BEHAVIOURAL ECOLOGY

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Sexual dimorphism, activity budget and synchrony in groups of sheep

Abstract The activity budget hypothesis has been proposed to explain the social segregation commonly observed in ungulate populations. This hypothesis suggests that differences in body size – i.e. between dimorphic males and females – may account for differences in activity budget. In particular, if females spend more time grazing and less time resting than males, activity synchrony would be reduced. Increased costs of maintaining synchrony despite differences in activity budget would facilitate group fragmentation and instability of mixed-sex groups. In this paper two prerequisites of the activity budget hypothesis were tested: (1) that males should spend less time feeding and more time resting than females in single-sex groups and (2) that lower activity synchrony should be observed in mixed-sex compared to single-sex groups. The activity budget and synchrony in mixed and single-sex groups of merino sheep (*Ovis aries*) of different sizes (2, 4, 6, 8 individuals) were measured in three contiguous 491-m^2 arenas located in a natural pasture. Three same-size groups, one of each category, were observed simultaneously. We found no sexual differences in the time spent inactive and active (i.e. grazing, standing, moving, interacting). Males spent significantly more time grazing and less time standing than females. These differences disappeared when yearling males were omitted from the group. Males and females had similar bite and step rates. Sheep of both sexes spent less time resting and more time grazing and moving and had lower bite rates when in mixed-sex groups than when in single-sex groups. The synchrony among visually isolated groups was near zero, indicating that they changed activities independently. On the contrary, within-group synchrony was high; however it was higher in single-sex groups, in particular for males, than in mixed-sex groups. Our results suggest that differences in activity budget and synchrony alone are insufficient to explain social segregation.

Keywords Allelomimetism · Body mass · Ruminant · Social segregation · Time budget

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Introduction

The current debate about sexual segregation in social and sexually dimorphic ungulates revolves around several related issues. Among these are the identification of the causes that are at the basis of this phenomenon and, consequently, the definition itself (Bon and Campan 1996; Bowyer 2004; Ruckstuhl and Neuhaus 2005). Various authors have distinguished between the social, spatial and habitat components of the sexual segregation (Bon 1991; Conradt 1998a; Mysterud 2000; Bonenfant et al. 2004), which are considered as outcomes at a population level that can be explained by different mechanisms (Bon et al. 2005). Most authors have claimed that sexual segregation is the result of different habitat choice (Main et al. 1996; Bleich et al. 1997) and may be understood within the framework of niche theory (Bowyer 2004; Bowyer and Kie 2004).

The two main hypotheses, 'reproductive strategy' and 'sexual dimorphism-body size' (or the 'predation risk' and 'forage selection' hypotheses), propose respectively that habitat segregation results from differential sensitivity to predation risks or from differences in forage selection between the sexes (Ruckstuhl and Neuhaus

2000). The second hypothesis has received little support (see Pérez-Barbería and Gordon 1999a; Bonenfant et al. 2004), while many studies have reported results that are in agreement with the reproductive strategy hypothesis (Kohlmann et al. 1996; Kie and Bowyer 1999; Corti and Shackleton 2002; Mooring et al. 2003; Bonenfant et al. 2004). The latter hypothesis predicts that females will select a safe habitat to reduce predation on their young; therefore it can explain habitat segregation between the sexes only during the period of maternal care, which stops at weaning (= some months after birth in most ungulates).

Studies of several ungulate species (Cransac et al. 1998; Conradt 1999; Bon et al. 2001; Bonenfant et al. 2004) have consistently reported higher degrees of social than habitat segregation, suggesting that if environmental factors are involved, they are insufficient to explain the low occurrence of mixed-sex groups in wild populations. This has led to other hypotheses based on non-ecological mechanisms being proposed – in particular, the social affinity and activity budget hypotheses, both of which focus more specifically on the mechanisms involved in group formation and cohesion.

It has been suggested that group cohesion depends on the capacity of individuals to synchronize their activities with other group members (Clayton 1978; Deneubourg and Goss 1989), a process also called contagion, allelomimetism or social facilitation. This synchronization of activity relies on the capacity of individual animals to obtain information about the activity of other group members. In ungulate species visual communication is likely to play a major role in maintaining social contact and exchanging information. A higher synchrony can therefore be expected within groups in which animals can maintain visual contact than among groups that are visually isolated. The degree of synchrony will also depend on the motivation of individuals to mutually adjust their activities. This would be achieved to some degree when individuals dedicate similar (but not necessarily identical) amounts of time to activity and inactivity (Ramirez Avila et al. 2003). Ruckstuhl (1998) argued that, in dimorphic ungulates, the smaller females would spend more time grazing and less time resting than larger males due to allometry in the efficiency to process food as well as in energy requirements (see also Mysterud 1998; Pérez-Barbería and Gordon 1999b). In a comparative analysis, Ruckstuhl and Neuhaus (2002) found a positive relationship between sexual differences in activity budget and body size. The activity budget hypothesis assumes that the sexual differences in time spent active (inactive) result in lower activity synchrony. The increasing costs of maintaining synchrony that are associated with differences in activity budgets results in the instability of mixed-sex groups (Conradt 1998b; Ruckstuhl 1998): if the costs become too high for a specific one age-sex category, the groups split (Conradt and Roper 2000, 2003).

