

HORNS AND FIGHTING IN MALE SPANISH IBEX, *CAPRA PYRENAICA*

FERNANDO ALVAREZ

*Estación Biológica Doñana, Consejo Superior Investigaciones Científicas,
Apartado 1056, Sevilla, Spain*

ABSTRACT.—As adult body mass is reached fighting force is greater, consequently horn growth in male Spanish ibex (*Capra pyrenaica*) must compensate to minimize breakage. This is done by increasing the value of the second moment of the area at the base of horns, which keeps the maximum horn-bending stress low. Transverse horn ridges are apparently involved in helping to control the length of the lever arm, hence the bending moment, thus helping to minimize bending stress and torques about the occiput. In the rear-clash type of fight, the probability of horn breakage is highest, but horn-bending stress is minimized by clashing against the basal sections of horns. I hypothesize that the most frequent, and harmless, types of conventional fighting serve as reliable tests of the fighting ability of an animal. Contenders resist dangerous rear clashes by their body mass and absorb the energy of fighting and prevent skull rotation by contraction of their neck muscles.

An understanding of bovid horn shape and structure should start by a knowledge of the exact use that the animals make of their horns while fighting, as suggested in Geist's (1966) evolutionary model. In this model, primitive forms have sharp, damage-inflicting weapons. Increasing body mass and inertia in the evolution of some species would have led to the use of frontal engagement during fighting and to development of greater horns, capable of controlling the adversary's head. From this evolutionary stage of frontal engagement, still heavier ramming horns would have developed and more complex horns used in wrestling and pushing combat techniques.

The species of the tribe Caprini have developed heavy skulls and large, massive horns used to deal and receive blows of considerable force. However, interspecific differences in fighting techniques and various degrees of skull and horn development occur within the group.

Backing off some distance, charging, and colliding at full speed in sheep (*Ovis*) and rearing up on their hind legs and crashing down in goats (*Capra*) are the most common types of fighting within the Caprini (Dunbar and Dunbar, 1981; Nievergelt, 1967; Schaller, 1977; Shank, 1972). The former liberates a higher amount of energy at the point of impact than the latter (Kitchener, 1985; Schaffer, 1968), corresponding to characteristic horn designs that resist different maximal stresses.

Among all possible modes of failure as a result of fighting, horns are most likely to fail in bending (Kitchener, 1988). According to beam theory, maximum bending stress must not exceed the strength of the horn (Kitchener, 1985).

If blows in the most forceful types of fighting are delivered on approximately the same point of impact, the length of the horn used will not change much and can be regarded as a constant. The same will apply to the radius of the base of the horn assuming that the horn is circular in cross section. Changes in the radius need only be small compared with the second moment of area to ensure that the maximum expected bending stress in the horn during fighting is constant as the force acting on horns increases (as a result of body mass increase in a growing animal).

The second moment of area of the cross section of the base of the horn, where bending stress is highest, is a shape factor. It describes the distribution of material in the cross section relative to the neutral axis of the cross section (where there is no net compressive or tensile bending stress). As such, the second moment of area of the cross section of the base of the horn is a relative measure of the structural stiffness of the horn, assuming material stiffness to be constant.

Another consideration relating to horn morphology is the way force is exerted to produce torque promoting rotation of the adversary's head. This torque can be either dorsoventral, lateral, or rotational with respect to the skull-cervical atlas vertebra joint. If unopposed by the neck

muscles, it would cause severe injury to the combatants. Horn shape may contribute in reducing torque by a curving of the horns about the center of rotation to reduce the length of the lever arm (impact site-occipital condyles—Schaffer, 1968).

Therefore, the two major factors apparently affecting horn design are animal body mass and fighting technique. The former directly affects impact force, therefore maximum horn bending stress and the torque intensity. The fighting technique has an effect both on the acceleration before impact (therefore on impact force) and on the location of the site of impact on the horn, affecting bending moment (Kitchener, 1985) and length of the lever arm (Schaffer, 1968). The affected horn features then appear to be the dimensions of the horn base, best represented by the second moment of area, and the horn features and shape contributing to the control of the point of impact and to the resistance to and the production of torques causing rotation of the head and neck.

The subjects of this study, the male Spanish ibex (*Capra pyrenaica*), are well endowed with horns, for which total length increases with the age of the animals, although at a slower rate when they reach maturity. The seasonal horn growth is revealed by the annual horn segments, limited by narrow grooves corresponding to the autumn and winter months (Fandos and Vigal, 1988; Fandos et al., in press). Horns are used in intense fighting during the mating season in November and December, mostly between animals of similar age. From these agonistic contests, winners appear to derive mating benefits from receptive females (Alados, 1986).

