

Seasonal range use by European mouflon rams in medium altitude mountains

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The dynamics of spatial distribution was followed in 18 radio-collared male mouflons *Ovis ammon musimon* (Pallas 1811) belonging to a population living in low mediterranean mountains. It was greatly modified with age and a marked inter-individual variability was observed in young males. The modification of spatial behaviour appeared to be based on the process of progressive segregation of the sexes outside the rutting period. Spatial distribution by adult males seems to be more structured. However, certain males of at least 4 years of age were seen to be sedentary throughout the annual cycle which suggests that the social segregation of the sexes does not necessarily involve spatial segregation. The hypothesis of neotenization in males of the genus *Ovis* is supported. The rut ground is used with fidelity, being a site of particular spatial attachment, which could be related to the fact that it seems to be the birth site. Nevertheless, with age, frequentation of the birth site steadily become reduced to functional use related to rutting activities.

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Introduction

In numerous species of ungulates, age has a great influence on space occupation patterns. In the bighorn *Ovis canadensis* (Geist 1971, Festa Bianchet 1986), in the Soay sheep *Ovis aries* (Grubb 1974) and in the white-tailed deer *Odocoileus virginianus* (Nelson and Mech 1984), it was shown that males have different seasonal home ranges which only become established after 3 or 4 years. During this period, the young males take a certain length of time to leave their mothers then start to set up their own home range (Nelson and Mech 1984, Festa Bianchet 1986). This last author presents evidence suggesting that ecological factors are unlikely to be the only modulators of the ram's seasonal home ranges.

For the above authors, setting up the home range not only indicates emancipation from the mother but also a steady social segregation of the sexes. This segregation outside the breeding season is well known in many species of wild

sheep (Pfeffer 1967, Geist 1971, Leslie and Douglas 1979, Gonzalez and Berducou 1985, Bon and Campan 1989) and other ungulates, such as red deer *Cervus elaphus* (Clutton-Brock *et al.* 1982) and mule deer *Odocoileus hemionus* (Lagory *et al.* 1991).

Limited published data are available on the yearly dispersion of individual mouflon *Ovis ammon musimon* (Pallas 1811) rams. In order to have a fuller description of the organization of rams' home range, and to analyse the expression of sexual segregation on spatial behaviour, an analysis of the home range behaviour of individuals of different ages is presented here. In addition, the aim of this paper is to estimate the validity of the neotenization hypothesis (Geist 1971, Gould 1977). This hypothesis suggests a correlation between morphology and behaviour in clinal members of *Ovis* which leads to a delay of the onset of adult characteristics. One potential effect of neoteny is a postpuberal maturation period of 5 to 6 years for rams in which they increase in body and horn size and mature in sociospatial behaviour.

Study area

The hills of Caroux-Espinouse are part of a mountain range forming the southern border of the Central massif (Fig. 1). They are situated between the Montagne Noire and the Causses in the north-west of the department of Hérault (South of France). The massif shows a great diversity in vegetation, experiencing a Mediterranean influence in its southern part and an Atlantic one in its northern part. The central part of our study area is occupied by a National Wildlife Sanctuary covering an area of 1800 hectares. The mouflon population was introduced there at the end of the 1950s (Pfeffer and Genest 1969).

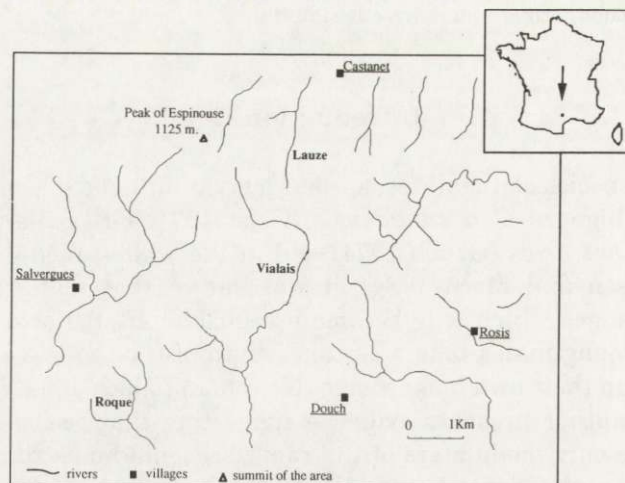


Fig. 1. Geographic situation of the study area.

