

Ram rut-involvement in a hunted population of mouflons

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This study was conducted during the rut in a protected valley (Vialais) inhabited by one permanent population of ewes. This valley forms part of a larger hunted area. Rams which segregate from ewes entered the Vialais during the pre-rut, first young rams while the oldest rams arrived later. These latter stay in the company of ewes only when most lambs are conceived. The removal of old males shifted the male population structure, favoring young males. Old males tended a low proportion of ewes in mating groups which was used as an index of the male mating success. A larger proportion of young males successfully tended estrous ewes than in protected populations of wild sheep. Despite that, the population is highly productive which contradicts the arguments that precocious involvement of young males in reproduction may be detrimental to population productivity.

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Introduction

In most ungulates exhibiting a polygynous or promiscuous mating system, it is reported that only a small proportion of dominant males achieve most mating (Gibson and Guinness 1980, Gosling 1986). The mouflon (*Ovis gmelini*), like other sheep species, is a medium-size, non-territorial, promiscuously breeding ungulate. Dominant males apply various strategies depending upon the social behaviour and space use of reproductive females (Emlen and Oring 1977, Gosling 1986). In *Ovis* species, the most successfully reproductive rams are those which tend an ewe (Geist 1971, Hogg 1984, 1987). The dominant males try to impede, directly or indirectly, attempts to mate of other male competitors. The relative reproductive success of dominant males depends on the time they tend reproductive females or on their capacities to detect when females come into estrus (Jewell *et al.* 1986). Subordinate rams employ alternative mating strategies, either breaching the defense of dominant rams (coursing) or blocking an ewe away from other rams

(Hogg 1984). As the number of subordinate competitors increases around an estrous ewe, the mating success of dominant males decreases and an ewe may mate with several different rams (Jewell *et al.* 1986, Hogg 1987).

Male sexual competition may increase consequent upon modification of the male population structure. Firstly, when the proportion of young subordinate males naturally increases (Byers and Kitchen 1988, Rubenstein 1986) and secondly, when dominant males are removed by hunting (Heimer and Watson 1986, Valdez *et al.* 1991). Logically when old dominant rams are less numerous, we can expect that young rams, i.e. rams ≤ 6 years old in our population, will successfully court more estrous ewes.

In Caroux-Espinouse massif, 80% of lambs are born in April which suggests that estrus are synchronous occurring in November (R. Bon *et al.*, in prep.). Even during the mating season when they widely move from group to group, the proportion of old rams ≥ 7.5 years old is very low in the population of Caroux-Espinouse (R. Bon *et al.*, in prep.). This suggests a higher competition between males as well as a stronger participation of young males in reproduction than in protected populations. In this paper, we test this hypothesis, examining the composition of the male reproductive population. We identify which males court estrous ewes and finally we will discuss the impact of such management on the mouflon mating system.

Study area

The Caroux-Espinouse massif (42° N, 3° E) is situated in the south of France. The vegetation, and both physical and climatic characteristics have been presented elsewhere (Bon and Campan 1989, Bon *et al.* 1990). The population of mouflons inhabits an area of approximately 10,000 ha and is partly protected from hunting in the Reserve Nationale de Chasse (1830 ha) where the data were collected in autumn from 1984 to 1988. This reserve is centred on a large N – S oriented valley (Vialais), with slopes ranging between 600 m to 1100 m of altitude. Woods covered 28% of the hillside and rocks 8%. In the open areas, moorlands characterized by heathers (*Erica cinerea*, *Calluna vulgaris*), and brooms (*Sarothamnus scoparius*, *Genista purgans*) are dominant but are frequently mixed with graminaceous species and bilberry (*Vaccinium myrtillus*).