It is my aim in the present study to analyze the relationship between the fighting behavior of male Spanish ibex and the features of their horns. I pay special attention to age variations both in horn morphology and behavior.

MATERIALS AND METHODS

I examined 35 trophy head mounts and 79 skulls with horns from the free-ranging population in Sierra de Cazorla, Spain. The specimens were maintained in institutional and private collections at Cazorla, Seville, Madrid, Andújar, and Jerez (Spain). Total length of horns was measured with a thin metallic tape applied to the irregularities along the anterior horn keel, from the tip to the base. Linear distances between successive growth grooves were measured with calipers along the inner arc of the horn sheath where growth grooves are most apparent. Width (lateral and anteroposterior) at the base of the horn also was measured, and the least distance between horn sheaths at their bases. For comparisons, the average values of measurements for both horn sheaths of each specimen were used. As horns of the Spanish ibex are roughly elliptical in cross section at all ages, the second moment of area was calculated from the two axes of the ellipse, according to:

$$I = \frac{\pi a^3 b}{4}$$

where:

a = half the major axis

b = half the minor axis.

For the purpose of the study, the transverse ridges on the front side of the horns were considered in the analysis only when their maximum depth was ≥ 1 mm. Their maximum depth and their distance to the horn base were measured for the left horns of 63 specimens.

Male fighting behavior was observed and video-recorded in the National Reserve of Cazorla (from where the horn specimens came), during two successive mating seasons, in an area where males traditionally gather in November and December. Daily observation periods were from 0700 h to 1200 h and from 1400 h to 1630 h. Males were filmed with a video camera, equipped with 400–1,200 mm zoom lenses, whenever at least two males were sufficiently close to each other to expect interactions among them. A 60 \times telescope was used for direct observations.

Age determination of skulls with horns and trophy head-mount specimens was based on counts of annual horn segments, a procedure found reliable for the same populations of Spanish ibex by Fandos et al. (in press). During direct observation and filmed behavior the following age classes were considered: subadult males, 2–4 years old with horns not yet S-shaped and tips bent backward and black stripes only on legs; adult males, 4–8 years old that when seen laterally, have S-shaped horns with tips pointing upward and inward, and black stripes on legs, shoulders, center of back, top of head, and flanks; old males, ≥ 8 years old

