Z. Säugetierkunde 58 (1993) 294–301

ISSN 0044-3468

Social grouping dynamics of Mouflon *(Ovis ammon)* during rut

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Receipt of Ms. 10. 6. 1992
Acceptance of Ms. 1. 4. 1993

Abstract

Studied grouping dynamics of mouflons in relation to the presence of males during rut in October-December. Before rut, older males and females were strongly segregated. During rut, the monthly group size distributions closely fit truncated negative binomial distributions. In October, mouflons lived in small groups and males entered female ranges. Single adult rams, especially older ones, wandered looking for œstrous ewes while younger rams were mostly in matriarchal groups in forested areas. In October, the observed sex ratio was male-biased. In November, mouflons used more open areas, the sex ratio declined and group size increased. The male population observed included few older rams per potentially receptive female. We suggest that the rut delayed the aggregative tendency and resulted in high social instability. Adult males provoked dissociation of mother-lamb bonds during the mating peak. Male lambs appeared more disturbed than female lambs but returned earlier in ewe groups. In December, males over 6 years old were rarely observed with females, whereas younger rams stayed with ewes up to January, when mouflons frequently formed large groups.

Introduction

Despite the great interest of ethologists and ecologists in the social behaviour and mating systems of ungulates, very little is known about the social organization of the mouflon *(Ovis ammon).* This dimorphic gregarious species exhibits a high degree of sexual segregation outside the rut (Pfeffer 1967; Gonzalez 1985; Bon and Campan 1989) like other wild sheep (Geist 1971) and feral sheep (Grubb and Jewell 1966). In Europe, the rut occurs from the end of October to the end of December (see Pfeffer 1967 for a review).

Wild sheep have a promiscuous mating system. Rams neither hold harems nor defend territories (Pfeffer 1967; Geist 1971; Hogg 1984, 1987), but wander in search of receptive females. The gathering of males and females entails large social modifications in open-membership groups (Bon and Campan 1989).

The aim of this study was to investigate when rams associate with ewes according to their age. To what extent social and ecological factors may account for the changes of composition and size of groups during rut is discussed.

Material and methods

Study area

The study area is situated in the Caroux-Espinouse massif (42.5° N, 3° E, elevation 300 to 1100 m) in France. After a summer dryness, cooler temperatures and rainfall allow a new growth of grasses. In winter, food availability decreases as reflected by mouflon rumen contents (Bon et al. 1990).

The study population is protected in the hunting reserve (1830 ha) and is hunted elsewhere from September to February (Cugnasse 1982). Between 1977 and 1989, 1437 males and 1403 females were hunted but the mean age of rams shot was higher than that of females (male range: 5–6.6 years, female range: 3.1–4.5 years). No natural large predators are present.

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Data collection

From July to January in 1984, 1985 and 1986, group sizes and composition were noted during 53 ground surveys along hiking routes, early in both morning and afternoon during the maximum feeding periods of mouflons. In 1984 and 1985, we walked along two routes in the hunting reserve. Throughout 1986, the sampled area was enlarged by eight new routes, covering about one half of the 10,000 ha used by the mouflon population. A group was defined as a set of animals within 25 m of one another. During the walks, 6460 observations of mouflons were collected, and ascribed to the following age/sex classes: male and female lambs (M1 and F1 respectively), females $\geq$ 1 year old (F), yearling males (M2), 2-year-old males (M3), 3 to 6-year-old males (M4), males $\geq$ 7 years old (M5). Groups were classified as adult or yearling male alone (M), adult and yearling male groups (MM), matriarchal groups, mixed sex groups were with or without lambs.

In the Caroux-Espinouse, the rut extends from October to early January with the peak of œstrus occurring in the first half of November (Bon et al. 1992). All ewes $\geq$ 1.5 years old were considered as potentially receptive during autumn (Cugnasse et al. 1985; Bon et al. 1993). The sex ratio of the breeding population (M/F) was measured including all mouflons $\geq$1.5 years.

Statistical analysis

The proportion of age/sex class, the group size and composition and the social tendencies of animals of each age/sex class were analysed monthly. Summer results are presented to underline social changes during rut.

Age/sex class proportion

Because few animals were marked and because the population was sampled repeatedly, our data are probably not independent and the age/sex proportions were only represented graphically. Because lamb sex could not be determined, lambs of both sexes were pooled in summer.

