How to Tell the Sheep from the Goats

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The challenge-first stage in a joust between two male Nubian ibex (Capra ibex nubian) in the Sinai.

In scientific research, as the practicing scientist knows from personal experience, not everything leads straight forward to the expected goal. The research described here began with one set of problems, basically archeological, and got diverted in part to another kind of problem, involved with the correlated evolution of the behavior and anatomy of sheep and goats.

The beginning was in 1954, when the senior author (Reed) went out to the Near East to help Robert Braidwood, of the Oriental Institute at the University of Chicago, excavate Jarmo, a prehistoric village-site in the foothills of northern Iraq. The villagers of Jarmo, some 8,500 years ago, were growing wheat and barley and rearing sheep and goats, pigs and dogs. We recovered the broken, scattered bones of these domestic animals, and also those of several kinds of hunted species, such as wild pigs, gazelle, deer, cattle, onagers (Asiatic asses), and many smaller wild animals.

Reed's original problems were to identify species and to distinguish which individuals were domesticated and which wild. However, the archeologists also wanted to know in what relative numbers the different kinds were present 8,500 years ago, at what age the animals were killed, and if any changes in fauna occurred during the 500 years the village was continuously occupied.

Many of these questions could be answered by comparison of the bones from Jarmo with the skeletons in the excellent osteological collections at Field Museum. Sheep and goats presented a special problem because, being rather closely related animals, their skeletons are extremely similar. However, as Reed sorted out the broken pieces from groups of mixed bones of sheep and goats, he noticed differences in the posterior parts of the skulls. Some were shorter and straighter; others were more elongated and bent down. These differences became more meaningful when the pieces of ancient, broken skulls were compared with skulls of some modern sheep and goats which had been sawed open lengthwise.

The skulls of the goats were the ones which were short and straight in the rear, a structure correlated with long but relatively light horns. The skulls of sheep not only had their rears elongated and bent down, they also carried heavier horns. Such characters, in the language of the evolutionary biologist, are "more specialized."

As an evolutionary biologist, Reed wondered about the functional significances of these differences, and how they were related particularly to the behavior of the two kinds of animals. Answers were not to be found in veterinary textbooks or in the books of hunters' tales, or even in the more technical wildlife literature of the period on sheep and goats.

Thus the matter rested until the spring of 1964, when Schaffer (the junior author, and then a freshman at Yale University) had an urge to try his hand at independent research. Reed, who was then mammalogist at Yale's Peabody Museum, suggested the problem of the sheep and the goats. Now, eight years later, we think we have some answers. It all took that long because we followed a few alleys toward blind ends, and of course each of us has done some other things too.

The common words "sheep" and "goats," as have been used here, make the situation sound much simpler than it really is. Actually involved is a definite group of animals, together called the Caprini, of which there are five different kinds (genera). Their names are: Capra (turs, ibexes, wild goats of several species, and the domestic goats); Hemitragus, (the tahrs, of which there are three species): Ammotragus (the Barbary "sheep," which is as much a goat as a sheep); Pseudois (the blue sheep); and Ovis (the several species of true sheep, including domestic sheep). All of these are Old World in distribution except the American bighorn, or Rocky Mountain sheep; it is a relatively late Ice Age immigrant from Asia into western North America.

Amongst the bovids (the general group of sheep, goats, antelopes, cattle, buffalos, musk-oxen, etc.), the Caprini are most closely related to the Rupicaprini, which group includes the chamois, a small mountain-living antelope-like animal of Europe and the Caucasus, and the Rocky Mountain "goat," which isn't a true goat but superficially looks like one. These two groups, the Caprini and Rupicaprini, are probably descended from a common ancestor—some antelope of several million years ago which had become more adapted for climbing and leaping in rocky hills than for swift running on the plains. Such agility, coupled with alert wariness, generally insured survival from such mountain-living predators as leopards, snow leopards, bears, and wolves. In other words, the rupicaprines and caprines have become so well adapted to a difficult terrain that what might seem to others to be a harsh environment is for them a favorable one.

