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A REVIEW OF THE SOCIAL BEHAVIOR OF FERAL AND WILD SHEEP AND GOATS[1]

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Summary

Feral sheep (Ovis) and goat (Capra) populations are found scattered throughout the world. Although generally separable by their morphology and ecology, the social behavior of feral sheep and goats is very similar. It also appears to be little changed from related wild species. Social organization is quite variable, particularly group size and composition, varying more among populations than between the genera. Although definite dominance hierarchies develop among males, they are weak or absent among female feral and wild sheep. Maternal care is similar among species, although the neonate goat may sometimes show a brief hiding phase. Suckling rates are high and durations short, but the process of weaning is poorly understood. Fighting behavior of sheep and goats is closely related to their horn structure, as is skull morphology. Horns are used both for overt fighting and as indicators of relative social rank. Many of the behavior patterns used by dominant male sheep and goats to subordinates in agonistic interactions are the same as those used by males courting estrous females. One of the major differences between feral sheep and goats is in their use of scent. Unlike sheep, male goats exhibit urine marking, possibly related to advertising a male's conditions, and to synchronizing estrus among females. Males court females with a series of increasing contact patterns culminating in copulation. Females may exert some choice in selecting a mate based on his courtship performance and social status.

(Key Words: Behavior, Social, Feral, Wild, Sheep, Goats.)

Introduction

The significance of animal behavior to domestic animal husbandry has been clearly documented (Hafez, 1975; Arnold and Dudzinski, 1978; Syme and Syme, 1979; Craig, 1981). Initially, before animal domestication, man used his knowledge of wild animal behavior to hunt them successfully. Later, whether by design or accident, he used behavior traits, particularly social ones, as key criteria in his selection of and success with domestic animals (Hale, 1962; Tennessen and Hudson, 1981). Knowledge of animal behavior may be more important today as intensive husbandry practices place animals in environments far removed from those they were originally selected for, and even more distantly removed from those their wild ancestors were adapted to. In many instances it may be easier to modify an animal's environment to provide or eliminate some key stimulus than to use artificial selection to exploit a favorable behavior or eliminate an unfavorable one. More recently concerns over animal welfare have led to the need for more information about domestic animal behavior (Craig, 1981).

Can we learn anything that may be usefully applied to domestic ungulate production from the behavior of their feral or wild conspecifics? This will depend in part upon the effect domestication has had on ungulate behavior. Although domestic ungulates often differ morphologically from their wild relatives, and learning, maintenance and social behavior may vary quantitatively (Shackleton, 1973; Horejsi, 1976; Arnold and Dudzinski, 1978; Berger, 1979), we

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can find no published data to show that significant qualitative changes in ungulate social behavior have occurred due to domestication. It would seem, therefore, that social behavior is not only important in animal husbandry but that it is also resistant to change. As a result we share the view expressed by others (Craig, 1981) that information about animal behavior under natural conditions is valuable for a proper understanding of domestic animal behavior. This information, we feel, would reduce possible insularity and potential misinterpretation of behaviors, and help in the design of environments for domestic animal production systems that most effectively take advantage of behavior. A detailed discussion of models suggesting how feral animal behavior may be applied to animal production is presented by McBride (1984). The objective of this paper is to provide a summary of social behavior studies of feral and wild sheep and goats, to be used as a reference source and hopefully as an initial comparative framework for the evaluation of domestic animal behavior.

Systematics and Distribution

Sheep (Ovis) and goats (Capra) both belong to the tribe Caprini, which also contains tahr (Hemitragus), aoudad (Ammotragus) and bharal (Pseudois). Differentiating species in the Caprini is often a problem due to close similarities within the group, the number of intermediate forms and the zoogeographic turmoil resulting from speciation during orogeny (Schaller, 1977). Goats are considered to comprise from one (Herre and Rohrs, 1955) to nine species (Lydekker, 1898), and sheep taxonomy is even more confused with as many as 37 subspecies being recognized (Herre and Rohrs, 1955). We will follow Schaller (1977) in recognizing six species in each of the two genera. To help reduce confusion in overlapping definitions we will refer to all Capra as "goats," all Ovis as "sheep," all never-domesticated species as "wild," species now or once subject to artificial selection as "domestic," domestic animals currently under human control as "farm sheep and goats" and all free-ranging domestic animals as "feral." In addition Capra aegagrus will be referred to as "agrimi" and North American wild sheep as "mountain sheep."