Material and methods

The study was based on radiotracking and visual sightings. From summer 1987 to the beginning of 1992, 18 male mouflons were radiotracked regularly for 4 to 20 months. The captures were made in three distinct valleys, 14 individuals in Vialais, three in Lauze and one in Roque (Fig. 1). Most individuals were trapped at the end of spring or in summer, except for the older males which were taken during the rutting season. The males were aged by counting the horn annuli (Pfeffer 1967), ranging in age from less than one year to around 9 years at the moment of capture. All animals were not sexually mature; i.e. in mouflons, only slight spermatogenesis have been found in yearling rams and in 2 years old, it was still weak (Colonna d'Istria 1988). The age of the rams was incremented by one on 15 April, the mean birth date, of each year (Bon 1991).

Three categories were distinguished: A ($n = 4$ lambs), B ($n = 8$ one year to three years old) and C ($n = 6$ four years old and more). The individuals were classified A01 to C18. A01 was observed out of the rut season and was not included in Table 1. The stability of ewes at the end of springtime (Dubois *et al.* 1992), allows us to consider that the lambs were trapped on mother's home range.

For these animals, we used radio tracking from the ground. We tested the accuracy of the system employed (Dubois *et al.* 1992) and determined that the error polygons around locations were 15 ha. Radio-collared mouflons were located six to twenty times a month throughout the year. Home range data were recorded on a detailed map (1:25000) of the study site overlaid with a scaled grid of 125×125 m quadrats (Dubois *et al.* 1992). The uncertain area due to the inaccuracies of radio tracking corresponds roughly to a polygon of nine squares (Dubois *et al.* 1992).

Home ranges were recorded on a daily basis. Daily location records, made at different hours of the day, were compiled by monitoring the individual from the day of capture. We cumulated all the error polygons of a given individual to obtain the area used for a given period. Direct observations were added to radio tracking data to specify and enlarge the data. Each home range was also characterized by calculating the barycentre (Hayne 1949) for a given period (month, season, rut season and non-rut season). The mating period occurs in autumn, from October to December (Bon *et al.* 1993) and we take these months to determine the rutting ground.

Movements were calculated as the distance between the centres of successive error polygons, or between these centres and the centre of the square where the animal was observed. Considering that the probability of presence of an animal at a given time fits a bi-normal distribution on its error polygon, and having then calculated the probability of an animal being in the same square twice when the error polygon of two successive radiolocations overlap, we consider only movements of more than 175 meters as significant (Dubois *et al.* 1992). We calculate a mean annual movement amplitude for each category.

For statistical analysis, we used the non-parametric Mann-Whitney *U*-test and Wilcoxon signed ranks test (Scherrer 1984).

Results

Home range area and occupation pattern

The surface areas (in ha) represented by the different home ranges (Table 1) do not show any large inter-class differences. Concerning the overlap between the rut and non-rut ranges, large inter-individual differences can be seen as well as a trend of decrease between A and C categories. The percentage of the complete range which is used only during the rutting season tends to increase with age. However, the actual proportion involved is fairly high in all age groups. For the area occupied on a month-by-month basis, a cyclic pattern appears in Fig. 2. The

Table 1. Home range usage and movements in all rams studied. S - surface in ha, n - number of locations, DIM - duration of home range usage (in months). For the complete range and the non-rut range, only results of rams followed for more than 7 months are presented. A01 was observed out of the rut season. * the breakdown of the transmitter is in December; the referring point is the single observation made in January, ** a limited amount of data during the rut lead us to hold the location of the trap site as referring point for the rut.

Animal number (Age)	Complete		Home range				Rut		% of overlap	% of home-range used only during the rut	Distance (m)	
	S	n	DIM	Non-rut		Rut		between rut and non-rut barycentres			from the rut barycentre	
				S	n	S	n					
A02 (Lamb)	-	-	-	-	-	214	21	-	-	900	850	
A03 (Lamb)	-	-	-	-	-	215	38	-	-	400	0	
A04 (Lamb)	467	170	11	453	133	225	37	45	3	0	350	
B05 (1Y)	480	102	8	375	84	117	18	03	22	2100	-	
B06 (1Y)	645	106	9	612	80	221	26	29	5	400	800	
B06 (2Y)	704	203	11	639	154	295	49	32	10	700	300	
B07 (2Y)	-	-	-	-	-	135	18	-	-	900	1050	
B08 (2Y)	520	155	11	518	139	118	16	22	0.5	100	200	
B09 (2Y)	710	138	11	646	101	259	37	27	9	110	450	
B10 (2Y)	567	96	8	396	62	367	34	34	30	250	900	
B11 (2Y)	485	95	7	328	52	323	43	34	32	250	450	
B09 (3Y)	629	152	9	500	107	323	45	30	21	900	400	
B12 (3Y)	-	-	-	-	-	262	40	-	-	300	300	
C13 (4Y)	-	-	-	-	-	119	12	-	-	1200	-	
C14 (4Y)	356	106	9	314	74	248	32	57	12	250	500	
C15 (4Y)	770	144	9	651	95	346	49	29	16	1350	250	
C16 (5Y)	443	58	7	304	45	142	13	0.7	31	1900	-	
C16 (6Y)	750	136	11	485	105	353	30	11	35	2200	1650	
C17 (7Y)	-	-	-	-	-	254	22	-	-	900	-	
C18 (9Y)	-	-	-	-	-	-	-	-	-	3600**	-	