The Caprini differ from their rupicaprine cousins in one fundamental pattern of behavior: sheep and goats are often seen banging their heads together. They butt. Rupicaprines, by contrast, either fight rarely or, if they do, they deliver blows of the head to the opponent's body.

Of the Caprini, the males mostly do the butting. But it is not an aimless, continuing activity. Serious fights—or better, "jousts"—occur only between strange males, adults or near-adults, who must settle the important matter of their social dominance. At least in sheep, whose behavior has been best studied, the winner of any such serious joust continues to act like a male, and the loser demonstrates his subordination by acting like a female.

The males with the larger horns are almost always the dominant rams. They not only intimidate or drive other males away from receptive females, but are seemingly preferred by such females, and hence sire a greater proportion of the next year's crop of lambs than do other rams. There is, thus, a natural selection for large horns amongst rams of *Ovis*. We believe that the same principle holds true for the males of the other Caprini.

However, the males of the different kinds of Caprini joust in quite different patterns, each style consistent for one kind; and each style of head-ramming or horn-clashing is related to the shape of horn and head of that kind of animal. If, for instance, two male goats (*Capra*), which merely clash their horns together from a standing position, were to try to act like the males of sheep (*Ovis*), which actually charge each other at the full run, the goats would kill themselves at the first contact. A ram's horns and head have evolved as a structural design which will absorb a much greater shock than does a goat's without addling his brain. This correlation between behavior, function, and structure is the crux of our story.

Wild male goats, for instance, have long thin horns curving like sabers up over their backs. On an old buck such horns will be forty inches or longer, and are handy for scratching his hips. When jousting, the males do not charge each other. Typically one stands firm while the other rears erect and then, with neck down-arched, crashes down upon his rival; or both may stand erect momentarily before clashing. Since the leading edge of the horn is sharp in male goats, cutting damage might result if the horn hit directly on the head. But the goat on the defensive is too clever to let that happen; he turns his head in the opposite direction of that of his challenger so that the horns cross and the bumpy edges interlock, thus preventing slippage and protecting the head from cuts. Accidents (miscalculations) may happen occasionally, as in all contact sports, but they are relatively few, and serious damage is rare.

A little contemplation of the paragraphs above should illustrate to one the niceties of the natural processes whereby horn, bone, brain, nerves, muscles, and behavior have evolved together. And we append here, as a footnote to our own thinking, the statement that we are amazed that some people, labeling their activities "sport," will with purpose aforethought destroy such wondrous animals as wild goats, tahrs and turs, sheep, and others.

In male goats and ibexes, horn-to-horn contact is not at the base, but usually about one-third of the distance from the base toward the tip. Receiving force in this region, the horns act as levers upon the skull, twisting it clockwise, as



The clash-a millisecond before male Nubian ibex make contact in a ritual "battle" for dominance.

viewed from the left. To compensate for this movement, which might if continued break the neck, the neck muscles which insert under the skull and pull it down are particularly enlarged in goats. What seemingly happens here is a reflex contraction of the muscles just at the moment of, or a millisecond prior to, horn-to-horn contact, to oppose the force of the blow and hold the head firm.

The males of Ovis, particularly of the populations with larger horns, have a pattern of jousting markedly different from that of goats. In the first place, the horns themselves are large, heavy, broad in front, and curled around the side of the head. Such horns are indeed veritable rams. A toss of a mature ram's head, bearing such formidable weapons, is sufficient to intimidate an adolescent male, who of course has smaller horns. Rams cannot see their own horns, but they are very aware of the relative sizes of the horns of all other rams-by experience of the force of blows which can be delivered by horns of all sizes. Young rams growing up learn quickly to respect rams with larger horns-i.e., their elders -and, indeed, for much of the year each older ram is followed by a group of younger males, each acting submissively toward him as a female would. The young rams in a group practice against one another, and by

the time the members of a group have reached adulthood, they have settled their own position of social dominance amongst themselves. But each of them will challenge any strange ram with horns of similar size to his own. A ram's ultimate goal seemingly is not to acquire females, but to reach such a position of dominance that all other sheep behave toward him as if they were females.