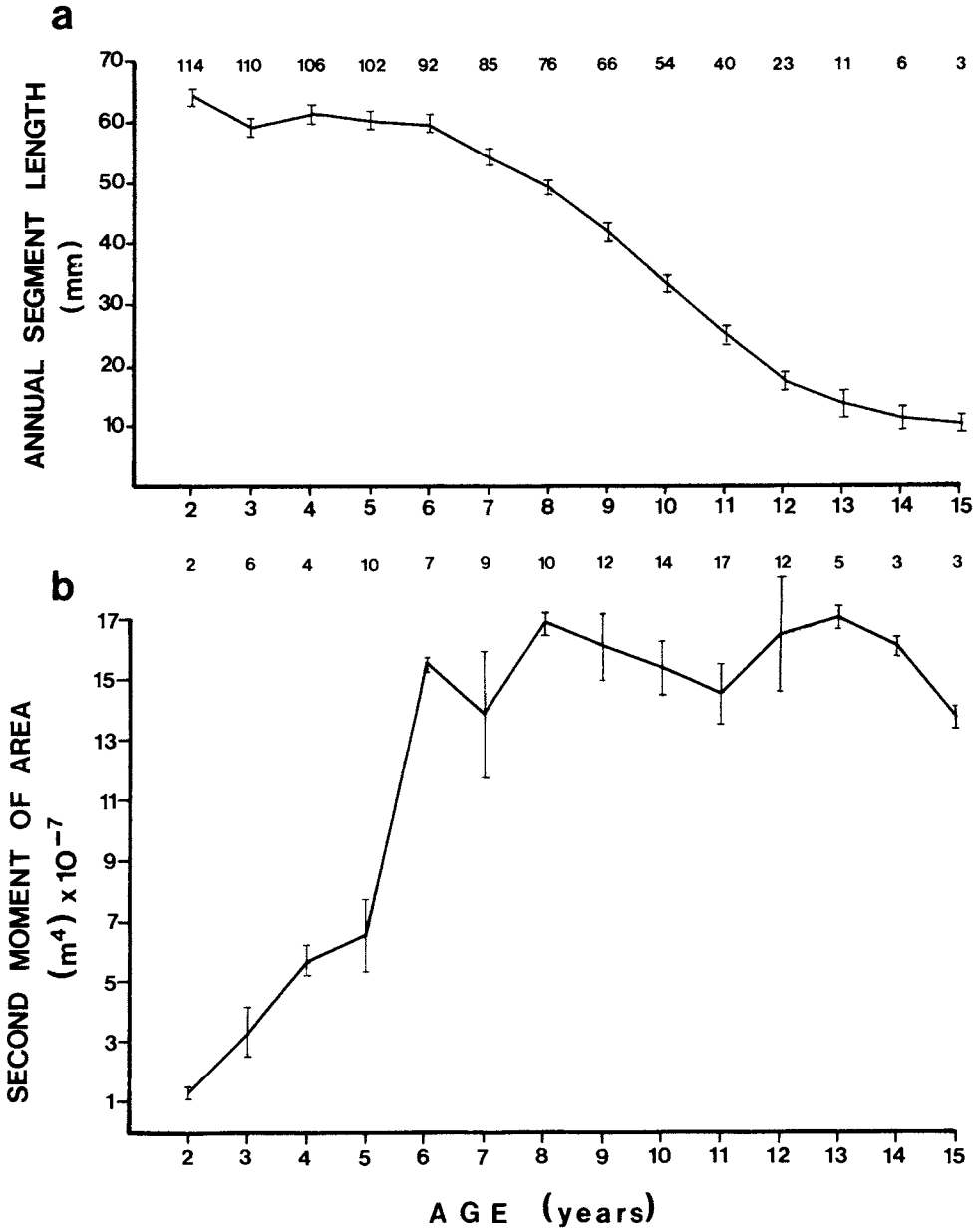


FIG. 1.—Variation ($\bar{X} \pm SE$) in: a, annual segment length (mm) and b, second moment of area of base of horns ($m^4 \times 10^{-7}$) of male Spanish ibex. Sample sizes are indicated above each value.

with black areas on shoulders, back, front legs, flanks, and rear legs usually connected and a black patch on top of the head extending to the face.

RESULTS

Horn Morphology and Growth

The horn sheaths of the ibex diverge to the sides and backward from their bases on the skull, then converge and turn upward at their tips in a characteristic lyre shape. The winding of about

TABLE 1.—Mean (\pm SD) number and maximum depth of cross-ridges in the sections of horns for three age classes of male Spanish ibex from Cazorra, Spain.

| Age and horn section | Horn cross-ridges | | | |
|-----------------------------|---------------------|----|----------------------------|-----|
| | Number ^a | | Maximum depth ^a | |
| | $\bar{X} \pm SD$ | n | $\bar{X} \pm SD$ | n |
| Subadult | | | | |
| Basal third ^b | 3.4 \pm 1.1 | 14 | 3.1 \pm 1.4** | 47 |
| Middle third ^b | 2.3 \pm 1.7* | 14 | 2.0 \pm 0.8* | 32 |
| Terminal third ^b | 0.9 \pm 0.9** | 14 | 1.4 \pm 0.2** | 12 |
| Adult | | | | |
| Basal third | 4.8 \pm 3.2 | 20 | 3.3 \pm 1.9* | 97 |
| Middle third | 5.0 \pm 3.0** | 20 | 2.8 \pm 1.3** | 99 |
| Terminal third | 1.0 \pm 1.0** | 20 | 2.1 \pm 0.7** | 21 |
| Old adult | | | | |
| Basal third | 6.2 \pm 3.6 | 29 | 2.1 \pm 1.0** | 180 |
| Middle third | 6.3 \pm 1.7** | 29 | 2.7 \pm 1.5 | 182 |
| Terminal third | 3.1 \pm 1.5** | 29 | 2.5 \pm 1.1 | 88 |

^a Friedman two-way tests used for comparisons within age classes. All $P < 0.01$ (Siegel, 1956).

^b Wilcoxon signed-ranked tests used for two-sample comparisons. Asterisks at basal value refer to basal-middle comparisons; asterisks at middle values refer to middle-terminal comparisons; asterisks at terminal values refer to terminal-basal comparisons (Siegel, 1956).

* $P < 0.05$.

** $P < 0.01$.

half a spiral turn in adult specimens is made more conspicuous by the well-marked longitudinal keel, which, starting at the inner side of the sheath base, ends laterally at the distal horn portion. The segmented horns show transverse ridges on their anterior faces, usually most prominent near the longitudinal keel. In relation to horn-sheath growth, the first annual incremental length was eliminated because it is significantly reduced with increasing age by breakage and wear ($r = -0.47$, $n = 114$, $P < 0.001$).

