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AGGRESSIVE BEHAVIOUR, SEXUAL STRATEGIES AND THEIR RELATION TO AGE IN MALE SPANISH IBEX (Capra pyrenaica)

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ABSTRACT

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This study aimed to investigate the factors determining male reproductive success during the rutting season of the Spanish ibex. The rut lasts about seven weeks. At the begining of this period the old males engage in contests with each other, while the adult and subadult males spend more time courting the females. In the second half of this period, the old males court and gain reproductive acceptance while the adult and subadult males decrease their courtship activity. The old males also differ from the adult and subadults in the daily pattern of courtship activity. The old males test their relative strength and show agonistic displays as their most typical behaviour, while younger males tend towards more overt and primitive forms of fighting. Most contests involving males of all age classes occur between animals of similar age and these combats often end unresolved. The older of two combatants usually wins. Older males are preferred to younger ones by the females. The older the males, the more energy they expend in activities leading to mating and representing energy expenditure and the less time they use in those representing energy saving or recovery.

INTRODUCTION

Variation in the mating success of males may depend on the preferences of females for certain males, on competition for females, or some combination of both forces (Darwin, 1871; Halliday, 1978; Payne, 1983). In species in which males provide neither resources nor parental care a female preference for large or dominant males is a common pattern (Trivers, 1972; Halliday, 1978). Theoretically, the choice of large or dominant males should have a genetic advantage and may minimize interference from other males (Searcy, 1982). However, evidence for long-term benefits relating to the genotype of a chosen mate is very weak and rigorous demonstrations of female choice are very rare (Halliday, 1983).

Because reproductive success is more variable for males than for females over their life span (according to sexual selection theory), the immediate and ultimate factors influencing success should be different for both sexes (Orians, 1969; Trivers, 1972; Parker, 1979; Gaulin & Schlegel, 1980). In line with this, sexual dimorphism in aspects such as body size, weaponry

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and growth rate may represent distintive results of reproductive success (Fisher, 1930; Maynard Smith, 1978, Janetos, 1980; Anderson, 1982; Cohen, 1984).

In our quest to understand the factors affecting reproductive success in the male Spanish ibex we set out to answer the following questions:

1. Is fighting success related to age?
2. Is fighting success related to reproductive success?
3. Do the successful males expend more energy in reproductive effort than the remainder?

METHODS

The study was carried out on the population of Spanish ibex (Capra pyrenaica) in the Sierras of Cazorla and Segura (Southeastern Spain) during rut (November and December) in 1982 and 1983. The age and sex classes considered were: a) adult females (over 2 years), b) yearling females (between 1-2 years old), c) kids (newlborns to 1 year old), d) old males, including class IV (8-10 years old) and class V (over 10 years), e) adult males, belonging to class III (6-8 years old) and class II (4-6 years old), f) subadult males (2-4 years old) and g) yearling males (1-2 years old).

The activity patterns, the criteria for age and sex classes, and the features of the habitat were described by Alados (1984, 1985). To summarise the activity patterns are:

Activity pattern

Normal clash (Cl): two antagonists face each other from a distance simultaneously; the antagonists strike downwards with the head.

Rear clash (RCl): the ibex rises on his hind legs in front of his opponent and inclines his head towards the latter; one hind leg is placed behind the other in line with the clash; the recipient strikes as in a normal clash with head to head contact occurring close to the ground.

Horn-push (frontal) (H-pF): a male hooks his curved horn through the horn of another male and pushes downwards.

Horn-push (sideways) (H-pS): the combatants hook their curved horns and pull in a parallel position.

Butting (Butt): the animal batters the neck, side or rump with either the blunt part of the horns or the tips.

Head to tail (H-T): the two opponents stand in reverse parallel position and hook each other in the rear with their horns, sometimes circling as they do so.

Shoulder (Sho): the two animals stand side by side and push with their shoulders.

Neck fight (NF): one animal places the ventral part of his neck over the neck or shoulder of another and pushes downwards.

Agonistic displays:

Head up (H up): by raising his head and standing stiffly erect, a male enhances his appearance.