Studied population, material and methods

Mouflons were introduced at the end of the 1950s – beginning of the 1960s in the Caroux-Espinouse massif. The population has developed well and reaches around 1000 animals. It is subjected to hunting, from September to February, primarily older and larger rams for their trophy, and beside animals are captured in spring-summer to be reintroduced elsewhere. Over the last 11 years, males and females were similarly removed but the mean age of males was higher (male range: 5 – 6.6 years, female range: 3.1 – 4.5 years). The first lambs were observed at the end of March and most ewes lambed in April (R. Bon *et al.*, in prep.). Then subtracting the gestation period, most of the successful copulations had been achieved in November though the rut lasted from the end of October up to end of December. We subdivided the rut in three periods: the pre-rut taking place in October, the full rut in November and the post-rut in December.

Only one class of ewes was considered, e.g. all ewes ≥ 1.5 year old (F). The age of males can be estimated by counting growth annuli but as it is difficult to appreciate at long distance without misdeterminations, 4 classes of rams were retained: yearling (M2), 2.5-year-old (M3), 3.5 to 6.5-year-old (M4), ≥ 7.5 years old rams (M5).

Data were collected during 69 ground surveys from October to December 1984, 1986 and 1988, during October and November 1985, and in October 1987, in the Vialais valley where most animals use the slopes during autumn and winter (Auvray 1983). The composition of all groups observed from fixed posts were noted.

In this population, most ewes ≥ 1.5 year old are potentially receptive (Cugnasse *et al.* 1985, R. Bon *et al.*, in prep.). Ewes were considered in estrus if they were only followed and courted consistently by one or several rams. We considered all males ≥ 1.5 year old sexually mature because yearling mouflons or bighorn sheep can reproduce in controlled conditions (Mottl, in Pfeffer 1967, Foreyt 1988). Grubb and Jewell (1973) also found that yearling Soay sheep establish tending bonds with ewes during the rut.

The M/F ratio is expressed as the males ≥ 1.5 year old/ewes ≥ 1.5 year old ratio. The ratio of each male class/ewes ≥ 1.5 year old reflects their abundance relatively to the potentially reproductive ewes. The male population structure is revealed by the ratio of each male class/males ≥ 1.5 year old.

When consorting with rams ≥ 1.5 year old, a ewe withdraws from its group, often followed by a lamb which tries to resist being separated before being chased, most often by young males. This type of group was called a mating group. In this study, the 6 copulations or attempts were observed in this social context. Then, we considered the mating groups as a good index of the timing of estrus. Following Hogg (1984), two categories of mating groups were distinguished: (1) one potentially reproductive ewe accompanied by one ram called a tending group and (2) one potentially reproductive ewe accompanied by several rams called a coursing group. We almost never observed blocking groups. As copulations were rarely observed, the involvement in coursing groups provides a good index of the male rut-involvement and the involvement in tending groups a good index of ram reproductive success.

Because very few animals were marked, data were surely not independent which prevented statistical comparisons (Machlis *et al.* 1985). The numbers of males and females in the figures are the frequencies of observation of anonymous mouflons.

Results

Outside the rut, male and female mouflon socially segregate with an intensity depending upon the age of the males (Bon and Campan 1989). A single ewe home range group permanently lives in Vialais valley (Dubois *et al.* 1992). In summer, rams observed in ewe home ranges are almost always yearlings (Fig. 1). During this season most animals lived in forested areas, to avoid the high temperatures and probably insect disturbances (Auvray 1983).

Population structure during the rut

In the beginning of October, while ewes and lambs still frequently used visually closed habitats, rams entered Vialais valley, widely roaming from group to group, so that they were more observed than ewes as indicated the high value of the M/F ratio (Fig. 1). In the pre-rut, 2.5-year-old and 3.5- to 6.5-year-old rams entered earlier than males ≥ 7.5 years old as shown by each male class/ewe ratio.