Feral sheep and goat populations are found scattered throughout the world. Rudge (1982) has collected data on 31 feral sheep and 64 feral goat populations presently extant. Feral populations derive either as escapees from domestic flocks or as deliberate releases. In the past, goats and other livestock were commonly loosed on remote oceanic islands to provide food for sailors.

Distributional maps for many species of wild sheep and goats can be found in Geist (1971), Schaller (1977) and Valdez (1982). Intolerance of deep snow together with requirements for xeric grasslands and mountain or foothill topography are the primary factors limiting the distribution of sheep and goats. Goats primarily occupy steep cliff areas, but also have a wide tolerance for altitude and habitat. Sheep are more typically found on gently sloping terrain such as alpine plateaus and foothills, often in close proximity to precipitous escape terrain.

Behavior of Sheep and Goats

Social Organization. Group size in sheep and goats (table 1) varies widely within species in response to local environmental conditions and to population characteristics. As in other ungulates, habitat structure is a particularly important determinant of group size, with larger groups occurring in populations inhabiting more open terrain (Eisenberg, 1966; Estes, 1974; Geist, 1974). This is generally interpreted as being one of several antipredator strategies: cover-seeking within the group (Hamilton, 1971), reduced detectability of a compact herd (Treisman, 1975), more effective predator detection (Pulliam, 1973) or cooperative defense (review in Wilson, 1975). Visual disruption in dense habitat may also reduce the ability of individuals to maintain large cohesive groups. Population size and density place obvious constraints on maximal group size. Considering these factors, there appears to be little difference between the group dynamics of the species and populations listed in table 1 whether they are wild or feral, sheep or goat. The generalization can be made that sheep and goats typically occur in groups of two to 10, with maximal group sizes of 100 to 150 dependent upon population density and terrain characteristics.

The degree and duration of sexual segregation in sheep and goat populations seems largely dependent upon the seasonality of breeding. Although photoperiod may be the proximal stimulus for the onset of estrus (Yeates, 1949), breeding seasons are more constrained and

TABLE 1. GROUP SIZES OF SHEEP AND GOATS

Species	Area	Mean group size	Range in group size	Modal group size	Population size	Source
Capra aegagrus (agrimi)	Pakistan	19–24	2–103	2–10	400–500	Schaller (1977)
	Pakistan	4–8	?–52			Schaller (1977)
Capra falconeri (markhor)	Afghanistan	16.5	1–?			Petocz and Larsson (1977)
		8.5	2–18		100–125	Schaller and Mirza (1971)
Capra hircus (feral goat)	California	3.8–11.0	1.–150	2	two populations = 300 and 250	Coblentz (1974)
	British Columbia		?–75		ca. 150	Geist (1960)
	British Columbia		1–100	4–6	ca. 150	Shank (1972)
	New Zealand	3.8	2–14		37	Riney and Caughley (1959)
	Hawaii		2–25	4	largest = 175	Yocum (1967)
	Seychelles	4.7	1–36	2		Gould (1979)
	Scotland		1–36	2	36	McDougall (1975)
Ovis orientalis (urial)	Pakistan	2.9–12.7	?–50			Schaller (1977)
Ovis ammon (argali)	Afghanistan		1–50	1–5 in summer 11–20 in winter		Petocz et al. (1978)
Ovis canadensis (mountain sheep)	British Columbia Alberta and	9.3	1–75	2–9	ca. 200	Blood (1963)
	British Columbia	10.7	1–40	2–9	ca. 150	Shackleton (1973)
Ovis aries (feral sheep)	Scotland	3.2	females 2–69 males 2–15		fluctuates between 174 and 425	Grubb (1974a)