Horn threat (HTh): with head lowered, muzzle pointing towards the ground or tucked close to the neck.

Lateral display (LD): the two antagonists face each other from a distance showing their horns frontolaterally.

Rubbing (Rub): the subject licks and nuzzles or rubs his face or horns against the face or neck of recipient.

Head under neck (HUN): the subject, with his head and neck extended, places his forehead under the neck of his opponent.

Back: the male shows his hindquarters to his opponent.
Low-stretch (L-S): the male approaches the female, holding his neck low and horizontally and straining his muzzle (this is also used during dominance interactions among males).
Mounting (Mo): as an expression of dominance; this is common in the Spanish ibex.
Twist (Tw): consists of rotating the head rapidly some 45º to 90º so that the horns are turned away from the female; these displays are often accompanied by a flicking of the tongue.
Chase (Ch): when a female is near the estrous cycle several males chase the female running behind her.
Retreat (Rtr): when a female rejects the male, presenting her horns to him or butting him in the head or neck, the male replies by moving back.
Estrous female: a receptive female stands or walks showily with her back slightly arched and her tail held limply horizontal.

Data recording

Data were recorded for 20 days during 1982 and for 21 during 1983. The observation periods being from 7a.m. to 16p.m. in 1982 and in 1983: 1) from 7a.m. to 11a.m. and 2) from 14.30p.m. to 16.30p.m.

The data recorded included the number of individuals in each group, their age and sex class, place, habitat, date and time of day.

Particular groups were observed continuously for one day at a time and the age and sex classes of all animals in the group, the activities performed by each of them and their position relative to each other, were recorded at 15 min. intervals. Whenever possible, all agonistic interactions and occurrences of courtship were recorded.

52 combats were observed in the two years. The average number of animals living in the study area was 22 in 1982 and 34 in 1983. The sex ratio (φ/σ) in 1982 was 1.14 and 1.33 in 1983.

RESULTS

Timing of rutting behaviour

If we consider how the different age classes of males are involved in

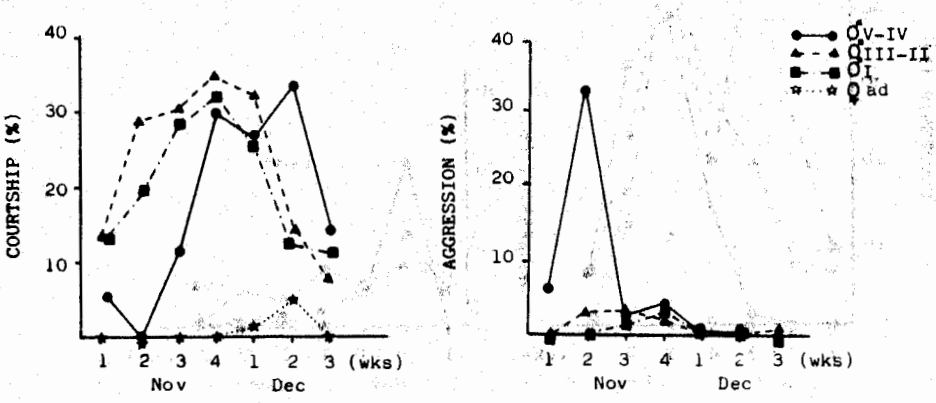

Fig. 1.- Percentage of time devoted to courtship activities by males and the frequency of receptive females during 1982 rut. (Observation period from 7a.m. to 16p.m.)

agonistic interactions and courtship, it can be seen in Fig. 1 that at the beginning of rut, when the older males engage in contests among themselves, the adult and subadult males start unsuccessfully courting the females. The old males start courting in the second half of the rut, displacing the adult and subadult males from the side of the females and gaining acceptance from the latter.