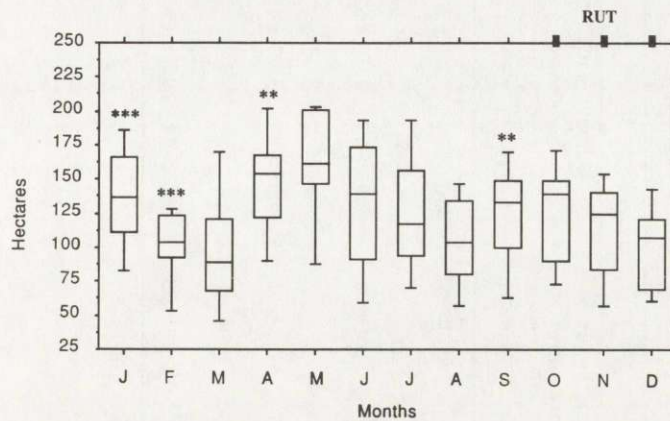


Fig. 2. Month-by-month range area for jointed categories B and C. Box-plots represent 80% of the distribution, and the horizontal line the median. *** - $p < 0.005$, ** - $p < 0.02$ (Wilcoxon signed ranks test. Two sided probabilities between the box-plot marked and the month before).

area occupied is the least in winter (February and March). It shows a clear increase in April, then decreases from May till August. Moreover, the rutting months from October to December do not show a large area used, and a decrease is even noted in this period. A certain spatial instability, even is recorded during the months on either side of the rut: September and January, shows a notable increase of the area used with respect to the months before. This cyclic pattern is not expressed significantly in locomotor activity. No significant differences in the movement amplitudes were noted during any month or season. The surface area occupied, although it does fluctuate a lot, is not correlated to the movement amplitude. The mean annual movement amplitude (Table 2) do not show any large inter-class differences.

Influence of age on spatial occupation dynamics

Category A (Lambs). The male lambs we observed did not disperse, occupying the same valley throughout the year except sometimes in the spring (see Fig. 3 for A04). The distance between successive monthly barycentres were lower than those observed on average for categories B and C ($z = -2.482$, $U = 754$, and $z = -2.512$, $U = 392$, $p < 0.01$, Mann-Whitney U -test, two-sided probabilities).

For 3 animals of category A that we able to observe during and outside the rut, the distances between rut and non-rut barycentres were not greater than 900 meters (Table 1), and they were significantly lower when compared to those obtained, on average, for category C (Table 2; $U = 2$, $p < 0.001$, Mann-Whitney U -test, two-sided probabilities). For A04, which was followed during the whole of its first year of life, the proportion of the total home range, which was only used during the rut, was 3%. This indicates a very large overlap between the rut range and the non-rut range. When their transmitter had broken down, the two lambs still alive were observed in their original valley during the rut until the end of

Table 2. Differences between categories of rams in home range usage and movements.

Cate- gory	Home range (ha)		Distance between rut and non-rut barycentres (m)	Monthly distance between barycentres (m)	Mean annual movement amplitude (m)	Distance (m)				
	Complete	Rut				Summer	Winter	from the rut barycentre Sep Jan		
A	467	453	218 ± 2	433 ± 104	400 ± 80	645 ± 41	-	-	400 ± 100	200 ± 70
B	592 ± 15	501 ± 24	242 ± 37	700 ± 85	662 ± 77	715 ± 23	479 ± 72	1134 ± 78	539 ± 55	1183 ± 62
C	579 ± 36	438 ± 37	243 ± 40	1629 ± 66	853 ± 100	740 ± 49	1858 ± 85	1781 ± 55	800 ± 93	1985 ± 49
Total	580 ± 36	480 ± 36	240 ± 19	985 ± 90	716 ± 90	695 ± 31	930 ± 118	1433 ± 66	563 ± 74	1386 ± 69