The joustings of the mature rams of large-horned sheep are indeed formidable. Two adult or nearly adult males with horns of approximately equal size who have not previously established their social rank relative to each other will almost always joust. If the opponents are unequal, the decision is settled in favor of the stronger after a few rammings. With a pair equally matched, though, the contest may continue for more than a day and night, marked by fifty or more full-powered rammings. The two will walk away from each other as if unconcerned, then, when some thirty feet apart, will whirl simultaneously and charge with all speed, finishing the charge bipedally. Each tries every possible trick to gain advantage. Particularly, each attempts to use the angle of the edge of one of his broad-fronted horns to cut the other. The other ram protects himself by catching the blow on his horns. So clever are they at simultaneous tricks

of offense and defense that some observers have thought the affair to be in the nature of a spirited but friendly tourney. This is not true. No aspect of friendly behavior is involved. Serious damage is rare, and death rarer, but one ram must emerge in the role of a male, the other finally signaling submissiveness by acting like a female.

During each episode of a serious set of rammings, the individual males achieve a speed of about thirty miles per hour before meeting hornbases to hornbases. Each then stands stiffly, head erect and horns displayed, so that the other can see what hit him, before strolling apart —perhaps even to feed momentarily and then repeating the ramming. Although no one has calculated the forces involved, the impact on horns and heads is obviously terrific.

If two people moving at this speed hit head to head, they die; the force of impact is that of hitting a wall at sixty miles an hour. The rams of course do not die; they live, usually uninjured, to repeat these contests with other rams on other days and in other years. The social system is so organized, however, that no ram is ever an outcast; each has his place in the dominance rankings, and each acts as a male toward those below him but as a female toward those above him.

Both males and females are usually capable of reproduction at the age of two years. Breeding is in the late autumn or early winter of their third year. Females do not compete for mates, and their horns remain relatively small in comparison with those of males. Males will breed successfully at the same age if no older males are around, but in a normal population the older males intimidate the youngsters and keep them from the females. Dominant males do try to keep other males from receptive females, but rarely succeed completely, and do not form harems; nor is monogamy the rule. Indeed, when a female is receptive, she may breed

with several adult males, and almost always becomes pregnant.

Although a young male is capable of breeding at the age of two to three years, his horns are still small, and he dares not assert himself against an adult with much larger horns. Horn growth continues throughout life, which may be as long as twenty years. The major horn growth is, however, achieved by the age of seven or eight years. By that time the young adult male is challenging and defeating any older male whose horns do not match his own in size. Amongst sheep at least, older males with smaller horns are subordinate to younger adults with larger horns; thus neither age nor adulthood is a guarantee of dominance and success in breeding. The evolutionary selection for larger-horned males is balanced in part by the fact that such "successful" males die vounger than do smaller-horned adults. who may breed less frequently each season but live to breed over a longer life-span.

There is thus a long adolescence for a male ram, almost a third of his life, during which time the females of his age-group are having a lamb each year. The young males, while capable and willing, are not necessary for the immediate reproductive success of the group, but are a kind of insurance, available if by some chance all adult males are killed.

We should not over-generalize for the several species of Caprini since prolonged behavioral and demographic studies have been made only on the Alpine ibex (Capra ibex) and the American bighorn (Ovis canadensis), and some behavioral studies have been made on the Barbary sheep. But for the latter, as for Hemitragus and Pseudois, as well as too often for many species of wild goats and sheep, the published accounts are predominantly those of successful hunters recounting their exploits. This kind of material adds little or nothing to our knowledge of an animal's behavior in intra-group



Male Nubian ibex sparring. Three photos by Uzi Pat, I/C Nature Reserves, Nature Reserves Authority, Kibutz Galuyot St., Tel Aviv, Israel.

associations, his place in the social structure, and his reproductive success. However, the behavior typical of the three species about which we do have good information, backed up by what we know of the male's anatomy in each of the five genera, suggests a similarity of basic pattern for all the Caprini.

