

BEHAVIOUR OF EWES (*OVIS GMELINI MUSIMON* x *OVIS* SP.) DURING THE RUT

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RÉSUMÉ

L'hypothèse que la cour des mâles induit une modification des activités des femelles en raison du système reproducteur de type promiscuité a été testée chez le Mouflon (*Ovis gmelini musimon* x *Ovis* sp.). On s'attendait à ce qu'en présence des mâles, les femelles soient plus fréquemment impliquées dans des interactions sociales et consacrent moins de temps à l'alimentation, plus de temps au « debout/observe » et au déplacement, changent plus souvent et diversifient davantage leurs actes. Nous avons donc comparé l'activité des femelles dans des groupes mixtes, reproducteurs (une femelle en oestrus avec au moins un mâle $\geq 1,5$ ans) et dans des groupes de femelles, au cours du pré-rut (16-31/oct.), du rut (01-30/nov.) et du post-rut (01-15/déc.). Du pré-rut au post-rut, tant dans les groupes mixtes que de femelles, le temps consacré à l'alimentation s'accroît au détriment du « debout/observe », alors qu'aucune variation significative n'est détectée dans la part allouée au déplacement. Durant cette même période, la fréquence de transition des actes et la diversité comportementale diminue dans les groupes de femelles. Ces résultats peuvent s'expliquer par une diminution de l'appétit des femelles pendant la période des œstrus mais aussi par des facteurs écologiques (amélioration de la qualité et abondance des ressources alimentaires).

Des différences entre groupes mixtes et de femelles n'ont été détectées que durant le plein rut. Les femelles passent moins de temps à se nourrir et plus de temps à observer dans les groupes mixtes. Bien que statistiquement significative, la relation entre fréquence de cour et pourcentage de temps consacré à l'alimentation et au « debout/observe » est faible. La relation disparaît si les données relatives aux groupes reproducteurs sont omises. L'impact de la présence des mâles sur l'activité des femelles semble donc minime, ce qui peut être relié aux faibles taux d'interactions impliquant les femelles, ou à la faible réactivité comportementale des femelles. Les groupes reproducteurs n'ont été observés que durant le pré- et le plein rut. En raison du petit échantillon (N = 8), les 2 périodes ont été rassemblées pour permettre une comparaison entre types de groupes. Dans les groupes reproducteurs, les femelles en oestrus broutent nettement moins, se déplacent plus, changent plus d'activité et sont plus souvent impliquées dans des interactions sociales que les brebis dans les groupes mixtes ou de femelles. Les résultats suggèrent que le comportement des femelles n'est sensiblement modifié que dans les groupes reproducteurs, pendant l'œstrus. Ce dernier ne durant que de 1 à 3 jours, les coûts énergétiques du rut sont vraisemblablement faibles pour les femelles.

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SUMMARY

It was tested whether male courtship induces changes in activities in female mouflon (*Ovis gmelini musimon* x *Ovis* sp.) due to the promiscuous mating system. For females in the presence of males, we expected a higher involvement in social interactions, reduced time spent feeding, increased time standing/scanning and moving, and a higher rate and level of act transition and diversity. We tested these hypotheses by comparing mouflon ewe activities in mixed-sex, mating (one oestrous female with at least one adult male) and female groups during the pre-rut (16-31/Oct.), the rut (01-30/Nov.) and the post-rut (01-15/Dec.). Females devoted more time to feeding and less to standing/scanning from the pre- to the post-rut, in mixed and female groups. At the same time, act transition and diversity decreased in female groups. Females could experience reduced appetite during the oestrus period but ecological factors (better quality and higher abundance of food) may explain these results.

Differences between mixed-sex and female groups were found only during the full-rut. Females devoted more time to standing/scanning and less to feeding in mixed-sex groups. Although significant, the percent of time dedicated to feeding and standing/scanning was weakly related to the interaction frequency. So the presence of males seems to have a low incidence on female activities, as seen through the low level of social interactions involving females, and their low behavioural responsiveness. Mating groups were observed only during the pre- and the full-rut. Because of small sample size ($N = 8$), data from the two periods were mixed in order to compare group types. Data on mating groups suggest that oestrous ewes feed much less, move more, change activity more often and are involved in social interactions more frequently than in mixed-sex and female groups. However, as oestrus lasts only 1-3 days, the energy costs of the rut are thought to be low for females.

