9-15.

Snedecor, G.W. 1956. Statistical methods. Iowa State Press, Ames.

Solbert, G.K. 1980. Social organization and behavior of aoudad (Ammotragus lervia) in Texas. Pages 66-72 in C.D. Simpson ed. Proc. Barbary sheep ecology and management symp. Texas Tech Univ. Press, Lubbock.

Southwick, C.H. 1955. Regulatory mechanisms of house mouse populations: Social behavior affecting litter survival. Ecology: 36:627-634.

Sprankle, G.D. 1980. Soil survey of Lincoln County area, New Mexico. Soil Conserv. Ser., U.S. Dept. of Ag.

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

Walther, F. 1974. Some reflections on expressive behavior in combats and courtship of certain horned ungulates. Pages 56-106 in V. Geist and F. Walther eds. The behavior of ungulates in relation to management. IUCN Publ. No. 24, Morges.

Watson A. and R. Moss. 1972. A current model of population dynamics in red grouse. Pages 134-149. Proc. 15th Int'l Ornithol. Cong. Leiden Brill.

Wynne-Edwards, V.C. 1959. The control of population density through social behavior: a hypothesis. Ibis. 101:436-441.

_____ 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, London.

_____ 1978. Intrinsic population control: an introduction. Pages 1-22 in F.J. Ebling and D.M. Stoddart eds. Population control by social behavior. Inst. of Biol., London.

Yoakum, J. 1980. Barbary sheep in the United States: Past, present and future. Pages 9-14 in C.D. Simpson ed. Proc. Barbary sheep ecology and management symp. Texas Tech Univ. Press, Lubbock.