Group size

Adult males joined females in October, so we only studied the effect of male presence on group size from October. In order to study the monthly grouping tendency during rut, we looked for the probability distribution of the random variable "group size" (noted Y).

Number of groups and group sizes might partially account for the observed group size distribution patterns. In order for these two variables to explain the variance in the data, we had to design a model in which each variable was represented by an appropriate theoretical distribution. The resulting mixed distribution was compared to the distribution of the mouflon data. We assumed that the number of mouflons in a group is given by a simple Poisson process with mean λ, where λ varies according to a gamma distribution from group to group.

Denote by y an observed value of Y, the probability function for the Poisson distribution is:

$$\lambda^y \frac{e^{-\lambda}}{y!} \tag{1}$$

where λ is an independently distributed gamma variable with a probability density function given by:

$$[p^k \Gamma(k)]^{-1} \lambda^{k-1} e^{-\frac{\lambda}{p}}; \lambda > 0; k > 0; p > 0 \tag{2}$$

where p is the scale parameter and k the shape parameter (if $0 < k < 1$ the density has a pole at the origin and decreases monotonously as $\lambda \to \infty$; if $k > 1$ the density is zero at the origin and has a single mode. The graphs of the densities are all positively skewed).

Making these two assumptions, we determined the probability function of Y when heterogeneous groups are mixed. With the joint distribution of y and λ obtained from the product of (1) and (2), we integrated over λ (from zero to infinity) to express the probability function of Y. For the compounding of a gamma with a Poisson distribution, this yields a negative binomial probability function (Johnson and Kotz 1969).

$$P[Y = y] = [p^k \Gamma(k)]^{-1} \int_0^\infty \lambda^{k-1} e^{-\frac{\lambda}{p}} (\lambda^y \frac{e^{-\lambda}}{y!})\, d\lambda$$

$$P[Y = y] = \left(\frac{y + k - 1}{y} \right) \frac{p^y}{(1 + p)^{k+y}}$$

The distribution of Y must be described by a truncated negative binomial distribution because groups of size 0 cannot be observed. The truncated negative binomial probability function is given by:

$$P[Y = y] = \binom{y + k - 1}{y} \frac{p^y}{(1 + p)^y[(1 + p)^k - 1]}$$

with expectation,

$$E(Y) = \frac{kp(1 + p)^k}{(1 + p)^k - 1} \quad (3)$$

and variance,

$$V(Y) = E(Y)\,[1 + p + kp - E(Y)] \quad (4)$$

We estimated the parameters k and p of the model by the maximum likelihood method.

With respect to the truncated Poisson distribution, the truncated negative binomial distribution becomes increasingly overdispersed as the value of the p parameter rises. At the limit, when $p \rightarrow 0$, $k \rightarrow \infty$ and $kp \rightarrow$ the mean, the truncated negative binomial distribution tends towards a truncated Poisson distribution ((4) $\Longrightarrow$ V(Y) = E(Y)). Thus, k and p (or E(Y) and V(Y)) can be viewed as aggregation indices because a p value which is not too small and a small k value (or V(Y) > E(Y)) indicate a non-random distribution of mouflons in the study area.

In order to assess the goodness of fit of the model to the data, we used a χ^2 test with degrees of freedom equal to the number of observed frequencies minus three because there are two parameters k and p and the sum of the predicted values must be equal to the total number of groups observed.

Results

Age/sex class proportions

In summer, rams ≥ 3 years old lived in more closed habitats than ewes (n = 452) so the observed ratios were strongly biased towards ewes (M/F = 0.29, M2/F = 0.13, M3/F = 0.035, M4/F = 0.13, M5/F = 0).

In October, we saw more males than females (M/F = 1.29) and the ratio of each male class to females (n = 157) peaked (M2/F = 0.22, M3/F = 0.14, M4/F = 0.8, M5/F = 0.13). From November to January, the yearling males/females ratio was similar to that seen in summer (respectively 0.13, 0.08 and 0.13) while the proportion of rams ≥ 2 years old decreased at a rate which rose with ram age. In November, when most conceptions occurred, for every 100 ewes (n = 930) we recorded 3 males ≥ 7 years old, 29 males 3 to 6 years old and 9 males 2 years old. In December, males ≥ 7 years old were rarely observed (M5/F = 0.007) whereas younger ones (M4/F = 0.2, M3/F = 0.08) stayed in the female (n = 772) ranges. As the rut progressed, adult ewes became more and more numerous in the samples (in January M5/F = 0.002, M4/F = 0.15, M3/F = 0.006 for n = 1235 females).