0.05

0.01

0.001

0.1

0.05

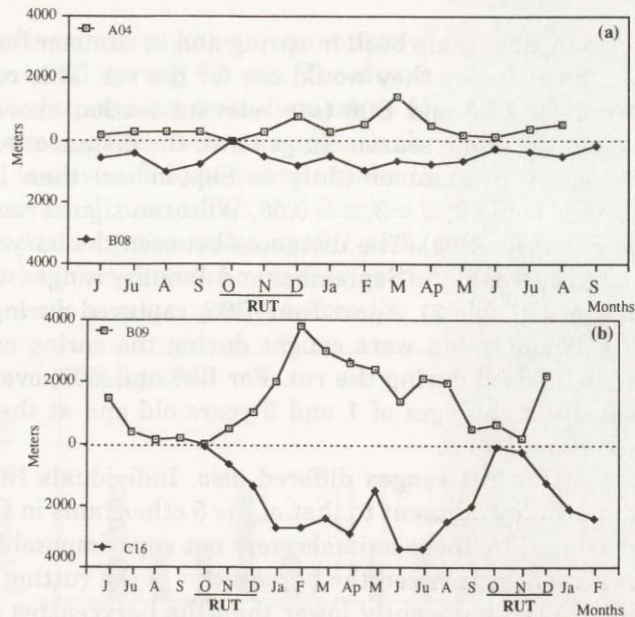


Fig. 3. Variation of the distance between the barycentre of the first October and the barycentres of the other months. (a) example of a lamb and a "non-disperser" male (b) example of disperser males.

the study, i.e. until the age of 2.5 years. We do not know if they left the valley outside the rutting period.

Category B (1 to 3 years). Although high inter-individual variability was seen between the rams, two types of spatial occupation patterns appeared. Two of the males (B06 and B08) did not leave their rut ground but did show instability in the spring visiting one or several other valleys to become stable once more in their original valley during the summer. Overlap between rut and non-rut ranges was extensive. The proportion of the complete range that was used only during the rut was 5% for B06 at one year of age and 10% at two years; it was 0.5% for B08 at two years of age. This spatial occupation pattern is very similar to that observed for lambs (Fig. 3 for B08) and females (Dubois *et al.* 1992). These males were located or observed in the same valley during the rut until the end of the study i.e. when B06 was 2.5 years old and B08 3.5.

The six other males aged 1 to 3 years left the valley where they had been captured during or at the end of the rutting period. The proportion of the total range used exclusively during the rut was between 9 and 32%. For B09 it rose from 9% at two years of age to 21% at three. Except for B10, which changed ranges as early as mid-November, the other individuals made this change from the last part of December to early January. However, the mean distance between the barycentres of the rut and non-rut ranges was lower than that observed in category C (Table 2; $U = 13.5$, $p < 0.05$, Mann-Whitney U -test, one-sided probability). Three

males, B05, B09 and B12, came back in spring and in summer for stays of varying lengths of time, to the valley they would use for the rut. This contrasts with the situation observed for B06 and B08 (see relevant section above) which left the same valley during the same season. In general, the distance from the rut range barycentre was lower in summer (July to September) than it was in winter (January to March) (Table 2; $T = 3$, $p = 0.05$, Wilcoxon signed rank test, one-sided probability; see Fig. 3 for B09). The distances between the barycentres of the rut range and the barycentres of the September and January ranges were intermediate in this male category (Table 2). Apart from B05, captured during the rut, all the other males of this age group were caught during the spring or the summer in the valley later to be used during the rut. For B06 and B09, overlap between rut ranges, respectively at the ages of 1 and 2 years old and at the ages of 2 and 3 years old was of 72 and 74%.

The positions of the rut ranges differed also. Individuals B07, B10 and B11 were captured in a valley adjacent to that of the 5 other rams in the group. During the rut, the areas used by these animals were not superimposable on those of the five others. The distances between the barycentres of the rutting grounds of these animals (07, 10, 11) is significantly lower than the barycentres of the males (05, 06, 08, 09, 12) from the neighbouring valley ($U = 0$, $p < 0.001$, Mann-Whitney U -test, two-sided probabilities).

Category C (4 years and more). In these males, we also observed the two types of spatial occupation pattern already described: sedentary and dispersed. After the rut, C13, until he lost his collar after 4 months of observation, never left the valley he had been caught in. For C14, the change of range after the rut was discrete only consisting of a shift of the range to a valley south of the one used during the rut. The proportion overlap between his rut range and the non-rut range was 57%.

Even in this age group, the proportion of overlap between the rut and non-rut ranges remained high. This could be explained by the periods of spatial instability on either side of the rut consisting of comings and goings between the non-rut and the rut ranges. The large surface area occupied during September (before the rut) and January (after the rut) could be the result of this instability (Fig. 2). Nevertheless, the proportion of the complete range used exclusively for rut increased for category C individuals being at least 12% and reaching 35% (Table 1). It was seen above (Table 2) that for rams of over 4 years of age, the non-rut range was established at a greater distance from the rut barycentre than for the two other age groups. This brings about a "lengthening" of the home range with age. The mean distance recorded between the barycentre of October and the most extreme monthly barycentre was 1.3 km for category A, 2.0 km for category B and 2.7 for category C. Three individuals were followed over two successive years and the above values were 2.0 km and 2.5 km at one and two years for B06, 3.8 km and 3.4 km at two and three years for B09 and 3.0 km and 3.4 km at five and six years for C16.