As for the other, more reliable annual incremental lengths of horns, although the corneous sheath continues to grow throughout life, horn growth is more rapid and sustained until 6 years of age, after which it decreases significantly. Consequently, the second moment of area of the base of horns shows a dramatic increase at 6 years, but remains rather stable thereafter (Fig. 1). As the age of the animal increases there also is a positive increase in horn length and second moment of area of the base of horns ($r = 0.77$, $n = 114$, $P < 0.001$; $r = 0.45$, $n = 114$, $P < 0.001$, respectively) and a decrease in the distance between horn sheaths at the base ($r = -0.34$, $n = 114$, $P < 0.001$).

The number and maximum depth of the transverse ridges on the horns were analyzed separately for the three age classes of males and their presence was considered in each of the three longitudinal thirds of each horn. The basal and middle thirds have higher numbers of cross ridges than the upper third of the horn. As for the mean depth of the transverse ridges, the highest values correspond to the basal third, followed by the middle and the upper third. However, for old males it is the middle third with the highest values, followed by the other two-thirds of the horn (Table 1).

Most of the specimens had surface defects on their horns, either superficial scratches (63.1%) or deeper cracks (13.1%), whereas 57.0% of them had blunt points on one or both horns. We also were able to examine seven specimens with one horn broken at its basal third and one specimen with the left horn reduced in length.

Patterns of Fighting Behavior

Rear clash.—At a distance of about 1–3.5 m from the opponent, in front but slanted with respect to the opponent's head and usually at a higher ground level (78% of 41 filmed cases), the initiator goes upright on its rear legs while the head and neck are twisted toward the receiver's head (73.2% of the cases). In this posture, the attacker may walk one to three steps toward the

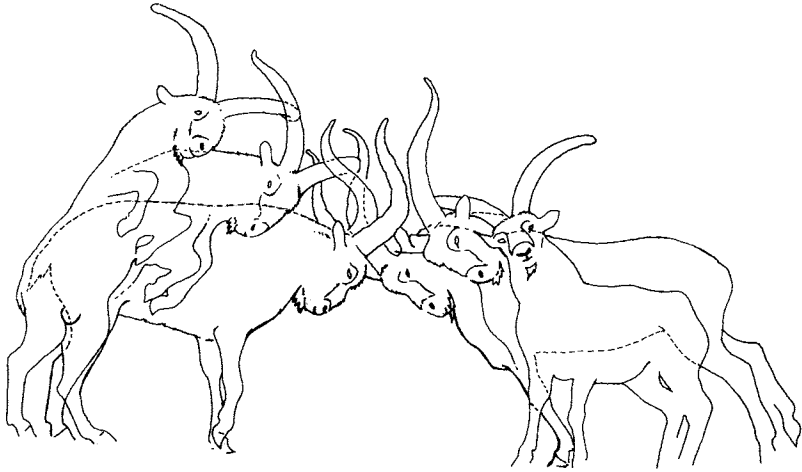


FIG. 2.—Overlapping views in stages of the rear clash in Spanish ibex.

receiver or, if sufficiently close, descend fast onto its front legs, delivering a strike mainly forward and downward (Fig. 2).

Sometimes (17.1%) both contestants lunge at the same time from bipedal posture, but most often the recipient remains on all fours. In this posture the recipient stands still and extends its horns in front of and above its face, usually twisting its neck to receive the blow on the front parts of the horns (73.2%), then striking at the last moment, just before receiving the blow.

Usually both horns of each combatant made contact, although in 19.5% of the cases both horns of the initiator struck against one horn of the receiver and in 9.8%, only one horn of the initiator contacted weakly one horn of the receiver. The basal third of the horns received most clashes, either for the initiators (82.9%) or for the receivers (75.6%); the middle third of the horns received the remaining clashes. On impact, the horns were crossed, although to a lesser extent when both contenders struck at the same time from bipedal posture.

As a result of the lunge and of the position of initiator and receiver and of the inclination of their heads, the recipient of the blow had its head thrust intensely downward in all observations and often (87.8% of the cases) also to the side. The initiator's head was thrust to the side in 29.3% of the cases and much more weakly than the receiver's.

On observing two males rear clashing it appears that both contenders cooperate to ensure exact horn-to-horn contact, the attacker even waiting to clash until the receiver is in good position to receive the blow. Serious injury may, however, occur. I observed an old male whose left horn fractured about 5 cm from its base while rear clashing, although the broken part did not drop to the ground.