One manner in which to test whether individuals synchronize their activity is to compare the degree of synchrony observed with that expected under the null hypothesis of independence between individuals (see Rook and Penning 1991). Note, however, that even independent subjects can synchronize because activity timing may be triggered by external factors, such as light intensity, and/or internal factors, such as the level of satiety. One way to assess the effect of social interactions on activity synchrony is to compare the degree of synchrony among individuals belonging to the same group to that of individuals belonging to independent groups submitted to the same conditions and at the same time.

Field studies are very helpful in addressing some of the candidate hypotheses to explain segregation. However, the identification of factors responsible for segregation in the wild is not straightforward. Various feeding, resting, interactions or vigilance may vary according to a variety of ecological and biological factors (Côté et al. 1997; Maier and White 1998; Blanc et al. 1999; Champion et al. 2004). Although experimental studies cannot account for all of the components observed in free-ranging populations (Bowyer 2004), they nonetheless enable different hypotheses to be tested. Studies of sexual differences in activity budget and synchrony according to age-sex categories and their relationship to group cohesion under controlled conditions are scarce (Pérez-Barbería and Gordon 1999a; Michelena et al. 2004).

Domestic sheep are a good model by which to assess some of the assumptions of the activity budget hypothesis. They display a relatively high level of sexual dimorphism, are easier to manage than wild sheep and groups of same-sex and mixed-sex groups can easily be formed and observed under controlled conditions. In a previous experiment, Michelena et al. (2004) found that 15 males and 15 females of dimorphic sheep (body mass ratio: 1.5) introduced simultaneously into 1-ha paddocks remained spontaneously in a single mixed-sex group. Rams and ewes within this group did not differ in time spent inactive. Moreover, males spent slightly less time grazing than females, and all individuals were highly synchronized in their activities. Such results suggest that despite there being a high difference in body mass between the sexes, males and females were able to adjust their activities. However, this preliminary study did not allow tests of predictions based on the activity budget hypothesis. In order for this hypothesis to be tested, the activity budget and synchrony in single-sex and mixed-sex groups have to be measured.

In the investigation reported here single-sex and mixed-sex groups of merino sheep were introduced simultaneously into the same pastures. The specific aims of the field study were to test the following predictions: (1) males should spend less time feeding and more time resting than females; (2) in mixed-sex groups lower activity synchrony should be observed than in single-sex group. Since the time spent grazing increases with group size (Penning et al. 1993; Dumont and Boissy 2000), we controlled for the effect of group size on activity budgets. In addition, the bite and step rates on which the

time spent grazing depends (Orr et al. 1997; Pérez-Barbería and Gordon 1999a; Ruckstuhl et al. 2003) were estimated for both sexes in both single and mixed-sex groups.

Materials and methods

Study area and subjects

The study was conducted from November 2003 to February 2004 at the experimental farm of Domaine du Merle (5.74°E and 48.50°N) in the south of France. We randomly selected 34 Arles merino horned males (median age: 3 years, range: 1–7 years) and 32 females (median age: 9 years, range: 5–11 years) from a group of males ($n = 66$) and a flock of females ($n = 900$). Five weeks before the start of the experiments the animals were placed into a 1-ha pasture to allow them to become familiarized with each other. On January 9, three additional 2-year-old males were introduced and allowed to familiarize with the experimental group for 18 days before participating in the experiments. All animals were painted with a number on both flanks and on the rump. Each ewe received a vaginal sponge containing 30–40 mg of progesterone (replaced every 14 days) to block oestrus and prevent any related sexual interactions. During the 15-weeks of the experiments, six ewes were isolated from the group for several days because of an infection arising from an irritation caused by the vaginal sponge. They were injected twice with 2-ml doses of penicillin (Duphapen, Fort Dodge Animal Health, 1 ml/10 kg). Animal care and experimental manipulations were in accordance with the rules of the French committee of animal experimentation ethics. The weight of the males and females changed significantly between the beginning (mean ± SD: $\bar{X} = 66.2 \pm 13.4$ kg and $\bar{X} = 47.9 \pm 5.0$ kg for males and females, respectively) and the end of the experiments (69.9 ± 11.1 kg and 49.8 ± 6.2 kg, respectively; paired t test, males: $t_{27} = -2.6$, females: $t_{30} = -2.65$, both $p = 0.01$), which is the consequence of wool growth. Females were lighter than males at both periods (Student t test: $t_{31,32} = 7.69$ and $t_{31,31} = 5.57$, both $p < 0.001$, at the beginning and at the end of the experiments, respectively; dimorphism index: 1.39). Whereas the weight range of males older than 1 year (59.5–88 kg) and females (39.5–56.5 kg) did not overlap (dimorphism index: 1.48), yearling males (range: 42–54 kg; $n = 9$) were about the same body weight as females. Therefore, we performed analyses on all of the subjects and without the yearling males.

