NOTES BRÈVES

DOES AGE INFLUENCE BETWEEN-RAMS COMPANIONSHIP IN MOUFLON (*OVIS GMELINI*) ?

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In non-territorial polygynous ungulates, adult male social behaviour is thought to be largely dependent on female social behaviour and distribution (Geist, 1974 ; Jarman, 1974 ; Bradbury and Verhencamp, 1976 ; Emlen and Oring, 1977). Ungulate species living under temperate or mountain climates, have a restricted rutting season and at other times adults are sexually segregated. It is commonly reported that males are less gregarious than females, and form temporary groups (*Ovis aries :* Grubb, 1974 ; Cervidae ssp. : Franklin and Lieb, 1979 ; Rounds, 1980 ; Clutton-Brock *et al.,* 1982 ; *Bison bison :* Lott and Minta 1983 ; *Tragelaphus oryx :* Hillman, 1987). Group living in ungulates is also often explained by anti-predator behaviour, feeding efficiency, and ecological factors. Although these important factors partly determine the grouping patterns, they are often insufficient to satisfactorily explain their social complexity (Bon *et al.,* 1990).

Little is known about the social behaviour of ram European mouflon (*Ovis gmelini*). It is a gregarious species but, like other wild sheep, grouping patterns vary frequently (Pfeffer, 1967 ; Auvray, 1983 ; Gonzalez, 1984 ; Rigaud, 1985) and no known permanent association between adults has been found. In a previous paper (Bon and Campan, 1989) we studied the tendency for different age/sex classes to become incorporated into different group types. One-year-old rams lived mainly within matriarchal groups although they tended to form peer groups during spring and summer. Rams exhibited an increasing tendency with age to live in groups apart from the females, restricting associations with ewes to the peak mating season only. However, in most cases, different age/sex classes mix in open-membership groups. Hence, little quantitative information was available about the social partners surrounding an individual animal.

Because of the absence of known permanent associations between adults, Hillman (1987) and Lott and Minta (1987) concluded that individuals associate at random. However, it has previously been shown that ungulates less than 2 years

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old prefer to interact, or frequently associate, with peers (see references in Bon 1991). Do adult males exhibit similar social preferences for peers ? Appleby (1983) has indeed shown that male red deer (*Cervus elaphus*) associated with individuals of close rank, or of similar age. In this paper we address the question of the extent to which mouflon rams associate in an unselective way. We examine the social environment of males to determine whether they choose any particular age/sex class to associate with. Moreover, we have attempted to detect any seasonal variation in such preferences.

STUDY AREA, ANIMALS AND SAMPLING METHODS

The Caroux-Espinouse massif (South of France, 42° N and 3° E) has already been described (Bon and Campan, 1989 ; Bon *et al.*, 1990), and further details on its vegetation and climate can be found in Baudière (1970) and Auvray (1983).

Following the introduction of 19 mouflons between 1956 and 1960, the population has now reached a total of *ca.* 1 000 heads (Cugnasse, pers. comm.) spread over *ca.* 13 000 ha. Around the « Reserve Nationale de Chasse », located in the central part of the study area, mouflons, mainly rams, are hunted from September to February. Inside the reserve, animals are trapped in order to be translocated. Over the last 10 years, males and females have been removed from the population in similar numbers.

The age of males was determined from horn size and annual growth annuli as done by Geist (1966) and Pfeffer (1967). But as age determination at distance was not very accurate, we only considered 6 age classes, 1-year-old males also called yearlings ($\male$ 1), 2 years old ($\male$ 2), 3-4 years old ($\male$ 3-4), 5-6 years old ($\male$ 5-6), 7 years old ($\male$ 7) males, and 2 further classes : females 1-year-old ($\female$) and lambs (L). We use the term « peer » for animals belonging to the same age/sex class.

In our study area, the rut lasts from the end of October to the end of December, but most copulations occur in November (Bon *et al.*, in prep.). Most lambs are born in April and the beginning of May.

In 1984 and 1985, 98 ground surveys were made along 2 fixed routes mainly in the « Reserve Nationale de Chasse du Caroux-Espinouse » (1 830 ha). In 1986 the study area was enlarged to almost 5 000 ha, 108 walks being made along our two previous routes and along 8 new ones. Routes were walked during the main feeding periods. Males in our study area frequently used closed habitats (Auvray, 1983). Despite frequent censuses, males over 3 years old were not seen as often as ewes. Hence, rams observed at random outside the routes were included in our samples. Only the groups of known size and composition were retained. In this study a group was considered as a temporary collection of animals. An animal was allocated to a group if it was less than 30 m away.