INTRODUCTION

In sexually dimorphic ungulates, the rut entails physiological, behavioural, and social changes for individual animals. Males and females, which segregate outside the rut, group together during the breeding season. Wild sheep are promiscuous and males move freely in search of receptive females (Hogg, 1984; Bon *et al.*, 1993b). Tending males typically approach females in a low-stretch position, twist head and nuzzle their ano-genital region. In response, females may stop their current activity, by moving some meters and urinating. According to a dominance hierarchy, males compete to monopolize oestrus females. During the rut, adult males spend considerable time courting females and competing with rivals, while spending less time feeding (Braza *et al.*, 1986; Miquelle, 1990; Bon *et al.*, 1992, 1995).

Few studies have investigated the behaviour of females during the rut in ungulates (but see Hogg, 1987; Byers *et al.*, 1994). Oestrus ewes isolate themselves from groups, seem to be less mobile, and may mate with one or several rams (Jewell *et al.*, 1986; Hogg, 1987, 1988; Bon *et al.*, 1992). However, non-oestrus females may also be courted within mixed-sex groups during the rut, which lasts several weeks in mountain or temperate climates. Courtship quality is dependent on the age and social status of the males (Hogg, 1984; Bon *et al.*, 1995; Hogg & Forbes, 1997; Guilhem *et al.*, 1997). Young males tend to behave more abruptly than elders, using alternative mating tactics, "coursing" or "blocking" the courted females (Geist, 1971, Hogg, 1987; Shackleton, 1991) and this is suspected to result in greater energy expenditure by ewes (Singer *et al.*, 1991; Valdez *et al.*, 1991). In addition, when females are courted by several males, an *ad-hoc* competition occurs among the males which may lead to a fuzzy competition (Geist, 1971; Hogg, 1984, 1987; Bon *et al.*, 1992). During blocking, females may be chased and may even be butted during coursing fights (Bon *et al.*, 1992), sometimes resulting in injury or death (Réale *et al.*, 1996).

In a promiscuous mating system, the alternative mating tactics (courting and blocking) likely involve greater social instability and drawbacks in females compared to mating systems where dominant males are territorial or hold harems (Byers & Kitchen, 1988). We assume that the behaviour of ewes is modified during the full-rut compared to non-rut periods. In particular, we hypothesize that ram courtship results in females spending more time moving and standing/scanning, a higher level of act transition and diversity, and accordingly less time feeding. On the other hand, animals experience physiological and behavioural modifications during the rut (Jewell, 1997). Males not only reduce their time feeding because of courting, they also experience a decrease in appetite during the rut (Miquelle, 1990). If females undergo similar physiological changes, they could feed less during the full-rut than before or after, independently of the presence of males.

These hypotheses were tested by comparing ewes' behaviour in mixed-sex, mating and female groups during the pre-, the full- and the post-rut, in a wild population of Mediterranean Mouflon (*Ovis gmelini musimon* x *Ovis* sp.). The frequency of interactions involving females was also measured to detect a possible relationship with the time devoted by females to feeding, to standing/scanning and to moving. In this population, most ewes ≥ 1.5 year old were potentially receptive (Cugnasse *et al.*, 1985). Most ≥ 3 years old (90 %) lambed in April, indicating that successful matings were achieved in November. The lambing period, and thus the oestrus period of 2-year-old females (*i.e.* which mated when 1.5 years old) was longer. By mid May, almost all pregnant ewes were estimated to have lambed (Bon *et al.*, 1993a). Therefore, the two age classes of females were distinguished, considering that courtship could have a longer effect for the younger than for the older females.

MATERIALS AND METHODS

The Caroux-Espinouse massif (42° N, 3° E) is located in the south of France. The vegetation, physical and climatic characteristics have been presented elsewhere (Bon *et al.*, 1993b, 1995). The Mouflon population (*ca.* 1,000 animals) used an area of *ca.* 10,000 ha, partly protected in a national hunting reserve (1,830 ha) where the data were collected. The reserve is centred on a N-S oriented valley (Vialais), with slopes ranging between 600 m and 1,100 m of elevation. Woods and rocks covered respectively 8 % and 28 % of the hillside. In the open areas, heather (*Erica cinerea*, *Calluna vulgaris*) and broom (*Sarothamnus scoparius*, *Genista purgans*) moorland were dominant but frequently mixed with graminaceous species and bilberry (*Vaccinium myrtillus*). The summer climate is characteristic of Mediterranean regions, whereas rainfall is more frequent and combined with cooler temperatures allowing vegetation re-growth in autumn (Bon *et al.*, 1990).