During the spring and the summer, no return of category C males was observed to the area frequented during the rut. The distance with respect to the October barycentre was never minimal from January to May for any individual, but from June, B category males were seen to approach their rut ground (Fig. 4). Rams of 4 years or more, however, did not start to make this type of move till September. Concerning maximum distance from the October barycentre, a greater dispersion was also observed among the males aged 1 to 3. For the older males, it can be noted that the maximum distance was only seen in winter or in summer arising from the fact that the summer range, before the rut, and the winter range, after

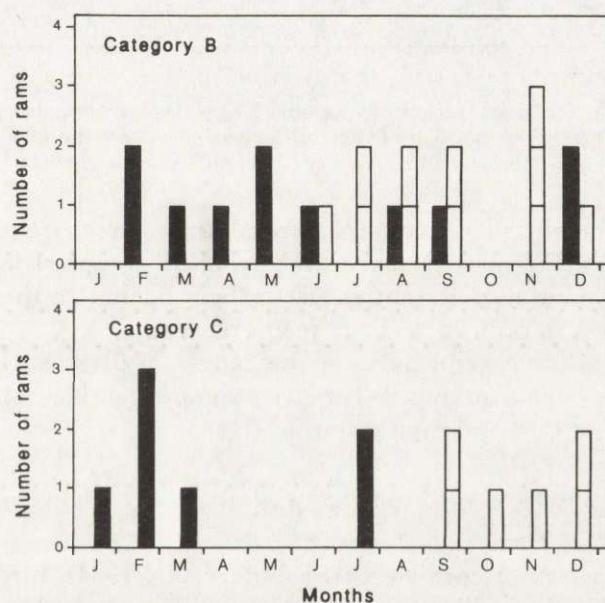


Fig. 4. Distribution during the annual cycle of the number of rams approaching (white bars) and withdrawing (dark bars) from their rut home range. The point of reference used for the rut is the barycentre of the first October, withdrawal and approaching being evaluated from the other monthly barycentres.

the rut, were more distant for category C males (Table 2). In summer, the distances from the rut barycentre are lower for rams of category B when compared to those obtained for category C (Table 2; $U = 5$, $p < 0.1$, Mann-Whitney U -test, two-sided probabilities). The dispersion of category C males with respect to their rut range was already high from January (Table 1). These observations seem to indicate more structured spatial occupation dynamics in males over 4 years of age.

The same rut range was used every year by C17 (marked at the age of 7 years old) up to the age of 10. For C16, overlap between rut ranges at the ages of 5 and 6 years old was 85%. He continued to frequent rut and non-rut ranges till the end of the study when he was 8.5 years old. Moreover, during winter and summer, this ram frequented remote plateaux at the limit of the area covered by the mouflon

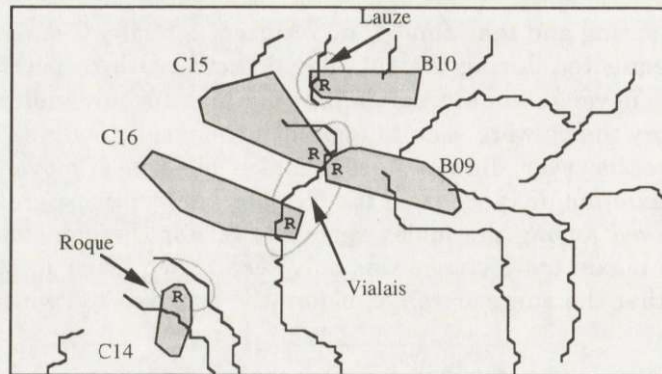


Fig. 5. Central parts of the home ranges represented by polygons determined from the monthly barycentres. The R indicates the position of the rutting ground at one end of the complete range. Ellipses of dashed lines show approximate boundary of the different rut grounds.

population where females never went (pers. obs.). In the areas frequented by other males outside the rutting period, there were resident groups of females. For the other animals, we have no information as to their fidelity to their rut grounds (death, transmitter breakdown without reobservation).

Fig. 5 represents the central parts of the ranges of 5 rams: (B09, B10, C14, C15 and C16). Three non-overlapping rut zones can be identified: that of B10 then that of B09, C15 and C16 and finally that of C14.