When we compare the equivalent periods for 1982 and 1983, some differences are evident (Fig. 2) although the general pattern is maintained. It is to be noted, however, that in 1983 the adult and old males courted more intensively and for a shorter period of time, whereas the rate of

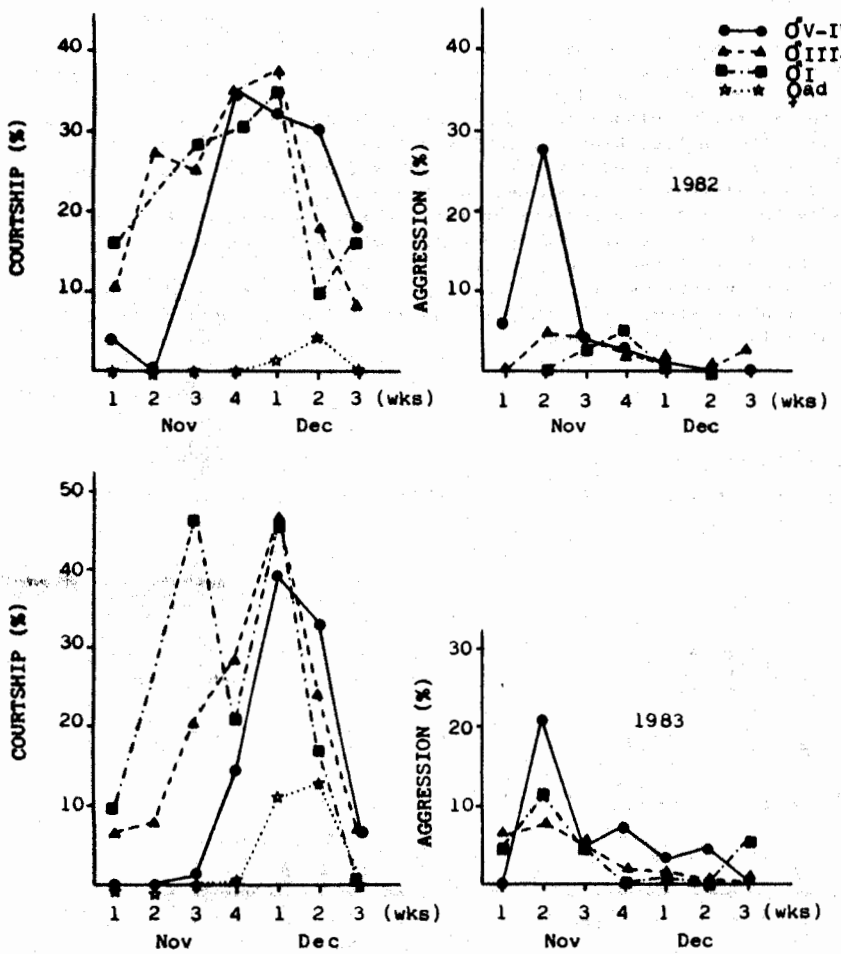

Fig. 2.- Percentage of time devoted to courtship activities by males and the frequency of receptive females during comparable periods (dawn and dusk time) during the 1982 and 1983 ruts. (Observation period from 7a.m. to 11a.m. and from 14.30p.m. to 16.30p.m.)

intermale aggression was lower in 1983.

Old males differ in the daily timing of courtship activity from the adult and subadult ones, the latter two being rather similar in this respect (Fig. 3).

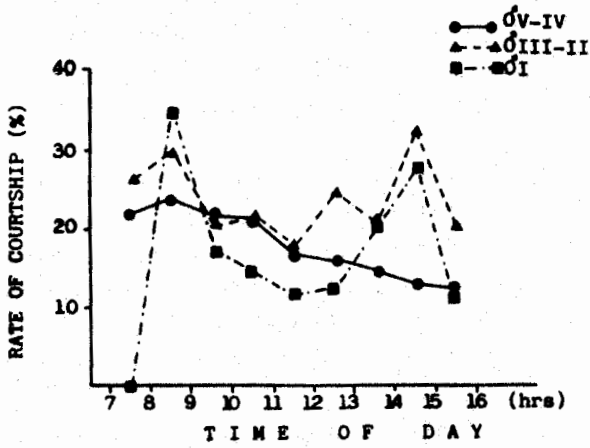

Fig. 3.- Time of male courtship activity during the 1982 rut.