Experimental set-up and procedure

The experiments were carried out in native wet Crau meadows consisting of graminoids, clover (*Trifolium* sp.) and plantain (*Plantago lanceolata*) (Bosc et al. 1999).

Three 25-m-diameter arenas were delimited around a 7-m-high tower erected 22.5 m from the centre of the arenas. Each arena was visually isolated by a 1.2-m-high green polypropylene net to prevent visual contact with the immediate surroundings and between sheep in adjacent arenas. In addition, the net allowed a waiting area around each arena to be delimited (Fig. 1). Single-sex and mixed-sex groups of two, four, six and eight individuals were introduced in the set-up. The experimental design consisted of the random allocation of a male group, a female group and a mixed-sex group (1:1 sex ratio) of the same size in each of the three arenas. The three groups were observed simultaneously. An experiment consisted of testing successively the four group sizes. Five replications of the experiment were conducted, and the order of testing as well as the allocation of each individual to one group size and type were randomly selected before each of the five replications. For example, the order of testing of group size and allocation of group types to arenas (A1, A2, A3) was the following for the first replication: two individuals (A1-females, A2-males, A3-mixed), six individuals (A1-males, A2-mixed, A3-females), four individuals (A1-females, A2-mixed, A3-males), eight individuals (A1-mixed, A2-females, A3-males). The individuals included in one group during the 6-h experiments participated only once in each
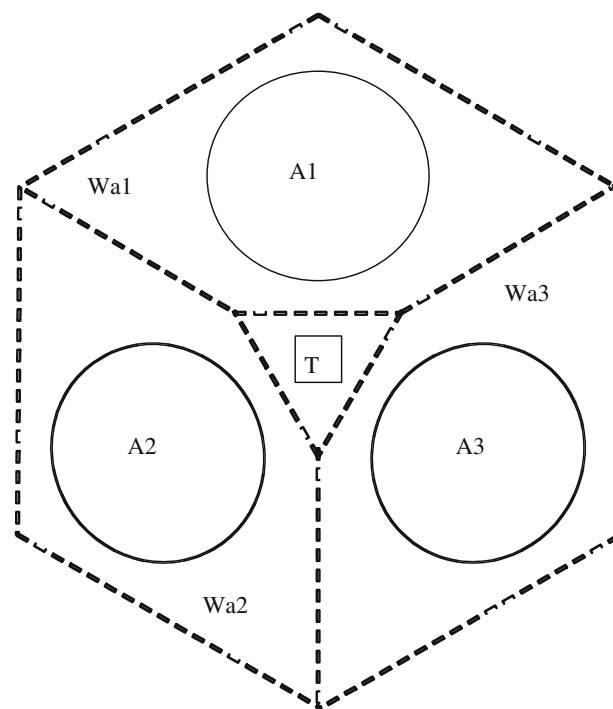

Fig. 1 Experimental set-up used to measure activity budget and synchrony in groups differing in size (two, four, six eight individuals, respectively) and composition (all males, all females and mixed-sex, respectively) during 6-h experiments. Three arenas (*A*) were delimited by electric fences (*straight line*) and enclosed by a 1.2-m-high green polypropylene netting (*dotted line*) delimiting three adjacent waiting areas (*Wa*). The 7.5-m-high observation tower (*T*) was located at the centre of the set-up

replication. Each individual was thus observed five times throughout the 15 weeks of experiments. In order to prevent food depletion within the arenas (i.e. when grass height became lower than 6 cm), the set-up was moved three times within the same pasture.

Early in the morning, the subjects constituting the experimental groups were removed from the flock maintained outdoors. At 10:00 on the day before the experiments, each group was introduced within the waiting area corresponding to its arena to allow familiarization with the experimental set-up and social conditions (group type and size). At 17:00 the same day, the tested groups were introduced within the arenas on the fenced side opposite the tower.