Frontal butt.—The two contestants are on all fours, facing each other at a distance of 0.5–1 m. The initiator, with horns up and chin tucked in, clashes its horns against those of the receiver by a quick downward motion of the head (Fig. 3). Of 32 filmed cases, a twist of the head was observed only in 37.5% for the initiator and 25% for the receiver. Although usually both horns of each animal made contact, in 12.5% of the cases both horns of the initiator struck against one horn of the receiver and in 18.7% one horn of each animal made contact on impact. The receiver's horn sections making contact were the middle third (56.2%) and the basal third (43.7%), whereas for the initiator it was mainly the horn's basal third (62.5%), followed by the middle third (37.5%). On impact, the receiver's head was thrust downward in all observations and in 18.7% of the cases also to one side, whereas the initiator's head and neck were never thrust laterally.

Lateral butt.—This behavior is much like frontal butt except that the body axes of the combatants are at right angles. The initiator strikes downward with both horns against those of

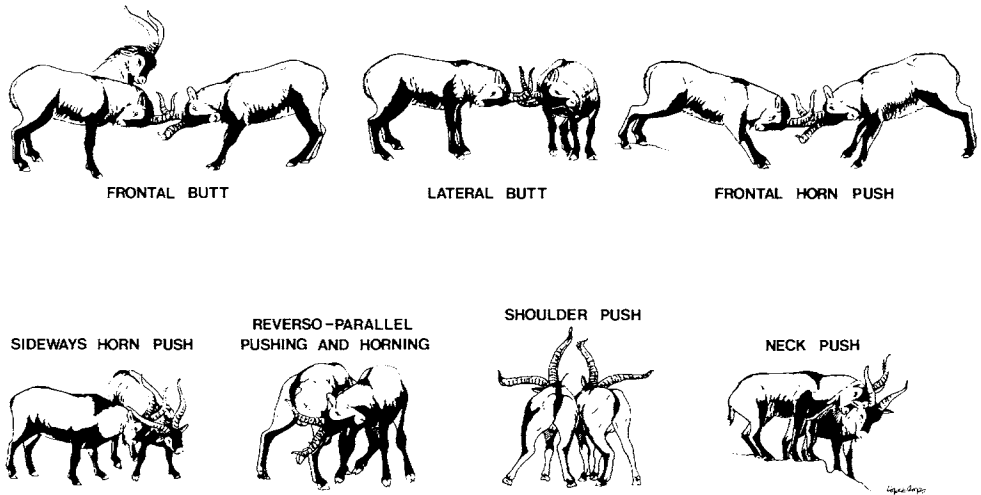


FIG. 3.—Patterns of harmless fighting behavior in Spanish ibex.

the receiver, who may receive the blow laterally in one horn (eight cases) or turn its head toward the attacker. The attacker's horns are pushed upward on impact (Fig. 3) whereas the recipient's horns were pushed laterally in all cases. The receiver's horn section making contact on impact were the basal third (10 cases) and the middle third (eight cases) whereas for the initiator they were the basal third (13 cases) and the middle third of the horn (five cases).

Frontal horn push.—This occurred either as a continuation of rear or frontal clash (6.8% of 380 filmed cases) or when both contestants lowered their heads to make horn contact. The horns usually were interdigitated (76.8%) or one or both were over (16.8%) or below (6.3%) those of the opponent (Fig. 3). The receiver's horn sections making contact were the basal third (64.2%), the middle (33.2%), and the upper third of the horn (2.6%), whereas for the initiator the horn sections contacted were the middle (55.8%) and the basal third of the horn (44.2%).

The receiver may be at the same ground level as the initiator (54.7%) or on lower (31.6%) or higher ground (13.7%). Its head was pushed in various combinations of backward (68.9%), upward (65.3%), downward (7.4%), and to one side (42.6%).

Sideways horn push.—For this behavior two males were side by side, often parallel to each other (although in 57.2% of the 290 filmed cases they were at right angles, 14.5% corresponding to the initiator being on higher ground). Their heads were lowered and horns either interdigitated (44.1%) or one or both horns over (25.5%) or below (17.2%) those of the receiver or contacting laterally with them (13.1%; Fig. 3). The receiver's horn sections making contact were the basal (53.8%) and middle third of the horn (46.2%), whereas for the initiator the horn sections contacted were the basal (61.4%), middle (37.2%), and upper (1.4%) thirds. The receiver's head was pushed in various combinations of backward (6.2%), upward (28.3%), downward (26.9%), and to one side (74.5%).

Reverso-parallel pushing and horning.—The contestants were parallel in head to tail position and rotated their heads toward each other; with their horns they contacted each other at the receiver's upper rear limb and hindquarters (16 of 21 filmed cases) or hooked one rear leg with the upper part of one horn (five cases) while sometimes pushing the opponent with the shoulders (eight cases; Fig. 3).