Now, after a necessary detour through the subject of the jousting behavior and age-related mating patterns of sheep and goats, we are ready to return to the beginning of our story and to understand why the skulls of different Caprini are built on recognizably different plans. As mentioned previously, if male goats, who merely clash their horns from a standing position, tried the charging ramming of male sheep, the goats would snap their horns, addle their brains, and possibly crush their skulls. The horns and skulls of each species of Caprini have become evolutionarily adapted by natural selection to resist successfully the stresses created by the behavior of their bearers. Thus, we can now begin to understand why sheep and goats, tahrs and turs, and ibexes and others have distinctive kinds of heads and horns.

Careful examination of the details of these structural differences, correlating them with behavioral differences, and working out some other evolutionary implications are what took us so long. We will explain some of these details.

Each horn of a caprine (and of all bovids) has two parts. The outer part is a sheath of keratin (horny tissue that develops from the skin, as does a human fingernail). The inner core is bone which is an outgrowth of one of the frontal bones of the skull. Since a bovid has two frontal bones, right and left, it normally has two horns. In all the caprines, as in all large bovids, the center of the bony core of a larger horn becomes absorbed as it grows, making the horn more or less hollow. The space so produced is an extension of the cavity of the animal's frontal sinus on that side, and both frontal sinus and the sinus of the horn (cornual sinus) are filled with air. In male wild goats and ibexes particularly, the cornual sinus may become so large that it extends to the tip of the core, leaving the bony wall at and near the tip paper-thin and fenestrated. In other caprines the wall of bone remains denser and thicker, and thus the sinus is smaller.

The cornual sinuses are not, however, occupied only by air. When forming, they retain several to many supportive bony struts which cross the sinus. These struts are usually longitudinal in the more goatlike species, while in others (tahrs and bighorn sheep, for instance) they form a complex pattern like a honeycomb. No matter how complex the interweaving pattern of struts, the cavities are all continuous, all air-filled, and all communicate by way of the frontal sinus with the nasal cavity and thus to the outside air.

Each frontal sinus is confined to one frontal bone and is separated from its partner of the opposite side by a thin vertical midline wall, and each such sinus also has some supportive struts. The sinus typically fills most of its frontal bone. In Capra, the frontal bone is smaller than in Caprini with heavier horns, in which the larger frontal bone extends backward to cover more of the brain. Also, in such Caprini with larger horns-the ones that ram instead of merely butt-the skull is bent down sharply at the back, so that all or almost all of the brain lies under the frontal bone and thus also underlies the frontal sinus. In these "rammers"-Caprini with larger horns-we also find the struts of the frontal sinus to be much more numerous, making as complex a honeycomb of bony bars as is found supporting the cornual sinuses of the same individuals.

Our conclusion is that the more the frontal sinuses overlie the brain and the more complex the pattern of struts is in the sinuses—within both the horn core and the frontal bone—the more forceful the male's butting or ramming behavior is. In other words, the behavior patterns are positively correlated with the detailed structure of skull and horns, and the evolution of behavior and structure has obviously gone forward together over long periods of time several millions of years—in the different populations of Caprini.

During this long period of complex evolution, generation by generation, the forces to which the head was subjected cannot have been so great as to injure the brain seriously. Any male with such an injured brain, whether the individual died immediately or not, was removed from the breeding population and, evolutionarily speaking, ceased to exist.

The potential types of brain damage, particularly in large-horned rams, are due to deceleration at the instant of contact or rotational acceleration if the heads meet off-center and are twisted.

The results in the brain may be torn



Honeycomb structure within cornual sinus of Ovis canadensis (top); and within frontal sinus of Ovis ammon (center); and Capra ibex sibirica (bottom). Back of skull is bent down much more sharply in Ovis ammon.

blood vessels, compression of tissue, shear, formation of internal vacuoles due to differential pressures within the brain (some possibly much lower than normal), or combinations of these types of damage. Obviously the problem of damage to the brain has been a limiting factor in the evolution of different Caprini, but has probably been most crucial in large-horned *Ovis*. However, just as obviously, the problems have been "met and solved," selected mutation by selected mutation, while the social and behavioral patterns were evolving. How was all this accomplished?