Data collection

The day after familiarization with the enclosures, the behaviour of the sheep in each arena was recorded from 10:00 to 16:00 with three digital cameras (Sony DCR-TRV950 E) anchored at the top of the tower. Each camera was programmed to take one snapshot at 1-s intervals ($n = 21,600$) which was then saved on the hard disk of a PowerBook laptop with three digital FireWire camcorders. Thus one image of each group was taken successively within each 1-s interval. At the end of the 6-h period, the sheep were returned to the flock which was penned in a paddock 500 m from the arenas. Preliminary video recordings of sheep in the same conditions confirmed that the relevant behavioural categories (grazing, standing, resting, walking, interacting) were reliably identified on each image. Walking was defined as a forward movement with the head maintained close to, or above, the column axis. Animals were considered to be grazing when standing with the nose in contact with the sward, including the time spent biting, cropping and mastication, and the time travelling between feeding stations.

In addition, two grazing sheep randomly selected in each arena were filmed (Sony CCD-TRV 67E) for 10 min following a resting bout to measure the bite and step rates when feeding. A bite was defined as "a jerking movement of the animal as it severed the grass already grasped" (Pérez-Barbería and Gordon 1999a). A step was defined as a forward motion with one of the front legs.

Vegetation measurements

Sward heights were measured (± 0.5 cm) within the arenas using an HFRO sward stick (Barthram 1986) the evening before the group was introduced. Twenty-four measurements were taken at 1-m intervals along two diameters of the arena. We also took 20 measures of the sward height along the side of 48 quadrates (1.4×0.14 m) before cutting the grass to ground level in the waiting area of the set-up. The dry matter (DM) of herbage mass was weighed after the quadrate samples had been oven dried at 85°C for 24 h. The calibration curve obtained by plotting the DM per unit height was used to estimate the biomass available in the arena.

Activity budget

During the 6-h experiments digital camera recordings were sometimes disrupted due to dysfunction of the computer system [median sum of disruption: 19 min; range: 18–56 min; mean occurrences ($\pm$SD): 10 ± 2; mean duration ($\pm$SD): 131 ± 55 s]. Consequently, when viewing the films in the laboratory, some of the activity of the sheep could not be scored (mean duration usable = 5:38:41; minimum = 5:03:28, maximum = 5:50:13). Accordingly, we computed for each animal the proportions of time spent grazing, standing, resting, walking and interacting over the duration that it was monitored within the 6-h period.

Activity synchrony

The coefficient of association r_ϕ, classically used for 2×2 contingency tables (Siegel and Castellan 1988), was adapted to estimate the degree of activity synchrony between individuals. For every individual i and j monitored the same day, we computed

$$r_\phi = \frac{A \times D - B \times C}{\sqrt{(A + B) \times (C + D) \times (A + C) \times (B + D)}}$$

where A is the time during which the two sheep were simultaneously active (i.e. grazing, standing, walking, interacting), D the time during which they were both inactive (i.e. resting), B the time during which i was active and j inactive and C the time during which I was inactive and j active. The coefficient r_ϕ, can range from -1 when i and j are never simultaneously active or inactive to $+1$ when both animals are always active or inactive at the same time, through zero when they behave independently of one another.

Because of the experimental design, all the pairs of individuals monitored during any single day could be classified into ten categories. If we denote the sex of the animals as M and F (male and female), and s and x designate the type of group to which the monitored individuals belong (single-sex and mixed-sex), there are five within-group categories, namely MsMs, FsFs, MxMx, FxFx and MxFx, and five between-group categories, namely MsMx, FsFx, MsFs, MsFx and MxFs. Accordingly, we computed the mean value of r_ϕ for each of these ten pair categories for each day of experiment. Our assumption was that among-group synchrony would be close to zero if same-sex sheep of adjacent groups are independent or do not follow the same behavioural rhythm. On the contrary, if there is contagious activity or allelomimetism within the group, the

synchrony will be higher within than among groups. In addition, the activity budget hypothesis assumes higher synchrony in single-sex than in male-female pairs.

Statistical analyses

We performed a MANOVA to assess the effects of sex, group type (single-sex versus mixed-sex) and group size on the proportion of time spent in the five activities studied. Means of the transformed individual proportions for each sex and group type within each day (the groups monitored during a single day having the same size) were computed. Individuals monitored during the same day were not considered to be independent because they were submitted to the same environmental conditions (weather, human perturbations, etc.). Accordingly, observation day was considered as a random factor. We first carried out MANOVAs, including separately the interactions sex × group type and size × group type. The analyses were limited to these two interactions because they were the most relevant and we wanted to avoid an excessive number of parameters. The same factors were analysed in a series of ANOVAs in order to study their specific effects on each of the five activities and on the step and bite rates. Additional ANOVAs tested the effects of sex, group type and group size on the mean sward height encountered by the different groups and the effects of pair type and group size on the activity synchrony r_ϕ.