Yearling females differ from ewes ≥ 2 years old by the lack of a white facial spot and slighter corpulence. A test with unknown marked individuals showed that the age of 93 % of the yearling (N = 15) was correctly determined, while no adult females (N = 19) were classified as yearling (Bon *et al.*, 1993a).

Data were collected in October 1987 and from October to mid-December in 1988, in the morning and the afternoon when most Mouflons were feeding. Three periods were considered: the pre-rut (16-31/Oct.), the full-rut (01-30/Nov.) and the post-rut (01-15/Dec.). Female groups were composed of at least two females (with

or without lambs) and mixed-sex groups included at least two females (with or without lambs) and one male ≥ 1.5 year old. Mating groups consisted of one ewe, presumed to be in oestrus, followed/courted consistently by one or several rams ≥ 1.5 year old. Ewe activities were recorded continuously during 10-mn focals (Altmann, 1974). The 10-mn focals containing only one activity pattern (3.3 %) were discarded from the analyses. Despite considerable time in the field, many focals were not completed since the animals were lost of sight, and so those lasting more than 300 sec were considered. The mean duration (\pm SE) of focals in female, mixed and mating groups was 566.8 ± 79.3 , 559.7 ± 98.8 and 565.4 ± 85.5 sec respectively, based on 7h21 mn, 9h25 mn, 3h08 mn of animal-focal collected in the pre-, the full- and the post-rut. Ewe behaviour was based on previous studies (Cavallini, 1987; McClelland, 1991; Shackleton, 1991, Valdez *et al.*, 1991). Six behaviour variables were measured: the time spent feeding, standing/scanning, moving, the frequency of interactions involving the focal females, the frequency of act transition and act diversity. "Stand/scan" included scanning the surroundings (including conspecifics) and the standing posture (Bon *et al.*, 1995). "Interactions" included all overt interactions and social displays exhibited by the females as actor or receptor. Act diversity was the absolute number of different acts/postures exhibited by the focal animal.

Data collected all around the year showed that marked females were re-observed infrequently in the study area (on average min = 3, max = 6 times/year on 8 successive years; Maublanc & Hewison, pers. comm.). Mouflons also live in flexible groups, so the individual-focal observations were considered as independent. Transformation failed to normalize data so non-parametric Mann-Whitney *U* and Kruskal-Wallis *H* tests (corrected for ties) were employed as appropriate. When *H* tests indicated significant differences ($P \leq 0.05$), Dunn's multiple comparison tests were applied to identify the source of the differences (Zar, 1996).

RESULTS

No significant differences were found between 1.5-year-old ($N = 28$) and older females ($N = 106$) regarding the 6 behaviour variables. Then all females were pooled in the subsequent analyses. We then compared data from mixed-sex and female groups in a first step and the comparison was extended to mating groups in a second step.

Females spent more time feeding and less time standing/scanning within mixed-sex ($H_2 = 6.37$, $P = 0.04$; $H_2 = 8.9$, $P = 0.01$) and female groups ($H_2 = 9.66$; $H_2 = 10.08$, both $P < 0.01$) from the pre- to the post-rut (Fig. 1a). Besides, the time spent moving did not vary significantly between the 3 periods in either of the group types (mixed-sex: $H_2 = 0.17$, female groups: $H_2 = 4.7$, both $P > 0.9$). The frequency of act transition ($H_2 = 6.7$, $P = 0.03$) and act diversity ($H_2 = 10.25$, $P < 0.01$) decreased significantly from the pre- to the post-rut in female groups (Fig. 1b). No significant differences were found regarding these two latter variables in mixed-sex groups (act transition: $H_2 = 4.03$, $P = 0.13$; act diversity: $H_2 = 1.7$, $P = 0.41$). Females were rarely involved in social interactions during the pre- and the full-rut and almost never during the post-rut, even when males were present in the groups (mixed-sex: $H_2 = 10.5$, $P < 0.01$; female groups: $H_2 = 5.7$, $P = 0.057$).