In the first place, the ram's horn itself, the outer sheath, is thick and presumably somewhat compressable. The shock-absorbing capacity of the bone of the horn core, with its honeycomb of supportive struts, must also be considerable; and it is "backed up," so to speak, by the system of struts below each horn, in the sinus cavity of each frontal bone. Finally, there is a correlation between the spot of impact-on the broad front of the horn directly above the forehead-and the fact that the whole of the back part of the skull is bent sharply downward. The direction of the force of the blow and the direction of the transmission of that force through the centrally bent posterior part of the skull are the same, and this line continues through the anterior vertebrae of the neck. Thus, in normal ramming, there is no tendency toward rotation of the head as occurs in goats, and the problem of whiplash is diminished. A structural correlation is that sheep do not need the enlarged ventral neck muscles of goats, and do not have them.

During the several million years of evolution within the Caprini, the usual evolutionary processes of mutation, differential selection in slightly different habitats, and geographical isolation have resulted in adaptive radiation within the group such that we now recognize five genera. Of these five, the goats (Capra) seem to be the least specialized for intense jousting by virtue of the structure of skull and horns. Jousting among male goats and ibexes-and also incidentally in the small-horned European sheep-is not forceful enough for any marked correlated changes in the shape of their skulls to have evolved. The angle between the plane of the palate and the plane of the back of the skull remains low (27°-48°) in these animals, in contrast to the angle (74°-92°) in the more specialized, large-horned animals with the backs of the skulls bent down sharply.

Clearly, the most specialized of the Caprini are the large-horned sheep of the genus *Ovis*. But even within the sheep there are differences. Those in western Europe have smaller horns and less specialized skulls (and hornless females, whatever that may mean), and Asiatic sheep generally have larger horns with correlated specializations of the skull, as do the North American sheep, which descended from late immigrants from one of these eastern Asiatic populations.

Evolutionary selection for behavior, population structure, and anatomy of head and horns has obviously occurred simultaneously for several million years. To have evolved a social system that allows the luxury of capable young males not reproducing until half their life is gone demands two conditions: several million years of evolution of behavioral patterns so that such a social system works; *and* the continuous presence of older males, generation after generation, to maintain a continuity of population pattern which would channel the evolution.

Obviously, the locomotor adaptations which allowed invasion of rocky hills and mountains have been long successful in the Caprini, and built upon that success came such certainty of population structure that the subsequent secondary and then tertiary adaptations we have been talking about did evolve.

We cannot say why the special evolution of the Caprini began to evolve in the way it did, when that of another crag-loving bovid, the Rocky Mountain "goat," proceeded quite differently. The males of this species do not usually "fight," no dominance is established, and the young breed as soon as they are physiologically capable. Jousting would be particularly dangerous in these animals because their small, straight, sharp horns can inflict extremely dangerous and often fatal stabbing wounds; even an adult could be killed by a youngster. The different pattern that the Caprini as a whole exhibit indicates that a common ancestor began to evolve several million years ago away from an animal also ancestral to the chamois. In the Caprini, this combined anatomical, behavioral, and social evolution was toward larger horns, male jousting, exclusion of the young males from breeding, and consequent extended adolescence.

So we have come full circle. The differences between skulls of sheep and goats which puzzled Reed in 1955 are better understood now in 1972. But we had to take a long way aroundthrough comparative study of the behavior, anatomy, and population structure, as determinable, of all caprines and some of their rupicaprine cousins, and put these factors into an evolutionary framework. This circle is spotted with gaps though, because we don't yet have intensive studies in nature of many of the caprine populations. The unstudied groups include Asiatic sheep and Asiatic goats. the single species of Pseudois, the three species of Hemitragus, and to a lesser degree the single species of Ammotragus.

There remains much research to be done by the field-naturalist—research of the kind now called ethology, the scientific study of the behavior of individuals and populations, as related to evolution, of free-living wild animals. These studies can be aided by modern techniques of telemetry and motion picture photography. Such studies must be done while natural populations remain to be studied!

FURTHER READING

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