Data normality was checked with the Kolmogorov Smirnov test and homocedasticity with the Levene test. The proportion of time (P) spent in each activity were logit-transformed, as $logit(P) = \ln(P/(1-P))$ to meet the assumption of normality. Statistical tests were performed with SPSS (Chicago, Ill.) the GLM (general linear model) procedure of SAS (SAS Institute, Cary, N.C.) and the nlme (linear and non-linear mixed effects models) package of R.

Results

Sward height and estimated herbage biomass (Table 1) were similar for the different group sizes and types

(group size: $F_{3,55} = 0.15$, $p = 0.92$; group type: $F_{2,55} = 0.35$, $p = 0.71$; group size × group type: $F_{6,55} = 0.52$, $p = 0.79$).

Activity budget

Overall a significant effect of sex, group type and group size was found, whereas the interactions sex × group size ($p = 0.18$) and sex × group type ($p = 0.21$) were non-significant in the MANOVA including all individuals (see Table 2). When examining the effect of the different factors on each activity, we found no sexual differences in the time spent resting (inactive). However, although the differences between sexes were small, males spent significantly more time grazing than females (Fig. 2a, Table 2). Females also differed from males as they spent more time standing and less time in social interactions (Fig. 2c, e, Table 2). No differences were found between the sexes when considering the step and bite rates while foraging (Fig. 3, Table 2).

Group size did not affect the time spent resting, and the sheep spent more time grazing and less time standing as the number of their conspecifics increased (Fig. 2b, c, Table 2). A significant effect of group size was also found on the time spent moving although no clear relationship was found between these two variables. We observed a trend for males to spend more time interacting in a group consisting of more than two individuals. Step rates increased with group size in grazing sheep but not the bite rate (Fig. 3b, Table 2).

Sheep spent less time resting (Fig. 2b) in mixed-sex than in single-sex groups (Table 2). The difference in time spent active was not explained by the standing time, which did not depend itself on the group types; sheep also allocated more time grazing and moving in mixed-sex than in single-sex groups (Fig. 2, Table 2). While no effect of group type was found on the step rate, bite rate was slightly but significantly higher in single-sex than in mixed-sex groups (Fig. 3).

Overall, the exclusion of the yearling males in the MANOVA did not substantially change the results. Also the results of the statistical analyses regarding the time spent resting and moving remained unchanged, whether data for yearling males were included or not. Significant

Table 1 Mean ($\pm$SD) sward height and estimated biomass before grazing in experimental arenas for each social condition and group size

Sward characteristics	Space allowance (m² per head)			
	245 (2 individuals)	123 (4 individuals)	82 (6 individuals)	61 (8 individuals)
Mean height before grazing (cm)				
Male group	7.6	8	7.6	6.8
Female group	7.4	6.7	7.6	6.8
Mixed-sex group	7	8.5	7.6	6.7
Estimated herbage mass (kg DM/ha)				
Male group	1086	1054	1060	1004
Female group	1058	989	1061	990
Mixed-sex group	1024	1126	1068	988

Table 2 Results of the MANOVA (using the Wilk's λ) and ANOVAs for testing the effects of sex, group type and group size on the proportion of time spent in each activity, and on the number of steps and bites performed per minute by grazing sheep. The results are shown for both the entire population and the population from which the yearling males have been excluded