At the end of the pre-rut, with autumn rains, a growing period provides new graminaceous. Consequently, ewes and rams used more the open areas grazing

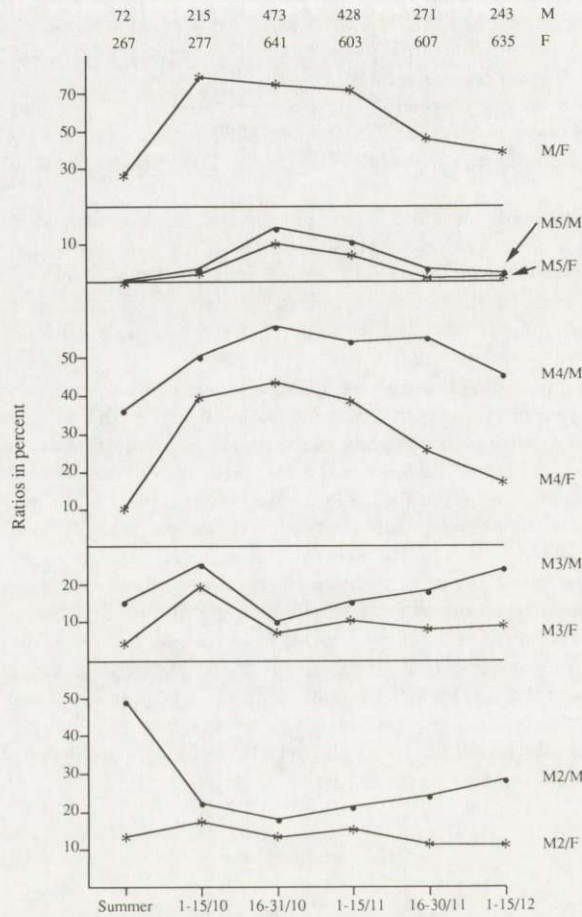


Fig. 1. The population structure of mouflons observed in open areas in the ewe "Vialais valley" group during the summer and the rut from 1984 to 1988. The M/F ratio and the ratios of each male class to the total number of females (F) or males (M) are represented by 15-days periods. Pre-rut: October; rut: November; post-rut: December. M2: yearling, M3: 2.5-year-old, M4: 3.5 to 6.5-year-old, M5: \geq 7.5 years old rams.

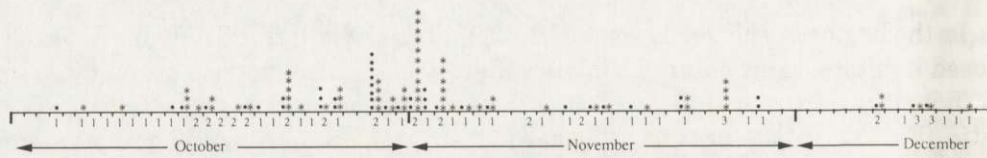


Fig. 2. Distribution of tending (*) and coursing groups (●) observed from 1984 to 1988 during the rut of mouflons living in Vialais valley. Each interval on the abscissa represents one day. The numbers of ground surveys for each sampled day are indicated on the abscissa.

graminaceous which represent more than 80% of the rumen contents (Bon *et al.* 1990). The proportion of the oldest ram is maximum so that the M/F ratio remained high. However, the M5/F and M5/M ratio revealed, during the full rut, (1) a low proportion of old males compared to the mature ewes and (2), a male population structure strongly biased toward the young males. The rams ≥ 7.5 years old remained in the valley only few weeks, from mid-October to mid-November. The younger rams left it more gradually, especially 2.5-year-old ones (Fig. 1).

Table 1. Observed frequencies of yearling, 2.5-year-old, 3.5- to 6.5-year-old and ≥ 7.5 years old males in mating groups during the rut from 1984 to 1988 in Vialais valley.

	Group type	Number of groups	M5	M4	M3	M2	Total number of males
1 - 15/10	a	6	0	5	1	0	6
	b	2	0	3	2	0	5
	a + b	8	0	8	3	0	11
16 - 31/10	a	22	2	16	4	0	22
	b	20	10	26	11	8	55
	a + b	43	12	42	15	8	77
1 - 15/11	a	24	6	12	6	0	24
	b	10	5	42	2	6	55
	a + b	34	11	54	8	6	79
16 - 30/11	a	8	0	5	3	0	8
	b	4	1	7	3	2	13
	a + b	12	1	12	6	6	21
1 - 15/12	a	7	0	4	1	0	5
	b	5	0	5	3	0	8
	a + b	12	0	9	4	0	13

a: tending groups, b: coursing groups, a + b: all mating groups. M2: yearling rams, M3: 2.5-year-old rams, M4: 3.5- to 6.5-year-old rams, M5: ≥ 7.5 years old rams.