No significant differences were found between mixed-sex and female groups regarding the 6 behaviour variables during the pre- and post-rut. Besides, females

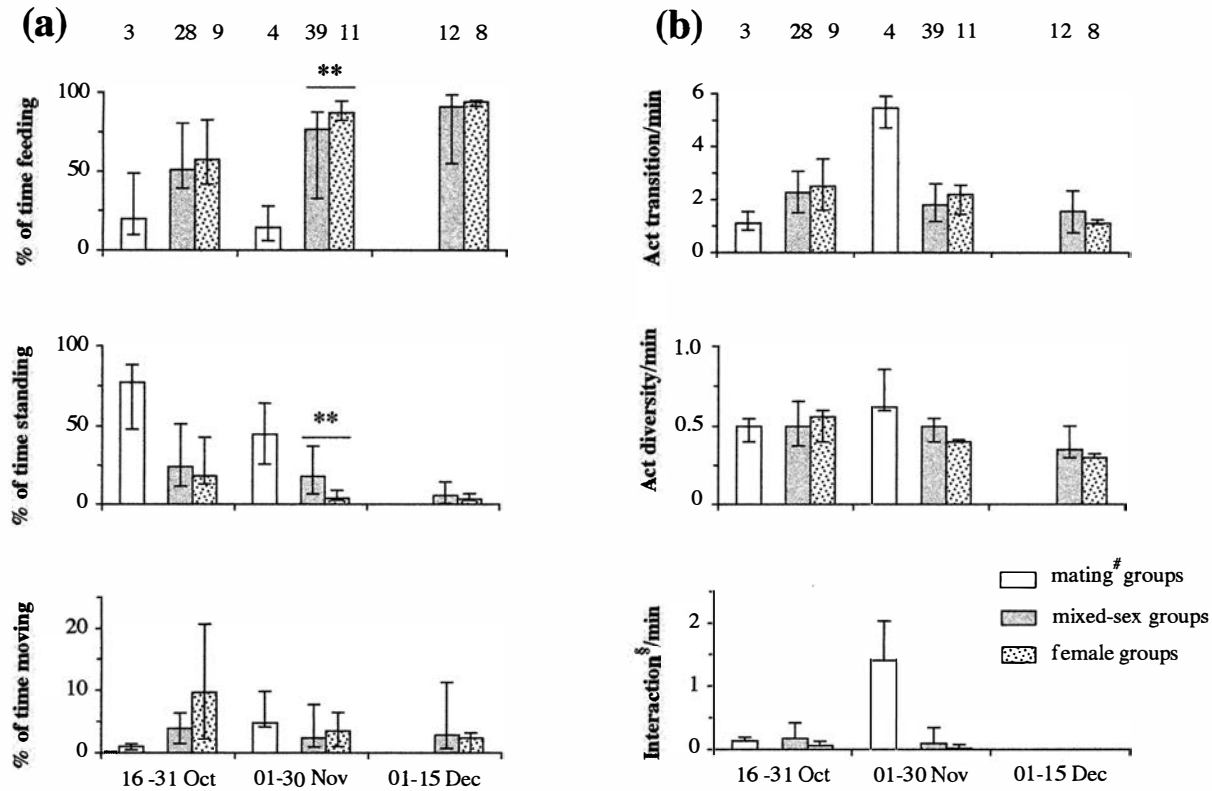


Figure 1. — Median with interquartile range of a) percent of time spent feeding, standing/scanning and moving by female Mouflons, and b) frequency per mn. of act transition, act diversity and interactions involving females during the pre-rut (16-31/Oct.), the rut (01-30/Nov.) and the post-rut (01-15/Dec.) in mixed-sex, mating and female groups, in the Caroux (southern France). Mixed-sex vs female groups: ** $P < 0.01$. Numbers of focal samplings are indicated above the charts. [§] For interactions, the median and interquartile is replaced by the mean and standard deviation as the median equals 0 in all but one case. [#] In the analysis, data on mating groups were pooled to statistically compare the three group types.

spent significantly more time feeding and less time standing/scanning ($U = 112$, $P = 0.017$ and $U = 106$, $P = 0.01$, $N_1 = 39$, $N_2 = 11$) in female than in mixed-sex groups during the full-rut. Ewes spent as much time moving in the absence and in the presence of rams in the groups ($U = 84.5$, $P = 0.14$, $N_1 = 39$, $N_2 = 11$). The presence of males had no significant effect on the frequency of either act transition and diversity in female behaviour, or on the frequency of interactions involving females (respectively: $U = 204$, $P = 0.81$; $U = 167.5$, $P = 0.27$; $U = 177.5$, $P = 0.38$, $N_1 = 39$, $N_2 = 11$).