Source of variations	Activities MANOVA	ANOVA Rest	Graze	Stand	Move	Interaction	Foraging behaviour ANOVA Step rate	Bite rate
Yearling included								
Sex	$\lambda=0.42$ $F_{5,51}=14.3$ $p<0.001{***}$	$F_{1,55}<0.1$ $p=0.86$	$F_{1,55}=3.7$ $p=0.06$	$F_{1,55}=10.1$ $p=0.002{**}$	$F_{1,55}=2.5$ $p=0.12$	$F_{1,55}=36.6$ $p<0.001{***}$	$F_{1,55}<0.1$ $p=0.92$	$F_{1,55}<0.1$ $p=0.84$
Group size	$\lambda=0.32$ $F_{15,141}=4.8$ $p<0.001{***}$	$F_{3,15}=0.2$ $p=0.91$	$F_{3,15}=3.1$ $p=0.03{*}$	$F_{3,15}=11.9$ $p<0.001{***}$	$F_{3,15}=5.2$ $p=0.003{**}$	$F_{3,15}=2.6$ $p=0.06$	$F_{3,15}=3.6$ $p=0.04{*}$	$F_{3,15}=0.3$ $p=0.85$
Group type	$\lambda=0.77$ $F_{5,51}=14.3$ $p<0.02{*}$	$F_{1,55}=5.9$ $p=0.02{*}$	$F_{1,55}=4.9$ $p=0.03{*}$	$F_{1,55}=0.2$ $p=0.68$	$F_{1,55}=5.6$ $p=0.02{*}$	$F_{1,55}=3.2$ $p=0.08$	$F_{1,55}=0.7$ $p=0.39$	$F_{1,55}=4.8$ $p=0.03{*}$
Yearling excluded								
Sex	$\lambda=0.56$ $F_{5,50}=7.7$ $p<0.001{***}$	$F_{1,54}=0.1$ $p=0.93$	$F_{1,54}=1.6$ $p=0.2$	$F_{1,54}=3.4$ $p=0.07$	$F_{1,54}=2$ $p=0.17$	$F_{1,54}=25.8$ $p<0.001{***}$	$F_{1,52}=0.2$ $p=0.63$	$F_{1,52}=0.2$ $p=0.65$
Group size	$\lambda=0.42$ $F_{15,138}=3.4$ $p<0.001{***}$	$F_{3,15}=0.4$ $p=0.77$	$F_{3,15}=2$ $p=0.13$	$F_{3,15}=8$ $p<0.001{***}$	$F_{3,15}=4$ $p=0.01{**}$	$F_{3,15}=2.1$ $p=0.11$	$F_{3,16}=3.7$ $p=0.03{*}$	$F_{3,16}=0.13$ $p=0.94$
Group type	$\lambda=0.81$ $F_{5,50}=2.3$ $p=0.06$	$F_{1,54}=5.4$ $p=0.02{*}$	$F_{1,54}=3.5$ $p=0.06$	$F_{1,54}=0.3$ $p=0.56$	$F_{1,54}=4.8$ $p=0.03{*}$	$F_{1,54}=1.6$ $p=0.21$	$F_{1,52}=0.1$ $p=0.71$	$F_{1,52}=4.7$ $p=0.03{*}$

Asterisk indicates the effect was significant at $*p<0.05$, $**p<0.01$ and $***p<0.001$

Fig. 2 Mean percentage of time spent grazing, resting, standing, walking and interacting by the females (*triangles*) and males (*squares*) in single-sex (*white symbols*) and mixed-sex groups (*black symbols*) as a function of group size
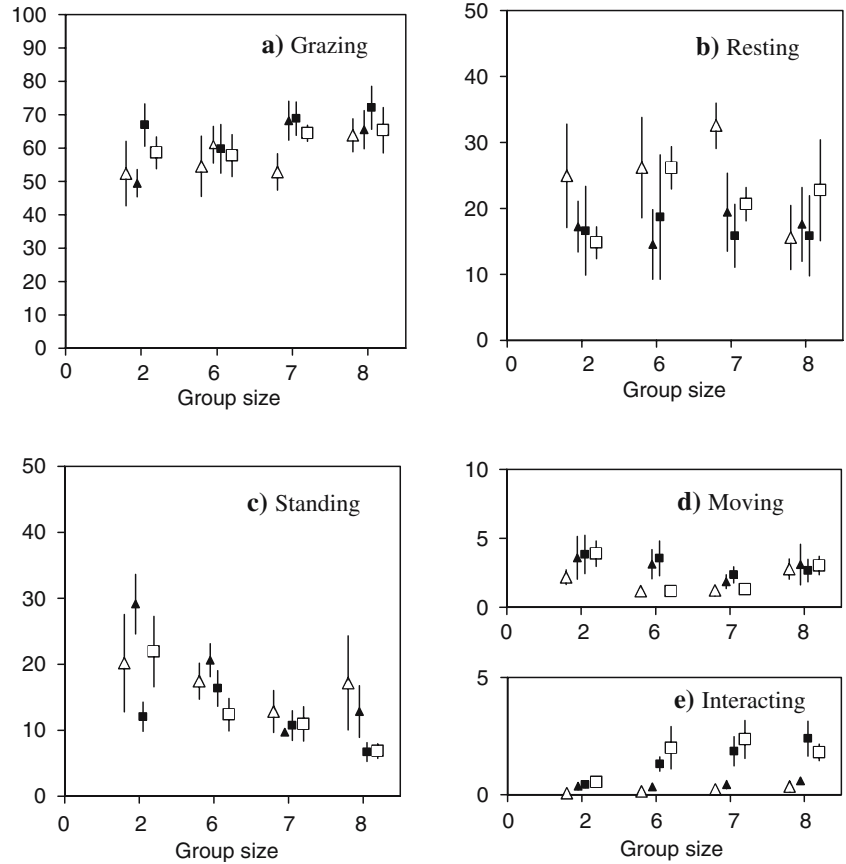