Shoulder push.—While standing side by side with their flanks or shoulders in contact, the opponents pushed against each other without using their horns. Walking in circles was common (seven of the 15 filmed cases) and sometimes (three cases) a sudden shoulder push threw the adversary away from body contact (Fig. 3).

Neck push.—While in a slanting position or at right angles with respect to each other and

TABLE 2.—Percent of the various fighting patterns initiated and received by male Spanish ibex in Cazorla (Spain) during the mating season.

| Interaction | Initiators | | | Receivers | | |
|--------------------------------------|------------|--------|------|-----------|--------|------|
| | Subadults | Adults | Old | Subadults | Adults | Old |
| Rear clash | 13.1 | 14.7 | 17.8 | 40.0 | 38.5 | 53.7 |
| Frontal butt | 13.8 | 14.0 | 8.9 | 36.0 | 44.2 | 29.3 |
| Lateral butt | 6.2 | 6.7 | 6.7 | 24.0 | 17.3 | 17.1 |
| Frontal horn push | 31.0 | 26.0 | 26.7 | | | |
| Sideways horn push | 18.6 | 28.7 | 38.5 | | | |
| Reverso-parallel pushing and horning | 9.0 | 6.0 | | | | |
| Shoulder push | 5.5 | 3.3 | 1.5 | | | |
| Neck push | 2.8 | 0.7 | | | | |
| Total frequency | 145 | 150 | 135 | 50 | 52 | 41 |

making neck-neck or head-neck contact, the males pushed dorsoventrally (four of five filmed cases) and laterally (one case) toward the other (Fig. 3).

While trying to evaluate the involvement of the three age classes of males in the five types of pushing fights, both contenders were considered to be performing the activity, because on direct observation it was not always possible to differentiate between initiator and receiver for those patterns (Table 2). Every frontal push bout comprised between one and 12 pushes and between one and six pushes for every sideways horn-push bout. The number of separate pushes in each bout was difficult to evaluate for the other types of pushing fights.

In the most forceful type of fighting (rear clash), horn breakage would be more likely to occur if the ibex used the middle or distal thirds of their horns. Therefore, to minimize the chances of breakage in the rear clash the ibex minimize the bending moment (and presumably the torsional moment) by only using the basal third of their horns (Fig. 4). This minimizes the bending stress, hence the likelihood of breakage. In conventional fighting the forces are much lower, so that bending moment is not constrained so critically and a much greater horn length can be used, even though most force is still directed toward the base. This is particularly true for adult and old males, those striking more forcefully while rear clashing.

DISCUSSION

The increase in the second moment of area at base of horns coincides at year 6 of life with the beginning of the slowing in growth of horn length. This is probably related to reaching adult body weight at that age (Fandos and Vigal, 1988). The differential allocation of horn material to increase the second moment of the area of the base of the horn to the detriment of horn length probably derives from the need to produce strong but light-weight structures (Kitchener, 1985, 1988) at an age when greater body mass may cause breakage of horns during combat.

The changes in body mass, fighting force, and horn structure in *C. pyrenaica* males when they reach the age of 6 years probably are related to the need to compete for access to females at the beginning of adulthood. An apparently similar pattern of growth in horn length was reported in two populations of *Capra ibex* studied by Nievergelt (1966) in the Swiss Alps.

Increasing impact force is also probably related to the tendency for horns to approach at their bases with increasing age. In that way they facilitate the distribution of the impact force between the two horns when dealing and supporting blows, reducing the risk of horn breakage. Also, the presence in the horns of transverse, forward-oriented ridges, more frequent in the basal horn sections where most of the force is applied, is of utmost importance in the control by the combatants of maximum bending stress of the horns and the torque about the occiput.

The transverse ridges may help to stiffen or strengthen the horn. They may be designed to prevent horns slipping past each other and causing accidental injury (as the upward horn turn also probably does). They also may prevent wear to the main horn structure through erosion in combat.