synchronous in harsher climates because of the greater necessity of producing young when climatic and forage conditions are favorable. In general, the harsher the climate, the shorter the breeding season and the longer the period of sexual segregation. Therefore, we observe that where climates are mild and uniform, typically on oceanic islands, feral goats breed all year around or in several peak periods with mixed groups forming at various times of the year (Geist, 1960; Yocum, 1967; Williams and Rudge, 1969; Shank, 1972; Coblentz, 1974, 1980; Gould, 1979). Where the climate is less favorable, feral goats may breed only once per year and tend to segregate sexually most of the time (Darling, 1937; McDougall, 1975; Rudge and Campbell, 1977; Rudge and Clark, 1978). Wild goats and both wild and feral sheep rarely occupy benign climes and usually show pronounced seasonality of breeding and sexual segregation throughout most of the year (Geist, 1971; Jewell and Grubb, 1974; Schaller, 1977; Bunnell, 1982). An exception is the Ethiopian ibex, which breeds year-round (Nievergelt, 1974).

The separation of males from female groups appears to take place as the young males become physically and socially dominant over adult females (Geist, 1971; Shank, 1972; Grubb, 1974a; Schaller, 1977). Grubb (1974a) has demonstrated that maternal groups of Soay sheep (a primitive feral sheep) are invariably composed of related females and that male groups are remarkably stable outside of the rutting period. Geist (1971) found great fidelity in the composition of mountain sheep groups at each season.

Sheep and goat populations are typically comprised of several intermixing groups occupying specific home ranges (Hunter, 1964; Geist, 1971; Coblentz,1974; Grubb and Jewell, 1974; Gould, 1979), which may vary seasonally but are used each year. Seasonal changes in size and location of home ranges are intimately linked with climate, plant phenology and breeding activities (Geist, 1971; Coblentz, 1974; Grubb and Jewell, 1974). Home ranges of different groups are not discrete and tend to overlap to varying extents. Defense of group areas has not been recorded. The only suggestion of territoriality has been made by Pfeffer (1967) for individual mouflon males (Ovis orientalis musimon) during the breeding season.

Dominance relations among males are strongly exhibited in wild and feral sheep (Geist, 1971; Grubb, 1974b; Schaller, 1977) and goats (Shank, 1972; Coblentz, 1974; Schaller, 1977). An individual's social status or rank is usually correlated with horn size, age, weight and behavior (Geist, 1971; Shank, 1972; Grubb, 1974b; Schaller, 1977). Some consequences of male social status are discussed later in Agonistic Behavior. Among females, however, dominance hierarchies are either weak as in mountain sheep (Eccles, 1981), or apparently absent as in Soay sheep (Grubb, 1974a). The female hierarchies reported for farm goats may, as Syme and Syme (1979) suggest, be an artifact of husbandry conditions that alter group composition.

Mother-Young Interactions. Almost invariably, female sheep and goats isolate themselves in rugged terrain before, during and after parturition (Pfeffer, 1967; Rudge, 1970; Geist, 1971; Grubb, 1974a; Schaller, 1977). The isolation period allows the mother-young bonds to develop without interference from other females (Arnold and Dudzinski, 1978). The separation may also function to reduce predation (Lent, 1974; Arnold and Dudzinski, 1978) and climatic stress (Geist, 1971; Lynch and Alexander, 1976) through selection of protected sites. Some Soay sheep give birth in sheltered cleits or enclosures (Grubb, 1974a) although most observations of births and of neonates were in the open.

Immediately after birth, all ungulate mothers, except camels and pigs, vigorously lick their offspring. This apparently functions in olfactory recognition (review in Lent, 1974) and in drying the neonate so that it does not cool too rapidly (Geist, 1971).