sexual differences in the time spent grazing disappeared when yearling males were excluded. In addition, the difference in the time spent standing between females and males subsisted only as a trend. The time devoted to grazing and interacting did not vary significantly with group size. Differences in grazing time between single- and mixed-sex groups decreased when yearling males were ignored.

Activity synchrony

The results of our analyses did not vary whether yearling males were included or not, therefore we report the results obtained for the whole population. The ANOVA revealed neither a significant effect of the interaction between group size × pair type ($F_{25,117} = 0.6$, $p = 0.89$) nor a significant effect of group size ($F_{3,15} = 0.9$, $p = 0.46$)

Fig. 3 Mean number of bites (**a**) and steps (**b**) per minute while grazing by females (*triangles*) and males (*squares*) in single-sex (*white symbols*) and mixed-sex groups (*black symbols*) as a function of group size
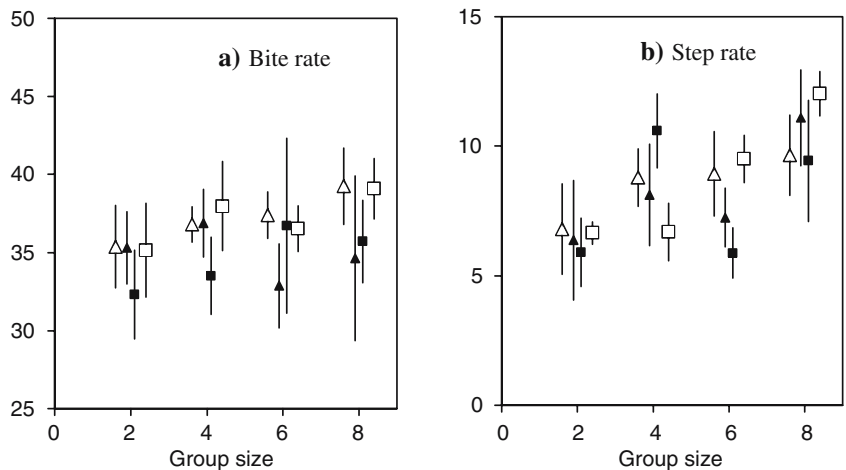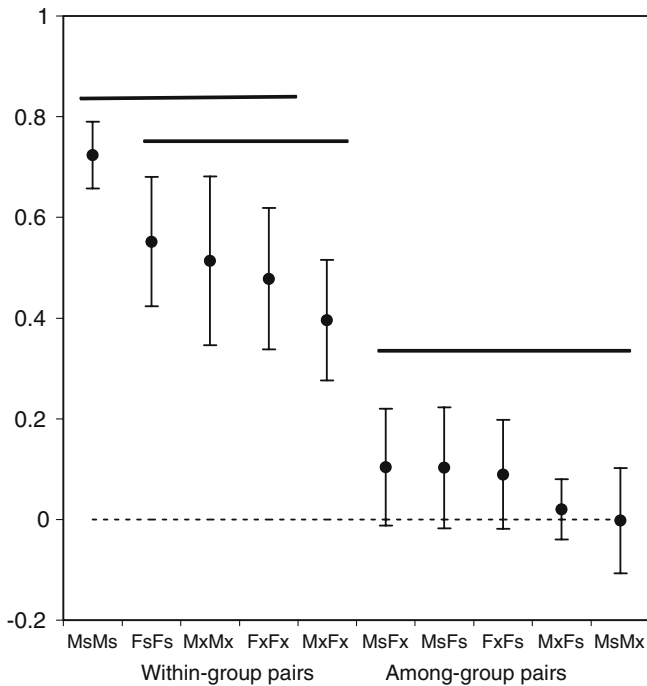
Fig. 4 Mean within-day index of synchrony ($\pm$95% CI) for the different pairs of sheep. *M* male, *F* female, *s* single-sex group, *x* mixed-sex group. The *horizontal lines* indicate the pair types that did not differ significantly at the experiment-wise error rate $\alpha_e = 0.05$ (Tukey post hoc test)