The proportion of lambs decreased from October (M1/F = 0.25, F1/F = 0.35) to November (M1/F = 0.14, F1/F = 0.22) and recovered in December (M1/F = 0.20, F1/F = 0.19) and January (M1/F = 0.20, F1/F = 0.27). In order to assess the possible effects of the presence of rams, the lambs/ewes ratio for both sexes were measured in mixed and matriarchal groups. The ratios were systematically higher in matriarchal than in mixed groups for both sexes, although the differences were not significant in October (F1/F = 0.42 vs F1/F = 0.36, G = 0.16, P = 0.69; M1/F = 0.35 vs M1/F = 0.25, G = 0.76. P = 0.38), December (F1/F = 0.20 vs F1/F = 0.19, G = 0.04, P = 0.85; M1/F = 0.23 vs M1/F = 0.195, G = 0.5. P = 0.47) and in January for male lambs (M1/F = 0.235 vs M1/F = 0.19, G = 1.56, P = 0.21). Male lambs were less numerous in mixed than in matriarchal groups in November (M1/F = 0.3 vs M1/F = 0.11, G = 22.4, P > 0.001) while a trend was found in November (F1/F = 0.315 vs F1/F = 0.22, G = 4.2, P = 0.04) and a significant difference in January (F1/F = 0.33 vs F1/F = 0.25, G = 5.13. P = 0.02) in the case of female lambs.

Group size

The χ^2 tests reveal no significant difference between predicted and observed frequencies of group size distributions. So, the truncated negative binomial distributions fit the monthly group size distributions well. The parameters of these distributions are summarized in the table.

Table 1. **Estimated parameters of the monthly truncated negative binomial distributions**

Parameter	October	November	December	January
k	1.000	1.413	4.196	3.138
p	1.865	2.470	1.282	2.115
Exp.	2.865	4.217	5.554	6.831
Var.	5.341	11.570	11.710	19.960
χ^2	8.925	12.390	20.020	23.960
df	10	11	15	17

k: shape parameter, *p:* scale parameter, *Exp.:* expectations, *Var.:* variances, χ^2: chi-square, *df:* degrees of freedom.

The mouflons had an increasing tendency to aggregate from October to January. In October, animals were frequently seen alone but most were in groups of 2 to 5 individuals (mean = 2.87 ± 0.64). In November the proportion of solitary mouflons decreased and almost no single animals were seen by January. At the same time, the large groups (> 10 animals) were more numerous; the estimated mean group size gradually rose from 4.2 (± 0.91) to 6.8 (± 0.99), reflecting the flexibility of the associations.

Social tendencies and group types

Social tendencies were defined as the tendencies of each age/sex class to join a particular group type (Bon and Campan 1989).

In summer, the rams' tendency to live in male groups increased with age (Fig. 1). As adult rams were much more difficult to observe than the ewes, matriarchal groups dominated in our samples (Fig. 2).

From summer to January, the social tendencies of yearling males changed little with an obvious trend to join ewe groups (Fig. 3). Conversely, older rams changed their grouping patterns. Two-year-old males exhibited similar tendencies to yearlings from October to January. At the end of the summer, adult male groups disbanded and rams were frequently alone in October and November. Males over 7 years old were alone in over 30 % of their

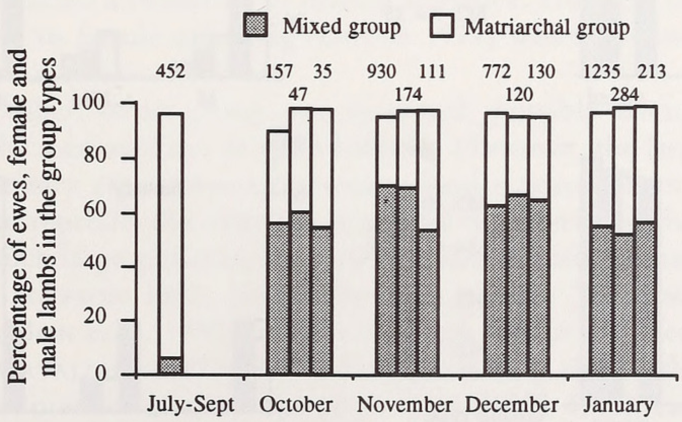

Fig. 1. Monthly percentages of adult females, female and male lambs seen in mixed and matriarchal groups during rut. Numbers of animals are indicated above columns