Ungulate young can be roughly divided into either "hiders" or "followers" (Walther, 1961; Lent, 1974), depending upon whether the young hides and the mother leaves the general vicinity, or the pair remains together with the neonate hidden or not. Most sheep are followers (Geist, 1971; Grubb, 1974a), the lamb keeping up with the mother from birth, although the pair may remain isolated from the group for 5 to 7 d after parturition (Geist, 1971). Neonatal mouflon are reported to remain hidden for their first 3 d (Pfeffer, 1967; Schaller, 1977). Data for wild, feral and farm goats indicate that many have a weak hiding phase lasting from 2 to 4 d after birth (Collias, 1956; Rudge, 1970; Coblentz, 1974; McDougall, 1975;

Schaller, 1977). Lent (1974) concludes that the hiding stage in goats is very plastic and is influenced by genetics, environment and tradition. After the initial hiding stage, goat kids become followers and remain closely attached to their mothers. Sheep and goats rarely defend their young (Schaller, 1977), although isolated instances of maternal defense have been recorded (Collias, 1956; Walther, 1961; Geist, 1971).

Nursing is the primary form of contact between young sheep and goats and their mothers. The act of suckling differs very little within or between ungulate taxonomic groups (Lent, 1974), but the frequency and duration of nursing is very plastic depending upon the number and age of the young, genetic factors and nutritional regimen. Suckling variables can vary significantly between populations of a single species (Shackleton, 1973; Berger, 1979) and between years in a single population (Horejsi, 1976). Phenyotypic differences are large enough to mask any interspecific differences. In general, sheep and goats nurse very frequently (ca. once per hour) and for short mean durations (typically 10 to 30 s), although maximal suckle times can be much longer. The frequency distribution of suckling duration is highly skewed towards shorter times.

There are few firm data relating to the breakdown of mother-young bonds. The process has two related aspects; weaning and loss of the close, functional social relationship. Wild sheep and goats are mostly weaned by 4 to 5 mo (Geist, 1971; Schaller, 1977), although occasional suckles are observed much later. There are no comparable data for feral sheep or goats. Lent (1974) suggests that we need to know much more about the frequency and significance of winter nursing.

The first hint of a weakening of the mother-young bond in sheep and goats is the "creche" or "nursery band" developed when infants form large groups apart from the females. This has been reported for wild sheep (Welles and Welles, 1961; Geist, 1971), feral goats (Coblentz, 1974) and wild goats (Walther, 1961; Nievergelt, 1967). In general, the mother-young bond is first disrupted during the rut, at which time almost all suckling ceases. An even more complete break occurs just before the mother gives birth again, although the yearling often rejoins the mother and her newborn. The breakdown in the bond is a complex interaction of gradually increasing independence of the

young coupled with increasing indifference or aggressiveness on the part of the mother. This basic pattern has been reported for mountain sheep (Geist, 1971), mouflon (Pfeffer, 1967), feral goats (Rudge, 1970) and agrimi (Schaller, 1977). As noted earlier, female Soay sheep remain in the same band as their mothers, whereas the males move off and enter a male group on a different home range. Schaller (1977) felt that yearling males of several wild sheep and goat species have a greater tendency to leave the mother than do the females. Little is known about this or other aspects of weaning and the deterioration in mother-young relations.

Agonistic Behavior. The agonistic behavior of male sheep and goats is closely linked to the morphology of the weapon and display systems. Darwin (1871) was the first to suggest that horns and similar weapons function primarily in intraspecific struggles between males for access to females rather than as antipredator devices. Horns in sheep and goats serve not only as offensive weapons, but also in defense and display (Geist, 1966, 1971). For offense, the horns are used to deliver the heavy blows, with often the whole body weight thrown behind to magnify the force. At the same time the horns have defensive functions as they are used to catch the blow of the opponent, and together with the internal structure of the horn cores and brain case, help absorb the impact forces thus protecting the brain (Geist, 1971; Schaffer and Reed, 1972). Relative social rank and possibly fighting ability can also be displayed in the size of the horns. Certainly in mountain sheep horn size appears to be recognized and fights are avoided between males of different horn size (Geist, 1971).

The overall significance of horns is perhaps demonstrated by the behavior of genetically polled, feral male goats. Although these individuals were often of large body size, they were very unsuccessful breeders, because their access to estrous females was prevented by the horned males in the population (Shank, 1972).