Timing of estrus

On the whole, 108 mating groups were observed from the beginning of October to mid-December but the mode for coursing groups occurred at 29 October and at 1 November for tending groups (Fig. 2). Signs of estrus are clumped in time, centred around the end of October beginning of November. All the copulations or mount attempts observed (N = 6 sessions) were observed during the 26 October to 5 November interval.

Consort and ram mating involvement

From all mating groups observed during the rut, 61.5% were tending groups and 38.5% were coursing groups. During the first 15 days of November the

proportion of tending groups reached 70.6%. The mean number of rams involved in coursing group was 2.4 ± 1.09 (mean \pm S.E.). In the pre-rut and post-rut periods, estrous ewes were consorted mainly by 2.5-year-old and 3.5- to 6.5-year-old rams (Table 1). Yearling males were never observed tending females and participated in the rut only in coursing groups. Rams ≥ 7.5 years old were involved in mating groups in late October and beginning of November (Table 1). But they represented a low proportion of rams involved in tending groups, reaching the highest proportion in beginning of November (25%). When considering all mating groups, rams ≥ 7.5 years old represented only 14.7% of rams consorted with ewes when most of conceptions occurred. During this period, 2.5-year-old rams tended ewes as often as rams ≥ 7.5 years old. From the 6 different sessions of copulations or mount attempts, 5 of them occurred in tending groups involving one ram 7.5 years old, three 3.5-year-old and one 2.5-year-old. In the last case, the ewe copulated with four 3.5- to 6.5-year-old rams which impeded one 3.5-year-old and two yearling rams from approaching her.

Discussion

The concentration of rams in the pre-rut period has been mentioned in other wild sheep populations (Festa-Bianchet 1991). Rams entered the rutting grounds well before first lambs were conceived. They travel from group to group investigating ewes as in other wild sheep species (Grubb 1974, Hogg 1987). In the pre-rut, ewes and lambs used more wooded biotopes than rams in our study area resulting in a high male proportion in the sampled population. However, in October, the observed M/F ratio may strongly vary depending on climatic conditions. When temperatures are high, ewes and lambs are hard to observe and the observed M/F ratio is strongly male-biased while with cold weather the M/F ratio is female-biased (R. Bon *et al.*, in prep). All the rams did not enter at the same period in Vialais valley. The young rams first congregated while the oldest ones entered the rutting grounds late in October. Yearling rams were never seen to tend ewes, while rams 2.5 to 6.5 years old did in the pre-rut. These mating groups may result from early estrus without successful copulation since first lamb conceptions occurred at the end of October (R. Bon *et al.*, in prep). It has been already shown that in mammals, subordinate and young males copulate with females early and late in the estrus period when dominant rams are still absent or when they have left the females (Jewell *et al.* 1986). Old rams consort with estrous ewes mainly during the major period of conceptions (R. Bon *et al.*, in prep.) and then stay little time in ewe home range as compared to younger rams.

Hogg (1987) showed that only "the first third of the males of the dominance hierarchy tended" and Shackleton (1991) reported that only the largest males successfully court females in un hunted populations. The survival of rams within our study area is around 13 years old as revealed by aging the trophy of hunted animals. Although we could not establish any dominance rank among the rams