DATA ANALYSIS

Knowing the seasonal proportion of each age/sex class (Table I), the expected frequency of individuals $N_{i(exp)}$ of each class found together with a male may be assessed as follows, if each individual associates unselectively :

$$N_{i(exp)} = (n_i/N) \cdot N_a$$

where $N_{i(exp)}$ = the number of animals of class i which would have accompanied a male of class j if he associated unselectively

n_i = the number of animals of class i seen in the population

N = the total number of animals seen in the population

N_a = the total number of animals seen with all the males of class j

According to Jarman and Southwell (1986) a preference index may be expressed as follows :

$$(N_{i(obs)} - N_{i(exp)})/N_a$$

where

$N_{i(obs)}$ = the number of animals of class i seen with all the males of class j.

Our samples being small, the data were pooled by season. Female wild sheep use the same seasonal home ranges in different years and males tend to behave similarly (Festa-Bianchet, 1986a, b). Since most animals were unmarked and likely to be re-observed during repetitive field samplings, our data are most probably not independent and so probably falsify *P* levels (Machlis *et al.*, 1985).

TABLE I

Observed seasonal structures of the mouflon population in Caroux-Espinouse massif.

Proportion of age/sex classes are expressed in percentage of the total number (N)
of mouflons observed.

	♂≥7	♂5-6	♂3-4	♂2	♂1	♀	L	N
Winter	0.2	0.8	2.2	3.3	7.8	57.5	23.8	3505
Spring	0.5	2.3	3	2.6	10.8	55.5	24.7	4279
Summer	0.2	1	4	1.9	6.9	55	28.9	829
Autumn	1.5	3.5	6.8	4.8	6.2	52.4	19.2	3569

RESULTS

Whatever their age, males associated unselectively with individuals belonging to the various age/sex classes during the rut. Outside this period, they exhibited different social preferences depending on their age.

Yearling males appeared to associate unselectively with other age/sex classes whatever the season, as indicated by the preference indices (Table II), except in summer where they tended to prefer peers.

In winter, 2-year-old rams continued to associate unselectively with all age/sex classes. Conversely, they avoided ewes and lambs in spring and summer, while associating preferentially with yearlings and 3 to 4-year-old males. They exhibited a preference for 5 to 6-year-old males only in summer, while associating unselectively with peers throughout the year.

TABLE II

Seasonal preferences indices of each male class towards each age/sex class of mouflons in Caroux-Espinouse massif.

	♂≥7	♂5-6	♂3-4	♂2	♂1	♀	L	N
♂1 with								
Winter	0	0	0	0	-2	+2	+1	1359
Spring	0	-1	-1	+1	+1	+1	-1	1621
Summer	0	+1	-2	0	+6	-2	-4	185
Autumn	0	-1	-2	0	-3	+4	+3	1174
♂2 with								
Winter	0	0	+1	-2	0	-2	+2	844
Spring	0	+5	+11	0	+6	-11	-11	471
Summer	-2	+11	+17	+3	+12	-25	-15	42
Autumn	-1	-1	-1	-3	0	+4	+2	885
♂3-4 with								
Winter	0	+4	+7	+2	+4	-15	-2	360
Spring	+2	+24	+19	+11	+2	-39	-21	285
Summer	+2	+17	+35	+7	+2	-38	-21	56
Autumn	0	+2	-1	+1	+1	-3	0	804
♂5-6 with								
Winter	0	+2	+19	+1.5	-3	-16	-4	159
Spring	+3	+18	+29	+6	-2	-35	-17	255
Summer	+4	+10	+65	+2	+5	-56	-30	26
Autumn	0	0	+4	0	0	-5	+2	426
♂≥7 with								
Winter	◄—+14—►			+4	-3	-23	+7	55
Spring	+14	+43	+21	+5	-10	-51	-22	82
Summer								2
Autumn	0	0	+3	-1	+1	-5	+3	191

Apart from the rutting season, rams over 3 years old avoided ewes, especially in spring and summer. In winter, 3 to 6-year-old rams associated unselectively with lambs whereas ≥ 7-year-old males associated frequently with lambs. In spring and summer, mature rams clearly avoided lambs. On the whole, the

preference indices between males were almost always lower in spring than in summer. Besides, according to their age class, males differed concerning their grouping preferences with the different age/sex classes.

In winter, 3 to 4-year-old rams had lower preference indices than older rams, with only a slight preference towards peers. Conversely, during spring and summer, they basically associated with peers, 5 to 6-year-old rams and lastly 2-year-old males.

In winter, 5 to 6-year-old rams clearly prefered 3 to 4-year-old males. The preference indices were lower with ⩾ 7-year-old males, 2-year-old males and yearlings. On the other hand, high preference indices were noted for peers and 3 to 4-year-old males in spring and summer.

The oldest rams were seldom seen, especially during the summer. In winter and spring, they associated with 3 to 6-year-old rams preferentially, and with peers only in spring.

DISCUSSION

The non-independance of our data makes a detailed quantitative analysis impossible. It is therefore difficult to assess whether or not there are significant differences in the level of social preference between the observed animals. However our observations indicate the following trends.