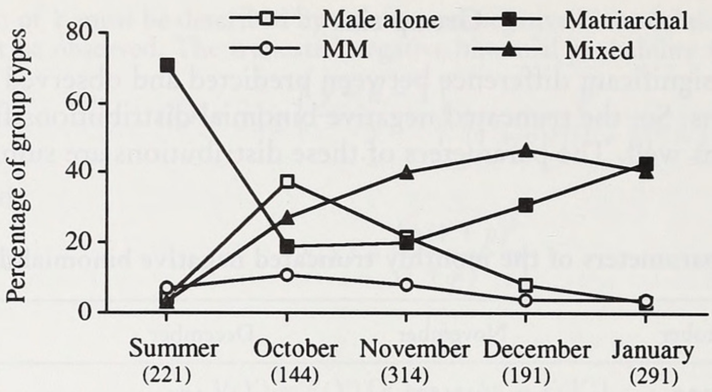

Fig. 2. Monthly percentages of group types during rut. Numbers in brackets indicate sample sizes

observations, but mature rams associated mostly with ewes so the proportion of mixed groups increased (Fig. 2).

Males over 7 years old left the female ranges after November. The younger males were almost never observed alone in December and January and more than 80 % of those which still stayed on rutting grounds lived in mixed groups.

During the rut, almost 100 % of the lambs observed associated closely with ewes. No significant differences were found between sexes about distribution in matriarchal and mixed groups except in November when male lambs were more often in matriarchal groups than female lambs (G = 6.75, P 0.009). Female lambs followed a pattern of distribution in mixed and matriarchal groups very similar to that of ewes (Fig. 1).