Male agonistic behaviour

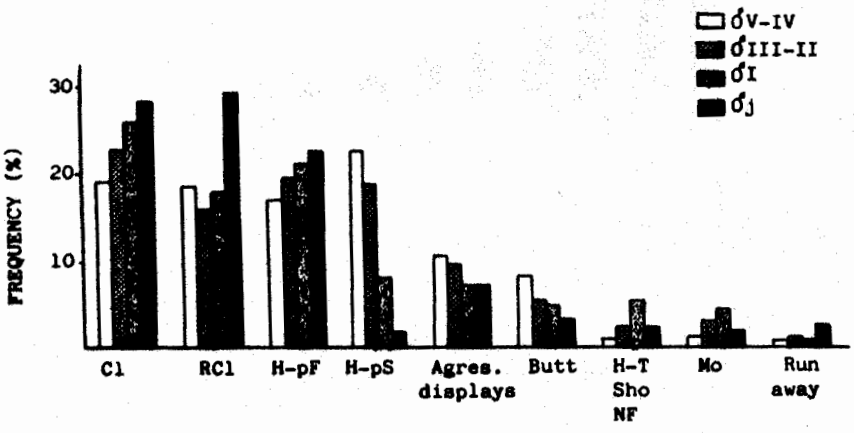

Fig. 4.- Frequency of different aggression patterns performed by each male age class.

Fig. 4 shows the frequency of various forms of aggression in males of different ages: we can see that frequency of horn clash from an all-fours position and horn push to the front decreases as age increases ($r_s = -1$, $N = 4$, $\alpha = 0.05$). A similar, although not significant, pattern was shown for the rear clash from a bipedal position ($r_s = -0.4$, $N = 4$, N.S.). On the other hand, the sideways horn push and the various aggressive displays (rubbing, head under neck and turning the back) and butting show a very different pattern, their intensities increasing with age ($r_s = 1$, $N = 4$, $\alpha = 0.05$).

Considering the aggressive patterns performed by the two opponents involved in a fight, we see that most are performed in approximately an equal amount by the older and younger of the combatants. However, displays of rubbing, head under neck and turning the back are performed mainly by the younger of the two animals (Wilcoxon Test, $T = 1$, $N = 7$, $\alpha = 0.05$; $T = 0$, $N = 6$, $\alpha = 0.05$, $T = 8$, $N = 8$, N.S. respectively) (Fig. 5), indicating submission.

As regards the level of aggression shown by the different male age classes (rate, calculated by dividing number of cases in which an animal was

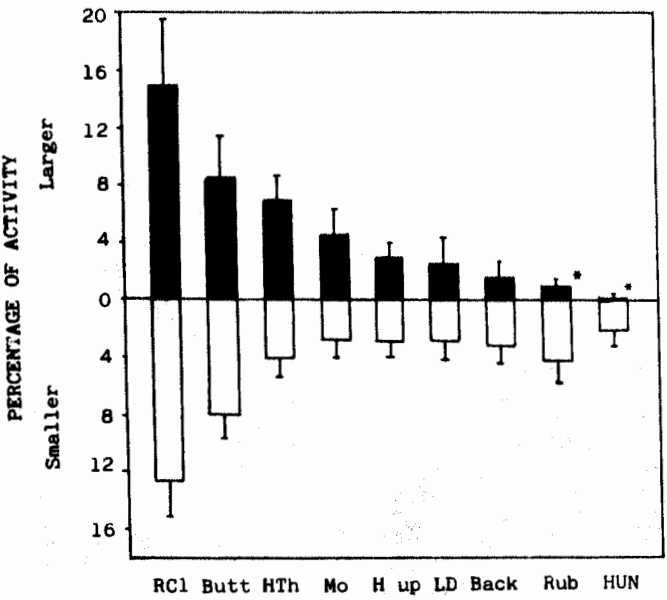

Fig. 5.- Mean frequency (%) of aggressive pattern performed by the larger and the smaller of the two males involved in a contest. *: level of significance of .05.

involved in a fight by the per unit value for the individuals of the same age class present in the study area), it can be seen in Fig. 6 that the various classes differ in this respect ($\chi^2 = 113.4$, d.f. = 3, $\alpha = 0.001$) the old males being the most aggressive.