Mating groups were observed only during the pre- and the full-rut and because of the small sample size, data were pooled to compare the three group types. No significant differences were found regarding the time spent moving ($H_2 = 0.84$, $P = 0.65$) or the frequency of act transition and diversity ($H_2 = 1.8$, $P = 0.39$; $H_2 = 109$, $P = 0.38$). In contrast, the time spent feeding ($H_2 = 10.6$, $P = 0.005$) and standing/scanning ($H_2 = 10.08$, $P = 0.006$) and the rate of interactions ($H_2 = 15.10$, $P < 0.001$) differed significantly according to the group type. Dunn multiple comparison tests indicated that, in mating groups, females allocated less time to feeding and more time to standing/scanning, and were more frequently involved in social interaction than in mixed-sex and female groups.

The rate of interactions of males ≥ 1.5 years toward females decreased from the pre- to the post-rut in mixed-sex groups (respectively mean \pm SE: 0.43 ± 0.84 , 0.17 ± 0.37 , 0.01 ± 0.03 interactions. mn^{-1}). Male courtship was less intense during the pre-rut than during the full-rut in the mating groups (0.07 ± 0.12 , 1.54 ± 1.14 interactions. mn^{-1} respectively). During the rut, the frequency of male interactions was related negatively to the time spent feeding ($r_s = -0.35$, $P < 0.001$), positively to the time spent standing/scanning ($r_s = 0.29$, $P = 0.002$) and near significance to the time spent moving ($r_s = 0.17$, $P = 0.06$) by females (Fig. 2). However, the strength of correlation was low in each case and the coefficients of determination (or shared variance) r^2 indicate that the variation of time spent in these activities is poorly accounted for by the variation of interaction frequency (Grimm, 1993). In addition, the highest rates of interactions were noted in mating groups, so the time devoted to feeding, standing/scanning and moving was no longer correlated with the frequency of interactions when only data from mixed-sex and female groups was considered.

DISCUSSION

During the rut, adult rams devoted a lot of time to courtship and much less time to feeding than ewes (Jewell 1997, Bon *et al.*, 1992). The time spent foraging by females remains unchanged during the rut in Fallow Deer *Dama dama* and Dall Sheep *Ovis dalli* (Buschhaus *et al.*, 1990; Singer *et al.*, 1991). In these species, the proportion of time devoted to feeding by females (65%) was close to that found during the full-rut in this study (60.2%). But the present results reveal that the period with respect to the rut has an effect on the basic female activity pattern. The reduced time spent feeding observed in mixed-sex and female groups (*i.e.* in the absence of males) in the pre- and the full-rut compared to the post-rut may be related to a change in female physiology. The rut occurs mainly at the end of October and in November in this population (Bon *et al.*, 1993a). This period is characterized by the end of the summer drought and a second period of vegetation greening (Bon *et al.*, 1990). Mouflons, which stay most of the day in wooded or