Agonistic behavior serves at least two purposes: for immediate gain or protection of resources and for determining and maintaining dominance relations that will determine future access to resources. The agonistic behaviors associated with these functions may be distinct. Shank (1972) differentiated between "rush" and "clash" associations for feral goats that correspond to the two functions. Rush association patterns refer to overt aggression solely for

an immediate, utilitarian purpose. Clash association patterns are far more stereotyped and are used to determine or reinforce dominance relations. The clash association differs from the rush association in being bilateral and to some degree, ritualized. In both sheep and goats, low intensity fights are common and occur between two individuals that appear to recognize each other's social rank. Much rarer are high intensity dominance fights in which relative rank is contested, usually between similar sized males. In both sheep and goats, such fights can last for hours. Overt aggression is very similar in all sheep and goats. It is essentially unilateral and consists primarily of butts with the horns to the body of the opponent, rushes toward the opponent with lowered head indicating the intent to butt, and the simple lowering of the head and point of the horns toward the opponent, often accompanied by a forward swing of the head. Overt aggression is primarily directed by older, larger, more dominant animals toward younger, smaller, more subordinant ones (Geist, 1971; Shank, 1972; Schaller, 1977). In this regard, horns, by their size alone, serve to display dominance status. Schaller (1977) has shown the ubiquity of rush association patterns in the Caprini.

In feral goats, the most obvious aspect of ritualized fighting is the clash in which two individuals crash their heads and horns together with great force (Shank, 1972). One of the opponents often rears up on his hind legs with the feet placed in a plane parallel to the line between the two animals and delivers a twisting, downward blow to the waiting opponent's horns (figure 1). The hair along the midline of the back may be erected. After the clash, one or both opponents may freeze in a head up and averted position (figure 1). Otherwise, they may engage in head-wrestling wherein they attempt to twist each other over with interlocked horns. Near the end of a severe dominance fight, the winner of the interaction begins to treat the loser as an estrous female by delivering courtship patterns such as the twist, kick, nudge and mount (see below). That the loser accepts such behavior rather than moving away may be appeasement behavior. However, unlike in sheep, sexual behavior in an aggressive context is rare in goats (Schaller, 1977). Schaller (1977) concludes that the basic aggressive repertoire is quite uniform throughout the genus and, more specifically, that he could find few differences between the behavior of feral

goats (Shank, 1972) and the agrimi (Schaller and Laurie, 1974).

The only available study in the agonistic behavior of feral sheep is for Soay sheep (Grubb, 1974b). Ritualized behavior in sheep differs from that of goats in the ubiquitous use of courtship patterns by sheep in an agonistic context. Geist (1971) considers mountain sheep society to be basically homosexual in that subordinate males and estrous females are treated identically by dominant males and respond to them in a qualitatively and quantitatively similar fashion.

The most common expression of ritualized aggression in Soay sheep is "nudging" (Grubb, 1974b), in which the displayer approaches with head lowered and nose up, tongue flickering, head twisted and uttering a low grunting. This is synonymous with the "low-stretch" and "twist" that Geist (1971) described for mountain sheep. The displayer may kick the opponent with a stiff foreleg; a pattern termed "front-kick" by Geist (1971). In both mountain sheep and Soay sheep, nudging is the prerogative of the dominant ram. The receiver typically moves away slightly and grazes.

Dominance fights consist largely of a series of clashes in which the opponents rush forward and bang heads. Geist (1971) analyzed films of the clash and showed that it is a complex behavior in which the maximal force is produced by snapping the head down, striking with the narrow horn keel and riding the blow home with the full body weight (figure 1). Mountain sheep and Marco Polo sheep (Ovis ammon poli) commonly rear up on their hind legs during the clash, but it is rarer in mouflon and urials (Schaller, 1977). Grubb (1974b) does not describe Soay sheep clashing bipedally and Schaller (1977) reports a personal communication with Grubb indicating that the latter had seen it on only one occasion. The rise onto the hind legs in wild sheep is significantly different to that of goats in that in the former the feet are placed in a line perpendicular to the line of the clash and the animal is out of balance (figure 1).