Fight duration can also be used as an index of aggressive intensity and a measurement of it could be the total frequency of all behaviour patterns involved in each combat. In connection with this it was found (see Fig. 6) that the rate increases with age.

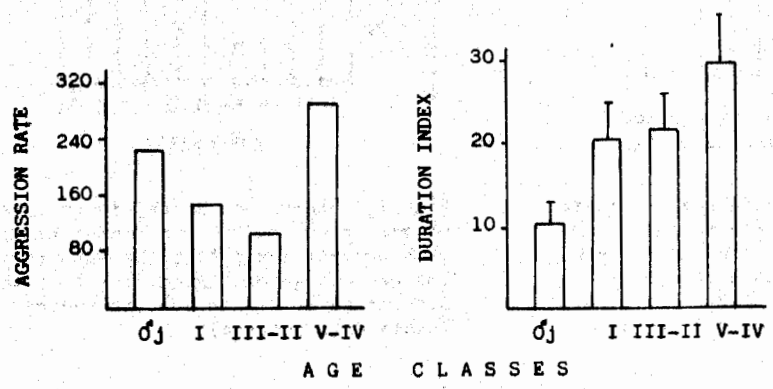

Fig. 6.- Left: aggression rate of the male age classes (rate calculated dividing number of cases where an animal was involved in a fight by the per unit value for the individuals of the same age class present in the study area). Right: duration index (frequency of patterns involved in each fight) of the male age classes.

If we now look at the frequency of fights depending on the age difference between opponents (Fig. 7), it was found that most contests are between animals differing in age by about two years. In Ibex the older the male, the bigger it is, so differences of two years of age are correlated with differences in body size.

The number of fights won or lost must be important. The criteria for winning in fights was the display of submission shown at the end of the fight by the loser. The problem was approached by concentrating on the older of the two animals of the different age classes involved in any fight, subtracting the frequency of fights lost from the frequency of those won. The results are shown in Fig. 8, where it is evident that the younger the two combatants are, the easier it is for the older of the two males to win ($r_s = 0.9$, $N = 5$, $\alpha = 0.05$).

Combats do not always end with a winner and a loser and are often not resolved. In Fig. 9, we observe that the probability of a fight being

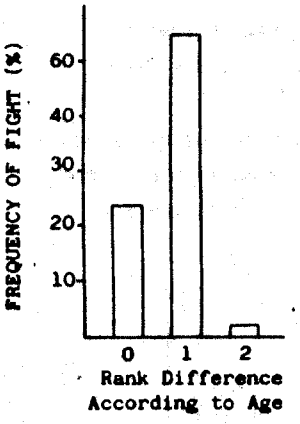

Fig. 7.- Frequency of fights versus difference in age (0: opponents differing by less than two years of age. 1: difference of 2-4 years. 2: difference of 4-6 years).

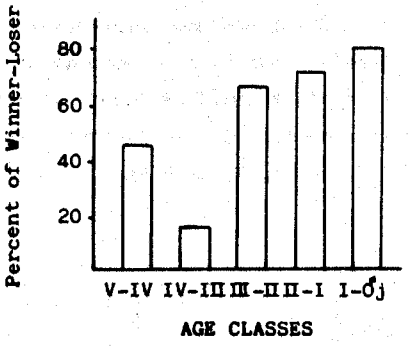

Fig. 8.- Fights won minus fights lost by the larger of the two opponents in each contest (calculated by subtracting the percentage of fights lost from the percentage of fights won; including fights not resolved).

resolved is much higher when there is an age difference in the pair of animals involved in the fight (χ^2 = 11.4, d.f. = 1, α = 0.001), whereas for animals belonging to the same age class the differences are not significant (χ^2 = 0.3, d.f. = 1, N.S.). In Fig. 9, we can also see that, as expected, the older animal of the pair was more frequently the winner.