Discussion

In numerous species of carnivores (Schantz *et al.* 1984), birds (Brown and Orians 1970) or ungulates like the moose *Alces alces* (Cederlund *et al.* 1987), caribou *Rangifer tarandus* (Gunn and Miller 1986) or bighorn (McCullough 1985) it has been shown that spatial occupation patterns depend, at least partly, on ontogenetic mechanisms related to sociality or to knowledge of the environment. Thus, home ranges and seasonal movement patterns in males become established only after a few years. Geist (1971) and Festa Bianchet (1986) observed this "settling down" period in bighorn as did Grubb (1974) in Soay sheep, and Nelson and Mech (1984) in white-tailed deer. The present study of European mouflon also shows the ontogenetic character of the spatial occupation patterns.

In numerous species of ungulates, the males are reported to disperse from the birth range, for examples: white-tailed deer (Nelson and Mech 1984) or red deer (Clutton-Brock *et al.* 1982). Certain studies carried out on sheep (Grubb and Jewel 1966) and bighorn sheep (Geist 1971) have shown that after the first year, the males leave the area they were born in and the home range of their mother's group. In the species mentioned above and in mouflon, this dispersion not only occurs spatially but also socially, since males group together, and, during their

growth, they have increasingly less tendency to associate with females (Pfeffer 1967, Geist 1971, Leslie and Douglas 1979, Grubb 1974, Arnold *et al.* 1981, Scarbrough and Krausman 1988, Bon and Campan 1989) even though some occupy the same areas.

The fact that the social segregation between sexes, especially in our study population (Bon 1991), becomes established only after several years, can also be seen from a spatial point of view. Mouflon rams, after their emancipation from their mother, exhibit social preferences for peers (Bon *et al.* 1993) and it seems that these preferences and the establishment of preferential bonds induces the dispersion of young males (Bon 1991). Festa Bianchet (1986) who notes a stronger sedentarity of young rams explains that these individuals have not yet permanently joined the ram bands. However, for the same author, at some times the tendency to follow attractive conspecifics may be greater than the tendency to stay on the familiar area. Pusey and Packer (1987) for monkeys, also underline the role of the attraction which leads to voluntary dispersal. Geist (1971), Festa Bianchet (1986) and Simmons (1985) note that spatial occupation of males under 4 years of age is very variable and that the degree of sexual segregation, as for sheep studied by Grubb (1974), depends closely on the individual concerned. Geist (1971) and Bon and Campan (1989) underline a stronger tendency for young bighorn and mouflon to remain with ewes even after the rut while observations of older ones decrease. These various elements seem to be able to shed light on certain points brought out by our study. In this way, the distance between the rut and non-rut ranges, which is lower for males of under 3 years than for males of 4 or over, stresses the ontogenetic character of the degree of dispersion. Similarly, Simmons (1985), in bighorn, reported a steady expansion of the home range over the years. As well as this process, which we found to vary from ram to ram, animals of 1 to 3 years of age were seen to be less selective in their spatial choices. They came and went between different valleys and also frequented their rut range in non-rut periods. When compared to older males, this seems to indicate both the establishment of the home range and a reduced influence of sexual segregation. In this respect, in the population studied, young males were seen to associate with their congeners fairly unselectively. On the other hand, rams over 3 years old avoid ewes, especially in spring and summer (Bon *et al.* 1993), i.e. in seasons during which 1 to 3 year-old males were seen to visit their previous rut range. Moreover, the distance from the rut range, which was less in summer than in winter for males of 1 to 3 years, indicates as noted by Bon *et al.* (1993), an early arrival to surroundings of the rut range. Spatial occupation by adult males seems to be more "structured", the separation between the two ranges (rut and non-rut) being clearer. This spatial occupation pattern seems to underline the degree of maturity of the males; i.e. rams over 6 years old are never observed in the company of females outside the rutting period (Bon *et al.* 1993). The neotenization hypothesis (Geist 1971, Gould 1977) predicts that all male sheep which have not reached ultimate size and proportions at 7 or 8 years old, are "juveniles", some sexually mature, some not, at various stages of social and psychological development.

Remaining with this hypothesis, the variability in the spatial patterns of our individuals is not surprising. Even if the ram's change in social preference appears to result from the female's unsatisfactory social responses (Geist 1971), this shift seems overlapped by their juvenile tendencies to act like females and so, to keep some characteristics of their sociospatial behaviour until full maturity.