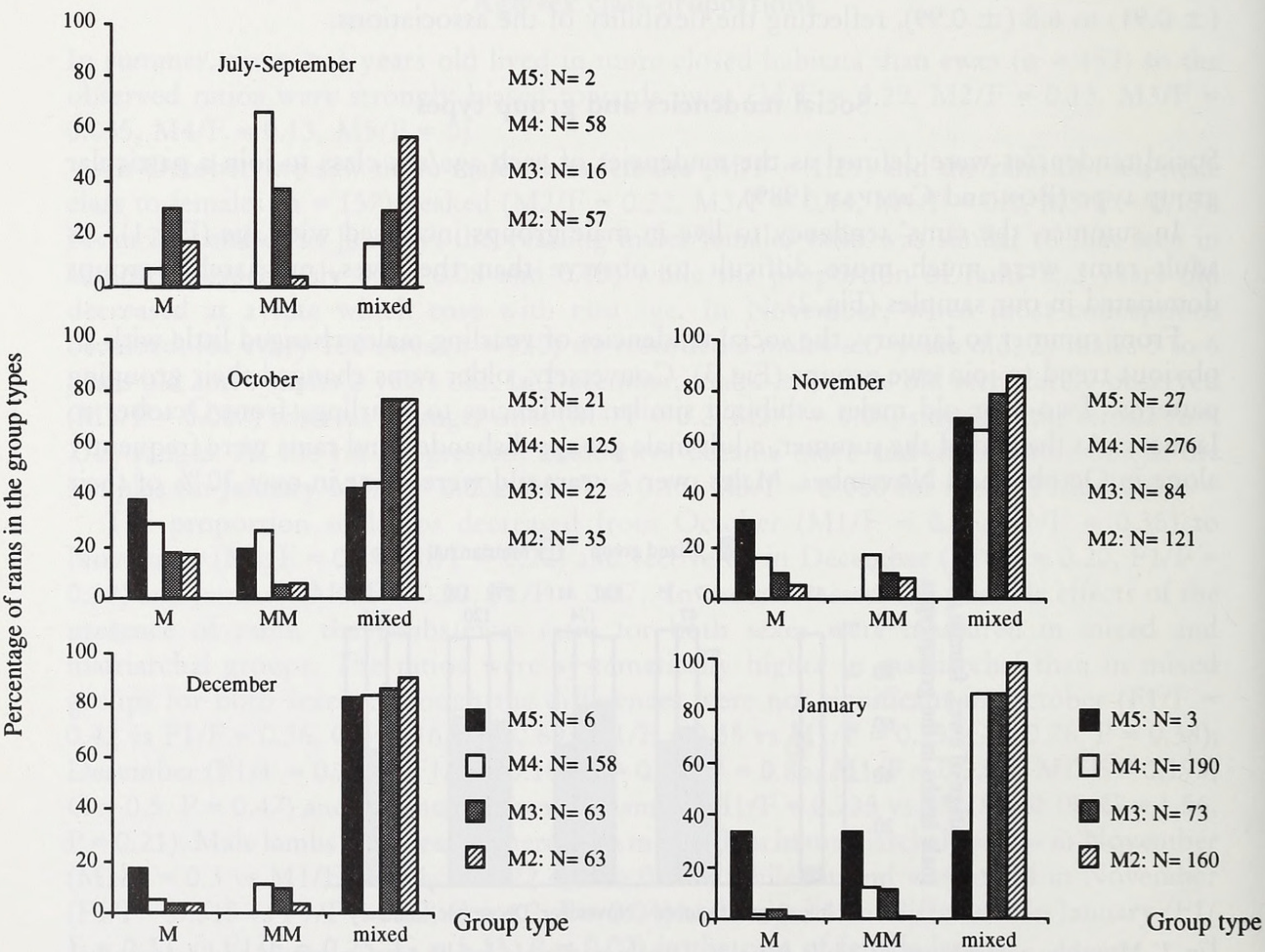

Fig. 3. Monthly percentages of males of each class, alone in male and in mixed groups during rut

Discussion

The advantage of adjusting the data to a truncated negative binomial distribution lies in the extension of the results given by the sample to the whole population. Such a distribution reflects the non-random association of mouflons. It provides the estimates of the parameters from which expectation and variance are issued. The expectation represents the mean group size which can be compared monthly. Indeed these comparisons could not be theoretically possible in using the empirical estimates of the mean and variance because of the monthly variation of the observed sample size.

Up to September, mature rams and ewes socially segregated as reported in wild sheep living under a seasonal climate outside the rut. During the pre-rut in October, large rams, either solitary or in small groups (Hogg 1987) enter the breeding areas and look for receptive ewes (Geist 1971; Grubb 1974; Leslie and Douglas 1979; Festa-Bianchet 1986; Van Vuren and Coblentz 1989) as observed for male ungulates (ibexes *Capra ibex* and *Walia ibex:* Nievergelt 1974; elk *Cervus elaphus canadensis;* African elephant *Loxondonta africana:* Barnes 1982; Poole 1989; feral goat *Capra hircus:* O'Brien 1984). Rams exhibit an increasing tendency to associate with ewes. The youngest rams for their part exhibit an intermediate social pattern as they still often associate with ewes (Geist 1971; Festa-Bianchet 1986, 1991). Females and juvenile live in small groups in woodland for a large part of the day, due to high temperatures, explaining the strong ram-biased sex ratio observed in October (Leslie and Douglas 1979).

In November, all animals increased their use of open areas. The proportion of ewes increased, explaining the ewe-biased sex ratio. Adult rams are often alone in search of receptive ewes. Most mouflons are observed in mixed sex groups.

The decrease in the proportion of lambs observed during rut coincides with the mating peak. Male lambs appeared more disturbed than females since during the full rut they obviously avoided the mixed groups possibly because of the presence of mature rams. It has been already found that reproductive males may repel male offspring or yearlings in Soay sheep *Ovis aries* (Grubb and Jewell 1966), impala *Aepyceros melampus* (Jarman and Jarman 1973, 1974) and wild boar *Sus scrofa* (Dardaillon 1989).

In December, the oldest rams leave the rutting grounds, spending less time with females than younger rams (Geist 1971; Geist und Petocz 1977; Leslie and Douglas 1979; Gonzalez 1985) like in other polygamous ungulates (Nievergelt 1974; Franklin and Lieb 1979; Dunbar and Dunbar 1981). Since 80 % of lambs are conceived in November (Bon et al. 1993), the presence of the oldest rams coincides with the conception peak, while younger males remain longer and serve some ewes in late œstrus (Cugnasse 1982; Bon et al. 1993) as reported by Heimer et al. (1984) in Dall sheep *(O. dalli).* The reobservation of male lambs in December and their similar rate of occurrence in mixed and matriarchal groups indicate a reduction of mating activities. This also suggests their higher independence relative to female offspring (Grubb 1974) which followed a social pattern rather similar to that of ewes.