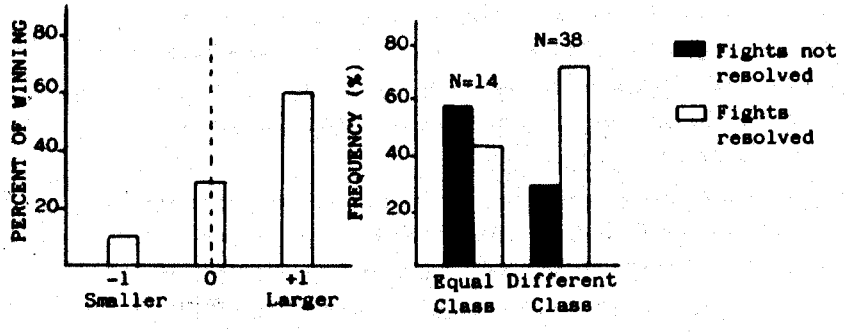

Fig. 9.- Left: percentage of fights won depending on age difference between combatants (0: equal age class, +1: winner is one age class step higher than loser, -1: winner is one step lower than loser). Right: frequency of fights ending resolved or unresolved between animals of various ages.

Male courtship behaviour: cost and benefit

Considering the various aspects of male courtship, we may first note that the behaviour units low-stretch and twist are the most frequent, the rest of the courtship patterns being rather rare (Fig. 10).

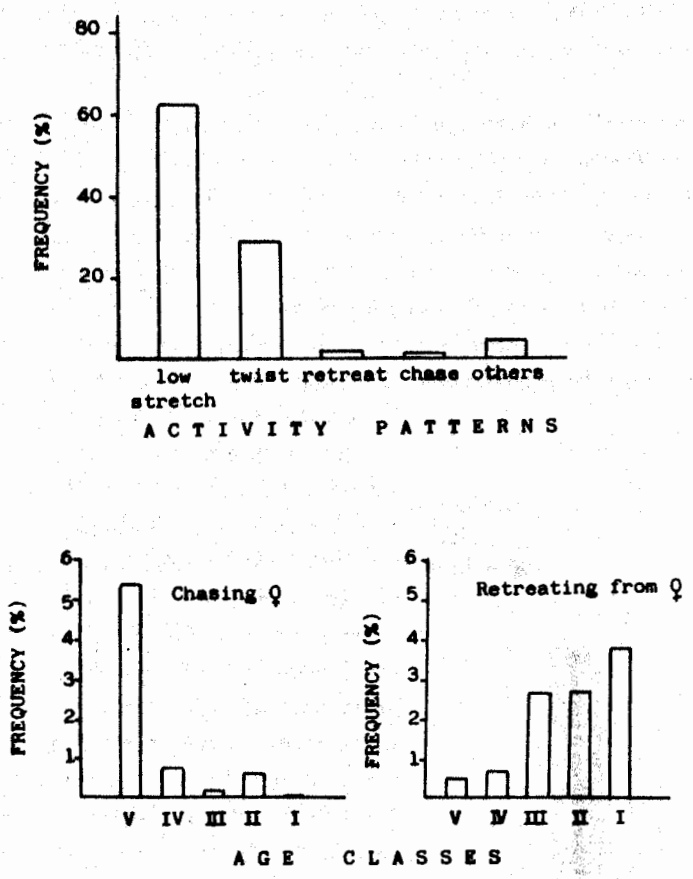

Fig. 10.- Above: frequency of performance of the various courtship patterns by all males. Below left: frequency of males chasing females, right: frequency of males retreating from females.

The various age classes of males also show differing tendencies to perform the various courtship patterns. So, chasing females is more often characteristic of the older males (r_s = 0.9, N = 5, α = 0.05), whereas the younger ones are more often rejected by the females (r_s = 0.97, N = 5, α = 0.05).

Since chasing females is one of the most frequent activities of the males at the peak of rut, it is of interest to consider the position of males following or chasing each female. Data collection was easy because

males arrange themselves approximately in single file behind each female. The line of males was divided into three parts (front, central and rear) and in each observation each individual male was assigned to one of those parts. These data were collected at two particular moments: when the males were actually running after the female and when they were all standing behind her and at least one of the males was performing low-stretch towards the female.