Apart from the lambs, which did not disperse, the spatial occupation dynamics of rams presents two types of spatial pattern: stability throughout the annual cycle and "dispersion" indicated by the occupation of a particular non-rut range. As an example of the first case, certain individuals, at least up to the age of 4, remained throughout the year in, or in the vicinity of, the same valley. They can be qualified as resident (Festa Bianchet 1986), their spatial occupation dynamics being similar to those of lambs and ewes (Dubois *et al.* 1992). Bighorn rams can become sedentarized in their birth range suggesting that avoidance of inbreeding (Greenwood 1980, Festa Bianchet 1986) does not appear to be a major factor in determining the choice of rut ground. Moreover, the observation of these resident males implies that the tendency for spatial segregation cannot be assimilated to a behavioural algorithm. It therefore appears that even though, owing to their sociality, males are predisposed to a great spatial dispersion, the attraction leading them to follow other individuals outside of their birth range, can be modified, or at least retarded, by attachment to the site or to certain congeners. Geist (1971) has suggested that the psychology of individuals could have an effect on dispersal, some individuals being more inquisitive and roaming than others. Following the neotenization hypothesis, this pattern could be in relation to the social status of these individuals; poorly developed males leave the female bands at a later age than well-developed males (Geist 1971) and consequently keep the spatial characteristics of females for a longer time. However, as far as we could see, the physiognomy of these sedentary males was no different. For the second case, i.e. dispersers, we noted departure from the valley where the animals were during rutting. This process was observed as early as one year of age (B05) but in general, it became established more progressively. These two types of males have already been observed by Festa Bianchet (1986) in bighorn and by Bunnell and Harestad (1983) in mule deer, where they note the existence of two phenotypes "non-dispersers" and "dispersers".

Different studies show that ungulates are faithful to their rutting area, for example bighorn (Geist 1971, Festa Bianchet 1986), red deer (Staines 1974) and fallow deer *Dama dama* (Chaplin and White 1970). Geist (1971) noted that, in general, more than 75% of bighorn rams are faithful to their seasonal home ranges. Furthermore, ungulates, which commonly show strong attachment to their home range (Jarman 1970), can be specially attached to the particular area where they have been reared. This has been reported for sheep (Hunter and Davies 1963), moose (Cederlund *et al.* 1987) and camel *Camelus dromedarius* (Arnold and Dudzinski 1978). The steady expansion of the home range that we observed indicates a greater separation from the birth area which still continued, however,

to be visited, not only during the rut but also, for males of 1 to 3 years, during other periods. This stresses that the strong attraction exerted by this area is not only linked, unlike with older males, to its functional role related to rutting activities. Nelson and Mech (1984) in white-tailed deer consider that the spatial affinities occur first during the first year of life explaining the fairly frequent return of intermediate aged animals to their birth area. It seems therefore, that there is no actual "dispersal" as such since, according to Kammermeyer and Marchinton (1976), dispersal consists in long range movements without return to original home range. Dispersal is obvious, for example, for red deer (Clutton Brock *et al.* 1982) where after the second year of life no overlap is observed with the maternal range. Even though an increasingly clear dissociation is observed between the rut range and the non-rut range, rams use with fidelity the same rut ground, a particular area which could be their birth area. This attraction for a particular site is clearly shown by the fact that females are to be found residing on the newly acquired range of "disperser" males which would not therefore be obliged to return to a particular area to reproduce. The fact that we captured animals in three valleys enabled three distinct rutting areas to be checked.

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References

- Arnold G. W. and Dudzinski M. L. 1978. Social organisation and animal dispersion. [In: Ethology of free ranging domestic animals. G. W. Arnold and M. L. Dudzinski, eds]. Elsevier Publ. Co., Amsterdam: 51 – 96.
- Arnold G. W., Wallace S. R. and Rea W. A. 1981. Associations between individuals and home-range behaviour in natural flocks of three breeds of domestic sheep. *Appl. Anim. Ethol.* 7: 239 – 257.
- Bon R. 1991. Trajectoires sociales chez le mouflon de Corse. Ph. D. thesis, Univ. P. Sabatier, Toulouse (France): 1 – 85.
- Bon R. and Campan R. 1989. Social tendencies of the Corsican Mouflon (*Ovis ammon musimon*) in the Caroux-Espinouse massif (South of France). *Behav. Process.* 19: 57 – 78.
- Bon R., Dubois M., and Maublanc M. L. 1993. Does age influence between-rams companionship in mouflon? *Rev. Ecol. (Terre.Vie)*. 48: 57 – 64.
- Brown J. L. and Orians G. H. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1: 239 – 262.
- Bunnell F. L. and Harestad A. S. 1983. Dispersal and dispersion of black-tailed deer: models and observations. *J. Mammal.* 64: 201 – 209.
- Cederlund G., Sandegren F. and Larsson K. 1987. Summer movements of female moose and dispersal of their offspring. *J. Wildl. Mgmt* 51: 342 – 352.
- Chaplin R. E. and White R. W. 1970. The sexual cycle and associated behaviour patterns in the fallow deer. *Deer* 2: 561 – 565.
- Clutton Brock T. H., Albon S. D., Gibson R. M. and Guinness F. E. 1982. Red deer: behaviour and ecology of two sexes. Univ. of Chicago Press, Chicago: 1 – 378.
- Colonna d'Istria R. 1988. La reproduction du mouflon de Corse. Veterinary Surgeon Thesis. E. N. V Toulouse (France): 1 – 200.