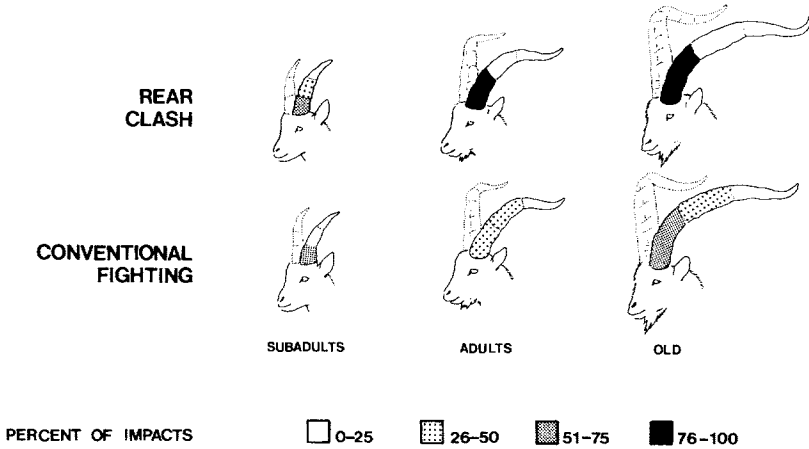


FIG. 4.—Percent of impacts received by the three longitudinal thirds of the horns of male Spanish ibex of different age classes for rear clash and for conventional horn-to-horn fighting.

Other than goats and ibex, the rear clash also is performed by *Pseudois nayaur*, *Ovis orientalis*, *O. ammon* (Schaller, 1977) and *O. canadensis* (Geist, 1971). Whereas the *Capra* species orient laterally toward the recipient before and during the rear clash, the other species of Caprini mostly orient frontally.

Among Spanish ibex, the most successful breeders, the old males, resort to the rear clash more often than the other age classes (Alados, 1986). This points to their readiness to bring into play the risk of injury, which seemingly contradicts the apparent cooperation between contenders to ensure exact horn-to-horn contact. Probably, great damage would occur in both contenders by misjudging the site of the clash, as seen in our observations of broken horns. The same apparently applies to *O. canadensis* (Schaffer and Reed, 1972), although serious injury occurs occasionally as a result of animal conflict (Geist, 1974).

It appears that fighting ability is most evident in the rear clash. Accordingly, the best assessment of the relative fighting ability of an opponent should be based on information about the body mass and age of an opponent (which would affect impact force and horn features) and on the capacity of the neck muscles inserting in the skull to absorb the energy of fighting and to oppose torque (Kitchener, 1988; Schaffer, 1968).

Accordingly, the other seven types of fights might be harmless tests of assessment of relative fighting ability. These fights would inform the contenders, unambiguously and without much cost, on body mass and body condition (through pushing), and on the power of contraction of the neck muscles (by the frontal and lateral butt, frontal and sideways horn push, and the neck push). The most frequent of these patterns of conventional fighting (frontal and sideways horn pushes) might also act to debilitate the adversary's neck muscles, precisely what it needs most to fight effectively.

The lack of more ritualized displays preceding fighting (as the parallel walk and roaring vocalization of red deer, *Cervus elaphus*—Clutton-Brock and Albon, 1979; Clutton-Brock et al., 1979) has probably compelled ibex to use conventional fighting as the best way to assess competitors. By gaining information on relative fighting ability, an animal would be able to withdraw without damage when its rival's resource-holding power (Parker, 1974) exceeds its own, as appears to be the case also among mountain sheep (Geist, 1971).

The relative power of contraction of the neck muscles, as displayed during test fighting, then qualifies as one of the most reliable signals of resource-holding power, once the evolutionary decision was made in goats and ibex to use the rear clash to assert themselves aggressively. However, direct trials of strength observed in our subjects appear to be widespread in animals

(Eibl-Eibesfeldt, 1970), probably because of the need for reliable information about the attributes of opponents. Under this view, a harmless fighting test would be of great value to a challenger. In addition, the seven types of conventional fighting in *C. pyrenaica* also fits the "war of attrition" model (Maynard Smith, 1974; Maynard Smith and Parker, 1976) because the costs of fighting amount to the duration of the contest. Conversely, horn development and fighting in *C. pyrenaica* appear to fit many of the predictions of the "truth in advertising" model (Kodric-Brown and Brown, 1984), as seen in the considerable intrapopulational variability in horn and body size. The latter two variables are directly related to nutritional condition, population density, and differential access to estrous females, because the cost of horn production and combat are high (Alados, 1986; P. Fandos, pers. comm.).

ACKNOWLEDGMENTS

I am indebted to A. Kitchener for constructive comments, to M. Calabrús, J. Garay, E. González, F. Hiraldo, P. Recuerda, J. Sañudo, and M. Simón for facilitating access to institutional and private skulls and trophies collections, to F. Campos for his help in data analysis, to J. López Rojas for his excellent drawings, to the Agencia de Medio Ambiente de Andalusia for assistance during the period of field work and to my wife, Cristina, for her help measuring specimens. The study was supported by a grant from the Comisión Asesora de Investigación Científica y Técnica (Spain).