In Fig. 11, we represent mean age rank on the ordinate: the older males are rank 1, descending in age through ranks 2, 3 and so on. When all males are chasing the female, those in the central position tend to be younger, although the differences were not significant (Kruskal-Wallis one way analysis of variance, $H = 5.43$, d.f. = 2, N.S.). When we look at the males standing behind a female, some of them performing low-stretch, the situation is clearer, those animals at the front being much older. In this case, the differences were significant ($H = 14.46$, d.f. = 2 $\alpha = 0.001$).

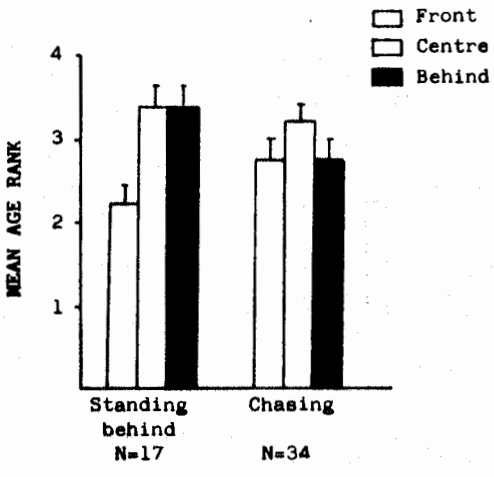

Fig. 11.- Different positions of males while chasing a female or standing behind her.

We consider that females reject males when the former threaten the latter with their horns in response to male advances. Conversely, we consider that females accept males by raising their tails. A significant difference was found in the acceptance and rejection of the different male age classes (Kolmogorov-Smirnov two-sample test, $D = 0.48$, $N = 5$, $\alpha = 0.01$; $D = 0.31$, $N = 5$, $\alpha = 0.01$, respectively). This fact is clearly seen in Fig. 12, where the relation of acceptance to rejection is represented for the various male age classes ($r_s = 0.9$, $N = 5$, $\alpha = 0.05$). Thus the benefit of male rutting behaviour is greater for old males.

As one of the principal functions of intermale aggression in many ungulates is mating with as many females as possible, it would be interesting to analyse the cost and benefit of rutting behaviour for male ibex at this time.

In order to get an idea of cost, the time consumed in the various activities leading to mating and representing energy expenditure, such as watching, fighting and courting, and in those representing a recovery or

saving of energy, such as feeding or lying down, was registered.

When analysing the rate of performance of those activities by the males of different ages, it was found that the older the animal, the more energy is invested and the less time is used in energy recovery (Fig. 13).

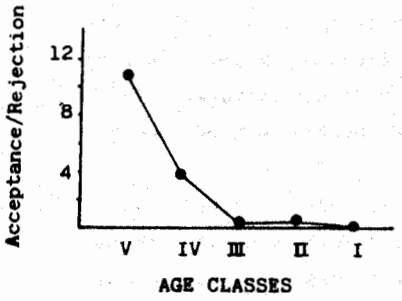

Fig. 12.- Relation of female acceptance to rejection toward different male age classes.

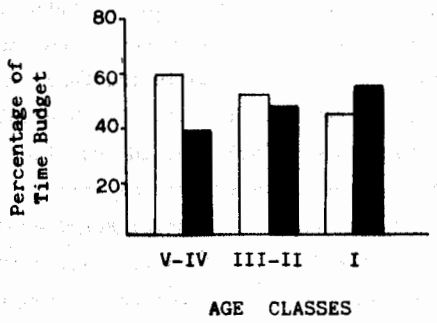

Fig. 13.- Time consumed in activities representing expenditure or saving of energy: ■ energy recovered, □ energy invested.

DISCUSSION

The social system of the Spanish ibex during rut is based on the establishment of a strong intermale hierarchy where the dominant animals displace the submissive ones from access to females at the time of rut. So multimale ibex groups exhibit a form of female defense polygyny in which males defend females only near the time of ovulation, as do macaques and baboons (Harcourt, 1981).