Beginning in October, mean group size increased, possibly because of higher food availability and by the increased use of open habitats. However, the large groups observed in December and January are unexpected because food is scarce (Bon et al. 1990). Some other causes linked to reproductive activities may lead mouflons to gather. Various authors have already noted such large gatherings in other ungulates (bison *Bison bison:* Lott 1981; aoudad: Gray and Simpson 1982; bharal *Pseudois nayaur:* Wilson, 1984; wild boar: Dardaillon, 1989; Bon et al. 1990). Male wild sheep do not herd females (Geist 1971; Hogg 1984, 1987; Cavallini 1987) and we have previously shown that even in matriarchal groups the mean number of ewes rises (Bon et al. 1990). In November, reproductive activities such as competitive behaviour among rams, the temporary departure of lambs and the isolation of ewes in œstrus could cause the groups to split, despite the grouping tendency of non-reproductive animals. This social instability may reduce the aggregative trend that we observed later. The tendency for males ≤ 6 years old to remain with ewes after the rut (GEIST 1971; BON and CAMPAN 1989) during a period of higher social stability (GEIST 1971) may explain the increasing mean group size as reported by ROUNDS (1980) in the post-rut for wapiti. The reduction of available and favourable habitats in winter may also partly explain the high aggregation tendency (BON et al. 1990).

Acknowledgements

We are grateful to R. CAMPAN, L. ARIAS DE REYNA, P. RECUERDA, L. FATTORINI, and M. FESTA-BIANCHET for their helpful comments on earlier drafts of the manuscript. We also thank D. DUBRAY and J. M. CUGNASSE of the Office National de la Chasse for the full facilities they gave us to achieve the field work. We are grateful to K. KOVÁTS and C. SPERISEN who kindly translated the abstract. This work was supported by a grant from the Spanish and French Foreign Offices to R. BON, and a French-Spanish project of university cooperation.

Zusammenfassung

Dynamik der sozialen Gruppierung von Mufflons (Ovis ammon) während der Brunst

Das Gruppierungsverhalten von Mufflons während der Brunstzeit von Oktober bis Dezember wurde in Bezug auf die Anwesenheit von männlichen Tieren untersucht. Vor der Brunst waren ältere männliche Tiere zu einem hohen Grad von weiblichen Tieren getrennt. Während der Brunst folgte die Verteilung der monatlichen Gruppengröße einer abgeflachten negativen Binomialverteilung. Im Oktober lebten die Mufflons in kleinen Gruppen, und männliche Tiere betraten das Streifgebiet von weiblichen Tieren. Während einzelne erwachsene, vor allem ältere Widder, auf der Suche nach brünstigen Muttertieren waren, lebten jüngere Widder vor allem mit Mutterschafen in bewaldeten Gebieten. Zu dieser Zeit war das Verhältnis von männlichen zu weiblichen Tieren mit einem systematischen Fehler der männlichen Tiere behaftet. Im November hielten sich die Mufflons vor allem in offenen Gebieten auf. Das Geschlechterverhältnis nahm ab, während die Gruppengröße zunahm. Die männliche Population zeigte ein niedriges Verhältnis von älteren Widdern zu empfänglichen weiblichen Tieren. Wir nehmen an, daß die Reproduktionsaktivitäten die Gruppierungstendenz verzögerten, und daß dies eine hohe soziale Instabilität zur Folge hatte: Die Anwesenheit von erwachsenen männlichen Tieren bewirkte eine Auflösung von Mutter-Lamm-Bindungen während der intensivsten Periode der Paarungszeit. Männliche Lämmer schienen stärker gestört als weibliche, aber jene kehrten früher zu den Mutterschafsgruppen zurück. Im Dezember wurden selten über 6 Jahre alte männliche Tiere in Gesellschaft von weiblichen Tieren beobachtet, während jüngere Widder bis Januar bei den Mutterschafen blieben. Während dieser Periode bildeten die Mufflons häufig große Gruppen.

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