There are several pattern types that may be interspersed with clashing. The most noteworthy is "shoulder-pushing" (Schaller, 1977) or "blocking" (Grubb, 1974b), in which the two animals stand side by side and shove with their shoulders. This behavior is very common in Soay sheep (Grubb, 1974b) and mouflon (Schaller, 1977), less so in mountain sheep and
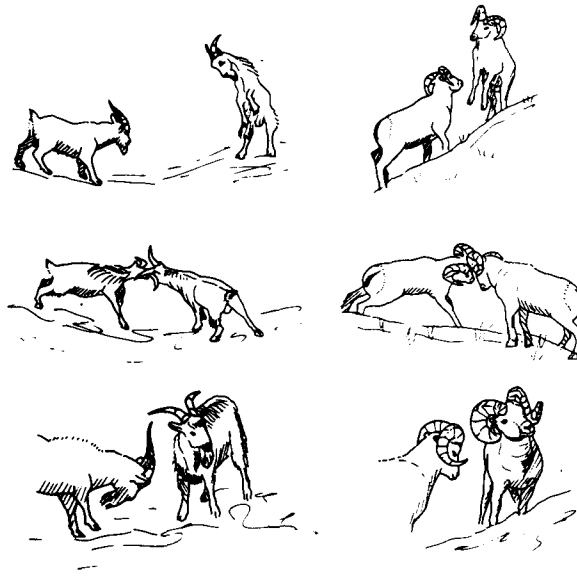
Figure 1. Comparison between feral goats and mountain sheep in their (upper) preclash jumps, (middle) clashes and (lower) postclash threat postures. Drawings taken from photographs; those for feral goats follow Shank (1972).

very rare in goats. By contrast, horn-wrestling, which is common in goats, is rare in all sheep except young mountain sheep (Shackleton, 1973) and mouflon (Pfeffer, 1967). Geist (1971) describes a "horn-present" in mountain sheep in which the opponents freeze after the clash with their heads averted in a position that best displays the horns (figure 1). The pattern is not conspicuous and Grubb (1974b) does not describe it for Soay sheep.

Goats and sheep differ markedly in their use of scent in an agonistic context. Sheep have pedal glands on all four feet as well as inguinal and preorbital glands. By contrast, goats have a tail gland and pedal glands on two feet at most. Male goats typically keep their tails raised whereas sheep do not; the significance of this difference is not clear but is presumably related to possession of a tail gland. Subordinate sheep commonly rub their faces on the horns and neck of dominants (Geist, 1971; Grubb, 1974b). Geist (1971) suggests that this serves to transfer preorbital secretions from the dominant and may have a recognition function among individuals in a group.

The most striking difference between sheep and goats in their use of scent is in the urine marking behavior of goats. While urinating, male goats typically hunch their backs and place the extended penis near the face or in the mouth (Shank, 1972; Coblentz, 1974, 1976; Schaller, 1977). The front quarters, beard and face become impregnated with a strong smelling scent. Shank (1972) speculated that the goat's beard may well have evolved as a repository for this scent. Coblentz (1976) suggests that the urine may well contain conspicuously scented metabolic by-products that advertize the state of the male's physical condition and also help synchronize estrus in females (Coblentz, 1980). Sheep may extend the penis and assume the hunched position, but they never urinate on themselves.

Courtship. The courtship strategies of the sexes are quite distinct despite the goal of production of offspring being the same. Females in most wild and feral populations begin breeding early in life, usually produce only one or two young per year, but continue to do so for the rest of their life. Males on the other hand usually delay reproduction until much later than females, then have a high annual reproductive contribution over a few years. Females would therefore be expected to exercise some level of choice among males for potential fathers of their offspring, while males would be expected to devote all their efforts into "convincing" as many females as possible to be inseminated. Whether females get the chance to exercise mate selection to any degree

is debateable. Competition among males, much of which is prior to the rut, serves to establish dominance relationships among the rams, so that during the breeding period dominant males can court females with less interference from subordinates (Geist, 1971; Jewell and Grubb, 1974). Thus the males themselves reduce the choice of potential mates for the females. However, at least in mountain sheep, males that do not use courtship patterns and merely attempt to mount, are not accepted by estrous females (Shackleton, 1973). Courtship by males tends to be prolonged and to consist of numerous patterns directed to the female, indicating its importance for successful copulation. These courtship patterns are similar to those described for male farm sheep by Banks (1964).