The narrower and higher courtship peak in 1983, as compared to 1982, was probably a result of the drought suffered in 1983. This caused a delay in the onset of rut, which became very pronounced for only a week and then declined rapidly in intensity as a result of physical deterioration of the old males, which, became noticeably thinner.

The lower aggression rate observed in 1983 was also probably caused by the same environmental conditions.

The higher female acceptance of males in 1983 may have been real although it could have been a result of an improvement in the researchers ability to detect the behaviour.

An interesting result concerning aggression is that old males tend to test strength, with aggressive displays, sideways horn push and horning the

opponent's body weakly whereas the younger males usually choose more overt aggression patterns, such as clashing and frontal horn pushing. A similar situation was found in mountain sheep (Geist, 1971). Like mountain sheep (Geist, 1971) and the ibex (Schaller, 1977), the younger males of the Spanish ibex are more prone than the older ones to performing the more primitive forms of fighting.

The fact that the older the males are the more intensively they fight and the more often they are involved in short fighting contests, with the exception of the yearling suggests that intermale aggression is affected on the one hand by variation in the benefits of fighting to get access to females, as in red deer (Clutton-Brock et al., 1979) and primates (Berenstain & Wade, 1983) and, on the other hand, by the need of young males to test the adult's fighting ability.

The fact that the male Caprini keeps growing in body and horn size during its whole life should help animals to differentiate easily between younger animals, where differences in body and horn size are greater and then the combats are easily resolved by the triumph of the older male, as also appears to be the case for red deer (Clutton-Brock et al., 1979). We may interpret the finding that most combats take place between animals of equal or similar age, and the fact that they are often unresolved as a need for the weaker of the two opponents to avoid risks, as appears to be the case in other ungulates (deer and sheep, Eibl-Eibesfeldt, 1970; mountain-sheep, Geist, 1971; Capra, Schaller, 1977; red deer, Clutton-Brock et al., 1982).

When an individual fights for a resource its decision on how to fight must depend not only on the value of the prize but also on its own strength compared with that of its opponent; therefore we might expect displays to demonstrate fighting ability and so allow the contestants to settle their dispute quickly without recourse to a costly fight (Parker 1974) which is related to the higher rate of aggressive displays by older males.

The observations of courtship behaviour, particularly the ratio of acceptance to rejection, shows that females prefer older males. Old males thus achieved high success by chasing younger males away from the proximity of a female when she stopped running, and being near her at the right moment, and, on the other hand, as a result of the female accepting their courtship and by threatening and butting younger males.

The effect of a female running is to attract the attention of males, so high rank male threats to low rank males make it impossible for low rank males to mate successfully. In this way, females of the Spanish ibex exercise a choice in favour of high status males.

The long-accepted role of female choice in the evolution of male

epigamic characters is challenged by recent studies of certain sexually-dimorphic species, notably birds of paradise and lekking species. These studies suggest that competition between males is a more potent force in these species than female choice (Halliday, 1983). So, whereas intrasexual selection has been widely accepted as the evolutionary process that has led to such male characters as large size, horns and antlers, intersexual selection has been the subject of considerable debate.

The question of whether animals can choose their mates on the basis of the quality of their genotypes is the most controversial issue in mate choice literature. Perhaps the only instances where it is tenable, on the basis of existing studies, are those where there is evidence that females choose older males, whose ability to survive may have an inheritable basis (Halliday, 1983).

Old males have demonstrated their ability to survive for a longer period and, by choosing them, females may ensure the transfer to their offspring of the right genes for survival (Trivers, 1972; Howard, 1978). In addition, the differences in reproductive success appear to be correlated with variation in fighting effectiveness in different animal species (Geist, 1971, in mountain sheep; Kucera, 1978, in desert mule deer; Clutton-Brock et al., 1979, 1982, in red deer; Berenstain & Wade, 1983, in some primate species).

Finally, we observe that, as in red deer (Clutton-Brock et al., 1982) the energy invested by ibex during rut is in relation with breeding success, measured in our case as female acceptance for copulation; so, the older the male is, the more energy he invests in mating activities and the higher is his breeding success. So the sexual strategy of males of different age classes differs in relation to breeding success, the most successful being the old males.

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