Whatever their age, rams seemed to associate with other age/sex classes unselectively in autumn, which may be explained by the promiscuous mating system of the mouflon. In almost all sheep species, rams do not defend a territory or a harem, and largely move from one group to another in search of receptive ewes. During the rut, the social organization is disrupted and animals freely intermingle (Bon, 1986). Grubb and Jewell (1966) showed that stability in groups of Soay rams during summer disrupted the following rut.

The absence of preference or avoidance for any age/sex class reflects the social instability of the yearling rams. Although they live most of the year in matriarchal group (Grubb and Jewell, 1966 ; Geist, 1971 ; Bon and Campan, 1989), out data indicate that they do not associate preferentially with ewes. When considering their association with older rams, a negative index could be expected. In summer, the preference for peers is in accordance with the tendency to live in peer groups (Grubb and Jewell, 1966 ; Geist, 1971 ; Bon and Campan, 1989).

As rams grew older, the gradual process of ewe avoidance outside the rut is consistent with adult segregation in wild sheep species (Pfeffer, 1967 ; Geist, 1971 ; Auvray, 1983 ; Festa-Bianchet, 1986 ; Bon and Campan, 1989). The present results provide further information to the between-male grouping tendency observed in other populations (Grubb and Jewell, 1966 ; Geist, 1971 ; Arnold *et al.,* 1981 ; Gonzalez and Berducou, 1985) and the tendency for young males to follow older ones (Geist, 1971 ; Festa-Bianchet, 1986). Indeed, rams tend to associate with individuals of similar age class. The tendency for males to associate with males of similar age or social status has already been reported in ungulates (Estes, 1974 ; Hirth, 1977 ; Leuthold, 1977, 1978 ; Estes and Estes, 1979 ; Clutton-Brock *et al.,* 1982 ; Appleby, 1983 ; Nievergelt 1967 *in* Gonzalez 1984). Jewell (1986), in particular, showed how wethers form self-contained groups, without interacting with other sheep. Geist (1971, p. 165) remarks that « rams prefer to interact socially with adult females and rams of equal horn size... », and

that « the tendency of sheep to interact voluntarily with old rams increases in the same fashion as their tendency to associate with males » as they grow older. Indeed, our results seem to fit the similarity principle proposed by the Waal and Luttrell (1986) inasmuch as rams associate with rams of similar age or social class. We cannot however answer the question « who is attracted to whom », at least for rams aged 2 years and more.

We also observed seasonal variations of the preference index. The weak winter values of preference towards rams and of avoidance towards ewes may result from the tendency for rams to remain with ewes after the rut (Geist, 1971 ; Bon and Campan, 1989). However, we cannot discard an underestimation of the preference index since rams, mainly the oldest ones, are much less observable than ewes. In spring, the lush vegetation of the pastures allows large groupings of animals of different age/sex classes in our study area (Auvray, 1983 ; Bon, 1986 ; Bon *et al.,* 1990). Such concentrations in spring also occur in other populations (Geist, 1971 ; Festa-Bianchet, 1986), and Festa-Bianchet underlines their importance since they allow rams to practice and develop social skills. It is also a period of dispersion of yearling rams which often wander alone or join male groups (Geist, 1971 ; Bon and Campan, 1989). Then, the social milieu of males is diversified, resulting in lower preference indices than in summer. At that time of the year, with the pasture impoverished and high temperatures prevailing, mouflons live mainly in forested or rocky areas, in smaller social units more largely based upon social affinities as revealed by the highest preference indices.

SUMMARY

During the rutting season, male mouflons, whatever their age, associate unselectively with individuals of the different age/sex classes. This applies to yearling rams throughout the year, except in summer when they tend to prefer other yearling males. Outside the rutting season, males, as they grow older, gradually tend to avoid ewes and lambs while grouping preferentially with similarly aged males. The preference indices are weaker in spring than in summer, probably because mouflons gather in large groups during the spring. We suggest that an interattraction between similarly aged animals is an important determinant of the social organization of mouflon rams.

RÉSUMÉ

Durant le rut, les mouflons mâles (*Ovis gmelini*), quel que soit leur âge, s'associent de façon non sélective avec les autres classes d'âge et de sexe. Ceci est vrai tout au long de l'année pour les béliers d'un an, avec cependant une préférence pour leurs pairs en été. En dehors du rut, on a observé une tendance croissante avec l'âge des béliers à éviter les brebis et les agneaux et une préférence marquée pour la compagnie de béliers d'âge similaire. Les indices de préférence étaient plus faibles au printemps qu'en été, vraisemblablement en raison de la formation de grands rassemblements durant la période de plus grande croissance de la végétation. Il est suggéré que l'interattraction entre animaux d'âge similaire est à la base de l'organisation sociale des béliers.

ACKNOWLEDGEMENTS

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