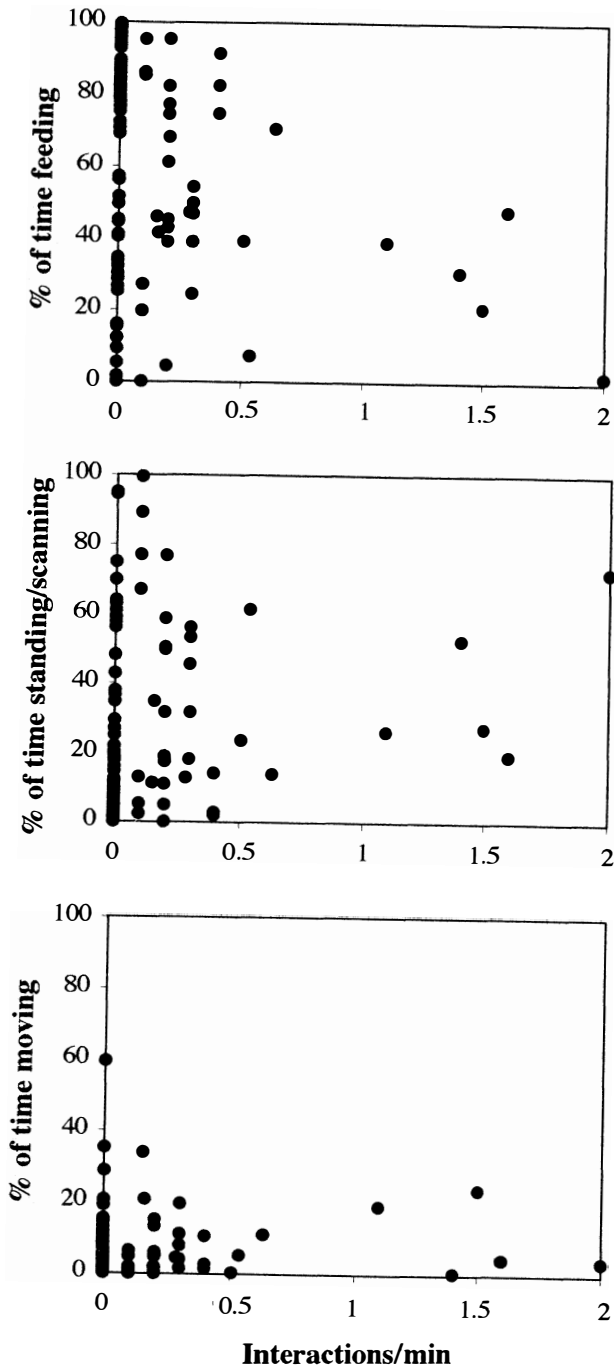


Figure 2. — Relationships between the percent of time spent feeding, standing/scanning and moving, and the frequency per mn. of interactions involving females during the rut.

shaded rocky areas in summer, use the open areas more in autumn. Accordingly, group size increased from October to December (Bon *et al.*, 1990, 1993b), which may result in scramble competition and increased time required to fulfil energy requirements. But, although not significant, the decreased time spent moving in female groups contradicts, at least partly, this argument. It was also unlikely that direct competition explains the increasing proportion of time spent grazing as, concomitantly, the frequency of interactions decreased as well as the time spent standing/scanning, even in female groups. Because the vegetation is less dry in autumn (Cransac *et al.*, 1997), feeding availability could have increased so the ewes would spend less time moving around in search of food.

During the pre- and full-rut, ewes perhaps experienced behavioural modifications due to reduced appetite and greater restlessness, which may in turn be hormonally induced. This could explain the large variability in time spent in basic activities and also the higher level of act transition and behavioural richness during the pre-rut and full-rut than during the post-rut.

Our main expectation, *i.e.* male courting will result in a change of basic female activities, was not clearly verified. Similar trends regarding the 6 behaviour variables were found in mixed-sex and female groups. Ecological and other social factors linked to group size could have blurred the effect of male courtship. The results may also indicate that, despite an intense involvement of males, courtship has a reduced impact on female activities. The presence of males seemed to disturb the females only in November, when they fed more and stood /scanned less in female than in mixed-sex groups. The low impact of male presence can be explained by the low frequency of interactions (addressed and received) involving female Mouflons, which was comparable in mixed-sex and female groups.

Ewes may also be weakly responsive to male displays. Lott (1981) reported that in the promiscuously mating American Bison (*Bison bison*), anoestrus females responded little to male presence. Both the low frequency of interactions and low female responsiveness probably explain the weak relationships between the frequency of interactions and the proportion of time devoted to feeding and standing/scanning. However, the absence of an observable behaviour pattern that could indicate female harassment does not preclude physiological consequences of male presence, *e.g.* a modified heart rate or a facilitation of the oestrus (male effect).

Although they must be taken cautiously, due to small sample size, our data indicate that female activities are modified mainly in mating groups. Oestrus females isolated themselves from other ewes, devoted less time to feeding, more time to standing/scanning, changed activity frequently and showed higher act diversity than in both other group types. The behavioural changes of oestrus females may result from male sexual interactions which can be very frequent, as documented in American Bison (Lott, 1981), but may also be physiologically induced.

Unlike in adult males, the mating period does not seem to disturb the time budget of females. It could thus entail low energy costs, contrary to what could be expected in a promiscuous mating system. This study indicates that the overt consequences of the mating season seem to affect females significantly only when they are in oestrus. Because oestrus lasts a short time in sheep species (Jewell *et al.*, 1986), females are unlikely to suffer a decrease in body weight. However, we must consider other direct or indirect consequences of the rut on the female. Male chases may be performed in steep rocky areas and so be dangerous (Schaller, 1977;

Festa-Bianchet, 1987), particularly when oestrous females are harassed (Hogg, 1987) and even butted by several coursing males (Bon *et al.*, 1992). Réale *et al.*, (1996) also showed that harassment may be an important cause of ewes' mortality in a feral sheep (*Ovis aries*) population with a sex ratio biased towards males. Whether aggression is detrimental for females is unknown in the present Mouflon population. Further data are needed to measure the extent to which females suffer directly or indirectly from the promiscuous mating system.

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