before the rut, we may suppose that rams ≥ 7.5 years old occupied the highest rank in Vialais valley since the dominance rank during the mating season is related to horn and body size. The low proportion of rams ≥ 7.5 years old tending ewes, representing their reproductive success, is due to their low proportion within the male population. Because the daily proportion of estrus ewes is largely lower than the whole proportion during the rut and because some ewes, failing to conceive at a first oestrus, may have a second one (Jewell and Grubb 1974), largest males would have higher probabilities of mating (Hogg 1987). However, in Caroux-Espinouse, most lambs are conceived in 4 weeks (R. Bon *et al.*, in prep.) as in other *Ovis* population living under temperate or mountain climates (Jewell and Grubb 1974, Hogg 1987), so that old rams most probably cannot defend many ewes. This surely explains why so many 2.5 to 6.5-year-old rams courted estrous ewes as revealed by their relative proportion involved in tending bonds in late October and November. Furthermore, a ewe may be sired by several rams (Jewell *et al.* 1986, Hogg 1987) confusing the likelihood of paternity. The precocious involvement of 2.5 to 6.5-year-old rams in mating group and especially in tending group in Vialais valley is typical of populations where there is a lack of mature dominant males (Heimer *et al.* 1984, Shackleton 1991, Valdez *et al.* 1991) strongly suggests the precocious involvement of young rams in the reproduction.

The low percentage of large dominant rams would have logically resulted in a high male-male competition and social instability (Byers and Kitchen 1988, Rubenstein 1986). However, most of the mating groups were tending groups (e.g. involving 1 ram) and the mean number of males following estrous ewes in coursing groups was low (i.e. 2.4 ± 1.09 rams). These results seem to contradict those arguing that a low percentage of large dominant male ungulates leads to an intensification of the competition between males (Gray and Simpson 1982, Peek *et al.* 1986, Rubenstein 1986, Byers and Kitchen 1988, Valdez *et al.* 1991).

It has been reported that the social instability consequent upon precocious young male involvement in competitive mating activities would lead to decrease the lambing rate (Heimer *et al.* 1984, Festa-Bianchet 1989). Despite the young male population structure observed in Vialais valley, the breeding performance was high since the lowest lamb/ewes ≥ 1 year old ratio was equal to 0.64 in 1985 (Bon *et al.* 1991). Hence, 2.5 to 6-year-old rams successfully copulate with estrous ewes as reported by Shackleton (1991) for bighorn sheep. A biased culling of large males does not lead inevitably to a decrease in the reproductive performance of the population. Nevertheless, such a young male population structure is invoked to be directly or indirectly responsible of an increase of winter mortality of young males precociously involved in reproduction (Geist 1971, Heimer *et al.* 1984, Festa-Bianchet 1989).

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BOOK REVIEW

Naked Mole-rats: A success story of sociobiology

The biology of the naked mole-rats. Eds. P. W. Sherman, J. U. M. Jarvis and R. D. Alexander. *Monographs in Behavior and Ecology*. Princeton University Press, Princeton, 1991; XVI+518 pp.; index ISBN 0-691-02498-0.

A central topic of this remarkable book is the evolution of eusociality as shown by a unique mammal species, the naked mole-rat (*Heterocephalus glaber*). Eusociality has a much narrower meaning than sociality in general and concerns multigenerational colonial species in which there exists a division of labour with a few, sometimes one, individuals capable of reproducing and many other sexually inactive ones doing all work necessary to maintain the colony. It had long been thought that only two orders of insects, *Hymenoptera* and *Isoptera*, fit to this definition until all attributes of eusociality were discovered in some aphids (*Homoptera*) and naked mole-rats, in the mid-1970s and in the early 1980s, respectively.

Charles Darwin was convinced that the phenomena of sterility and self-sacrifice as seen in extreme form in social insects were of critical importance to his theory of natural selection and were potentially able to falsify it if not reasonably explained. He initiated the approach which yielded the theory of kin selection put forward by W. D. Hamilton in the 1960s and the development of sociobiology or behavioural ecology in the 1980s. The prevailing view is now that it is a haplo-diploid genetic system of Hymenoptera that is conducive to the evolution of eusociality and in fact this happened several times independently in these insects. However, haplo-diploidy is not a necessary condition for eusociality to evolve and some other factors causing an increase in mean relatedness between individuals in a population may act in favour of a similar result.