- Dubois M., Gerard J. F. and Maublanc M. L. 1992. Seasonal movements of female Corsican mouflon (*Ovis ammon*) in a mediterranean mountain range, southern France. *Behav. Process.* 26: 155 – 166.
- Festa Bianchet M. 1986. Site fidelity and seasonal range use by bighorn rams. *Can. J. Zool.* 64: 2126 – 2132.
- Geist V. 1971. Mountain sheep: a study in behaviour and evolution. Univ. of Chicago Press, Chicago: 1 – 383.
- Gonzalez G. and Berduco C. 1985. Les groupes sociaux d'isards et de mouflons au massif du Carlit. *Gibier Faune Sauvage* 4: 85 – 102.
- Gould S. J. 1977. Ontogeny and phylogeny. Harvard Univ. Press, Cambridge: 1 – 501.
- Greenwood P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* 28: 1140 – 1162.
- Grubb P. 1974. The rut and behaviour of Soay rams. [In: Island survivors: the ecology of the Soay sheep of St. Kilda. P. A. Jewell, C. Milner, and J. M. Boyde, eds]. Athlone Press, London: 131 – 159.
- Grubb P. and Jewell P. A. 1966. Social grouping and home range in feral Soay sheep. *Symp. zool. Soc. Lond.* 18: 179 – 210.
- Gunn A. and Miller F. L. 1986. Traditional behavior and fidelity to caribou calving grounds by barren-ground Caribou. *Rangifer* 1: 151 – 158.
- Hayne D. W. 1949. Calculation of size of home range. *J. Mammal.* 30: 1 – 17.
- Hunter R. F. and Davies G. E. 1963. The effect of method of rearing on the social behaviour of Scottish blackface hoggets. *Anim. Prod.* 5: 183 – 194.
- Jarman M. V. 1970. Attachment to home range in impala. *E. Afr. Wildl. J.* 8: 198 – 200.
- Kammermeyer K. E. and Marchinton R. L. 1976. Notes on dispersal of male white-tailed deer. *J. Mammal.* 57: 776 – 778.
- Lagory K. E., Bagshaw C., and Brisbin I. L. 1991. Niche differences between male and female white-tailed deer on Ossabaw island, Georgia. *Appl. Anim. Behav. Sci.* 29: 205 – 214.
- Leslie D. M. and Douglas C. L. 1979. Desert Bighorn sheep of the River Mountains, Nevada. *Wildl. Monogr.* 66: 1 – 56.
- Mc Cullough D. R. 1985. Long range movements of large terrestrial mammals. [In: Migration: mechanisms and adaptive significance. M. A. Rankin, ed]. *Contrib. in Marine Science* 27: 444 – 465.
- Nelson M. E. and Mech L. D. 1984. Home range formation and dispersal of deer in northeastern Minnesota. *J. Mammal.* 65: 567 – 575.
- Pfeffer P. 1967. Le Mouflon de Corse. Position systématique, écologie et éthologie comparées. *Mammalia* 31: 1 – 262.
- Pfeffer P. and Genest H. 1969. Biologie comparée d'une population de mouflons de Corse (*Ovis ammon m.*) du parc naturel du Caroux. *Mammalia* 33: 165 – 192.
- Pusey A. E. and Packer C. 1987. Dispersal and philopatry. [In: Primates societies. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker, eds]. Univ. of Chicago Press, Chicago: 250 – 266.
- Scarbrough D. L. and Krausman P. R. 1988. Sexual segregation by desert mule deer. *S. West. Nat.* 33: 157 – 165.
- Schantz T. 1984. Spacing strategies, kin selection and population regulation in altricial vertebrates. *Oikos* 42: 48 – 58.
- Scherrer B. 1984. Biostatistique. Gaëtan Morin Press. Chicoutimi (Canada): 1 – 850.
- Simmons N. M. 1985. Behavior. [In: The desert bighorn. Its life history, ecology and management. G. Monson and L. Summer, eds]. Univ. of Arizona Press. Tucson: 124 – 144.
- Staines B. W. 1974. A review of factors affecting deer dispersion and their relevance to management. *Mammal. Rev.* 4: 79 – 91.