LITERATURE CITED

- ALADOS, C. L. 1986. Aggressive behaviour, sexual strategies and their relation to age in male Spanish ibex (*Capra pyrenaica*). Behavioural Processes, 12: 145-158.
- CLUTTON-BROCK, T. H., AND S. D. ALBON. 1979. The roaring of red deer and the evolution of honest advertisement. Behaviour, 69:145-170.
- CLUTTON-BROCK, T. H., S. D. ALBON, R. M. GIBSON, AND F. E. GUINNESS. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). Animal Behaviour, 27:211-225.
- DUNBAR, R. I. M., AND E. P. DUNBAR. 1981. The grouping behaviour of male *Walia ibex* with special reference to the rut. African Journal of Ecology, 19:251-263.
- EIBL-EIBESFELDT, I. 1970. Ethology. The biology of behavior. Holt, Rinehart & Winston, New York, 625 pp.
- FANDOS, P., AND C. R. VIGAL. 1988. Body weight and horn length in relation to age of the Spanish wild goat. Acta Theriologica, 33:339-344.
- FANDOS, P., C. R. VIGAL, A. MACHORDOM, J. M. FERNÁNDEZ, T. MARTÍNEZ, AND F. PALACIOS. In press. Horn segments and dental cementum lines as age criteria for the Spanish wild goat, *Capra pyrenaica* Schinz, 1838. Säugetierkundliche Mitteilungen.
- GEIST, V. 1966. The evolution of horn-like organs. Behaviour, 27:175-214.
- . 1971. Mountain sheep. The University of Chicago Press, Chicago, 383 pp.
- . 1974. On fighting strategies in animal combat. Nature, 250:354.
- KITCHENER, A. 1985. The effect of behaviour and body weight on the mechanical design of horns. Journal of Zoology (London), 205:191-203.
- . 1988. An analysis of the forces of fighting of the blackbuck (*Antelope cervicapra*) and the bighorn sheep (*Ovis canadensis*) and the mechanical design of the horns of bovids. Journal of Zoology (London), 214:1-20.
- KODRIC-BROWN, A., AND J. H. BROWN. 1984. Truth in advertising: the kinds of traits favored by sexual selection. The American Naturalist, 124:309-323.
- MAYNARD SMITH, J. 1974. The theory of games and the evolution of animal conflicts. Journal of Theoretical Biology, 47:209-221.
- MAYNARD SMITH, J., AND G. A. PARKER. 1976. The logic of asymmetric contests. Animal Behaviour, 24:159-175.
- NIEVERGELT, B. 1966. Der Alpensteinbock (*Capra ibex* L.) in seinem Lebensraum. Mammalia depicta, Verlag Paul Parey, Hamburg, 85 pp.
- . 1967. Die Zusammensetzung der Gruppen beim Alpensteinbock. Zeitschrift für Säugetierkunde, 32:129-144.
- PARKER, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. Journal of Theoretical Biology, 47:223-243.
- SCHAFFER, W. M. 1968. Intraspecific combat and the evolution of the Caprini. Evolution, 22:817-825.
- SCHAFFER, W. M., AND C. A. REED. 1972. The co-evolution of social behavior and cranial morphology in sheep and goats (Bovidae, Caprini). Fieldiana: Zoology, 61:1-88.
- SCHALLER, G. B. 1977. Mountain monarchs. The University of Chicago Press, Chicago, 425 pp.
- SHANK, C. C. 1972. Some aspects of social behaviour in a population of feral goats (*Capra hircus* L.). Zeitschrift für Tierpsychologie, 30:488-528.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, 312 pp.

LINKED CITATIONS

- Page 1 of 1 -



You have printed the following article:

Horns and Fighting in Male Spanish Ibex, *Capra pyrenaica*

Fernando Alvarez

Journal of Mammalogy, Vol. 71, No. 4. (Nov., 1990), pp. 608-616.

Stable URL:

<http://links.jstor.org/sici?sici=0022-2372%28199011%2971%3A4%3C608%3AHAFIMS%3E2.0.CO%3B2-J>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

Literature Cited

Truth in Advertising: The Kinds of Traits Favored by Sexual Selection

Astrid Kodric-Brown; James H. Brown

The American Naturalist, Vol. 124, No. 3. (Sep., 1984), pp. 309-323.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28198409%29124%3A3%3C309%3ATIATKO%3E2.0.CO%3B2-N>

Intraspecific Combat and the Evolution of the Caprini

William M. Schaffer

Evolution, Vol. 22, No. 4. (Dec., 1968), pp. 817-825.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28196812%2922%3A4%3C817%3AICATEO%3E2.0.CO%3B2-V>