Courtship strategies dictate that males should not bother with anestrous females but should be ready to breed them as soon as they come into estrus. Therefore, male goats and sheep test the estrous condition of females constantly during the rutting season by approaching the female from the rear in the low-stretch position with crouched legs, nose up, head down and tongue flickering and producing a gutteral whickering, grunting or gobbling sound. The nose is extended towards the female's perineum or flank. If the female continues to stand, the male may front-kick her and nudge her flank. These patterns are identical to those seen in the agonistic interactions among male sheep (Geist, 1971; Grubb, 1974b). Usually, the female will respond to these attentions by urinating and then moving away. The male sniffs the urine or takes some into his mouth and "lipcurls" by raising his head with the mouth open and upper lip curled back. Often the head is waved from side-to-side. During lipcurl, odorant molecules are being aspirated into the vomeronasal organs in the roof of the mouth (Ladewig and Hart, 1980). Lindsay (1965) showed that lipcurl is an important aspect of estrous detection in farm sheep but that other cues are sufficient. It is interesting and puzzling that sheep and goat males rarely compete for opportunities to lip-curl; two or more males are often seen side-by-side, lipcurling.

Although herding of ewes by rams has been reported in bighorn sheep (Shackleton, 1973) and Marco Polo sheep (R. G. Petocz, personal communication), sheep and goats do not maintain harems. Dominant males tend single estrous females. When an estrous female has been detected by a male, he will attend her continually, following her and performing the courtship displays of nudging and front-kicking. At each nudge, initially the female typically moves a few paces forward, but when receptive, she stands and accepts mounts. The male remains closer to the female and rests his chin on her rump and back. This stage is shortly followed by repeated mounting. Successful copulation is signified by the male performing a thrust with a slight jump. A mating rate of 1/h, similar to domestic sheep, was reported for Soay sheep (Jewell and Grubb, 1974). The male typically remains with the female after copulation, which may help ensure that he is the only male succesfully to breed the female.

During the male's courtship the female is only apparently passive. She actively determines whether the courtship will be successful by standing and allowing the male to mount her. Female sheep and goats also perform courtship themselves (Geist, 1971; Shank, 1972; Shackleton, 1973; Coblentz, 1974; Grubb, 1974b; Jewell and Grubb, 1974), which is usually directed at large males. Female courtship is typified by her turning in front of the male, rubbing her body along his chest and down his side. When male interest is flagging, females may even mount the male, which usually stimulates him to mount her in turn.

The picture painted here is the theory-satisfying one of male dominance and female choice invariably leading to dominant males doing all of the breeding. In fact, the system often seems to break down, particularly where subordinant males are at high density. Geist (1971) describes mountain sheep females breaking into a run and followed by a large group of males that the dominant is unable to control. Fighting between the males is overt and vicious, with a loss of many dominance conventions. The success of subordinant males in such interactions is difficult to assess, but may be significant in some circumstances. The same behavior was reported for Soay sheep (Grubb, 1974b), feral goats (Shank, 1972; Coblentz, 1974; Gould, 1979) and urial (Schaller, 1977). The major differences are the ability of the dominant to control copulation attempts by subordinants and the intensity of the interaction. In feral goats, the action often becomes frenetic and may represent a major source of mortality through falls from cliffs (Shank, 1972; Gould, 1979). The significance

of such behavior in terms of successful breeding by subordinant males is unknown.

Conclusions

The review presented here suggests that, at the descriptive level of analysis, there are few significant differences between the social behaviors of wild and feral species of sheep and goats. Although we feel that knowledge of the behavior of feral sheep and goats is valuable for an adequate understanding of farm animal behavior, we feel that data from wild species should also be considered. With the impending extinction of many forms of wild Palearctic caprids (Schaller, 1977), it is essential that we learn more about them, and do so soon. Without such a body of information, we will have only limited biological baselines against which farm animal behavior can be interpreted and evaluated.

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