on the r_ϕ index of synchrony. However, the activity synchrony differed significantly between pair categories ($F_{9,117} = 28.5$, $p < 0.001$, Fig. 4). The degree of synchrony for all pair categories consisting of sheep of adjacent groups was close to 0, suggesting that sheep in adjacent arenas exhibited quite independent activity rhythms. In contrast, activity synchrony was much higher between sheep belonging to the same groups, as revealed by the Tukey post hoc tests comparing the between-group and the within-group pair categories ($p < 0.005$). Among the within-group pair categories, the male pairs in single-sex groups exhibited the highest degree of synchrony, and the male-female pairs in mixed-sex groups the lowest degree (Tukey post hoc test comparing these two categories of pairs: $p = 0.005$). As a consequence, the mean within-group index of synchrony differed between male groups, female groups and mixed-sex groups (respectively, mean $\pm$ SD: 0.72 ± 0.15; 0.58 ± 0.26 and 0.43 ± 0.26; $F_{2,30} = 6$, $p = 0.006$) and was significantly higher in male groups than in mixed-sex groups (Tukey post hoc test: $p = 0.01$).

Discussion

The aim of our investigation was to test some of the assumptions of the activity budget hypothesis proposed by Ruckstuhl (1998) and Conradt (1998b), specifically whether the activity budget differs between the sexes and how these differences affect the degree of activity synchrony. Although the subjects were reared in an experimental farm and thus could not display the social patterns exhibited by their wild counterparts, we believe that our experiments are relevant for the testing of these predictions. Most of the male and female sheep studied differed substantially in their body mass, with males being 1.4-fold heavier than females. Both sexes also fed in the same pastures, thereby reducing the possible effects of different ecological factors met by females and males in the wild. By comparing single-sex and mixed-sex groups observed simultaneously, we measured the activity budget of individuals of the same sex and opposite sex and the synchrony within and between groups. These measures allowed us to test the extent to which individuals in the same and distinct groups actually engaged in different activities independently. They also provided us with the means to measure how activity synchronization or contagion operates between members of the same group.

Some of the yearling males participating in the experiments were lighter than their older counterparts and had a weight comparable to that of the females. Therefore, given the overall reduction of the difference in body mass between sexes due to yearlings, the results for the activity budget of males could have been biased – i.e. the activity budget of the males may have been found be more similar to that of the females than it is actually the case. We found greater differences between sexes with respect to the activity budget when yearlings were included than when they were excluded. In particular, yearlings tended to graze more than older males which may be explained by their energetic needs driven by body growth. When only the heaviest males were considered in the analysis were few differences found between sexes and group types.

Contrary to our expectation, we did not find significant differences between females and males for the time spent resting (inactive). When active, adult males and females did not differ in the time they allocated to feeding and resting. Males only tended to spend less time standing than females. The question of whether the lack of differences between sexes in activity budget is an effect of sex or body mass per se did not fall within the aim of the present investigation and remains unsolved. This question can only be answered by further experiments and statistical procedures. Although the sheep were grouped and grazed in the same pasture, we cannot be sure that males and females shared the same diet. Also, females may be more selective than males in their choice of food. However, the lack of sexual differences in the step and bite rate, which is considered to be an index of feeding selectivity (Ruckstuhl 1998; Mooring et al. 2003), is not in agreement with a presumed higher female selectivity. Females have been found to spend more time grazing and less time resting than males in unisex groups of bighorn sheep *Ovis canadensis* and ibex (Ruckstuhl 1998; Neuhaus and Ruckstuhl 2002). On the other hand, no differences have been found in the time budget of

males and females in black-tailed deer *Odocoileus hemionus*, muskoxen and desert bighorn sheep *O. c. mexicana* (Weckerly 1993; Côté et al. 1997; Mooring et al. 2003). Other contradictory results can be found in the literature on ungulates: in some cases males spend more time feeding than females while the opposite is true in other instances (see Ginnett and Demment 1997; Pérez-Barbería and Gordon 1998, 1999b). Further experiments on other ungulate species conducted in similar experimental conditions would be required to confirm the present results.

A comparison of the activity budget in mixed and single-sex groups revealed no significant interactions between sex and group type, indicating that the activities of males and females were similarly affected when they were in a mixed-sex group. In particular, both sexes spent slightly more time foraging and moving and less time being inactive than in single-sex groups. The longer time spent feeding in mixed-sex groups may be related to a lower bite rate. The similar bite rate between sexes in mixed-sex groups is in accordance with the results found in the Roosevelt elk *Cervus elaphus roosevelti* (Weckerly et al. 2001). However, male deer had lower cropping rates in single-sex than in mixed-sex groups while we found the opposite for merino males. The equivalent bite rate between sexes in mixed-sex and in unisex groups is also at variance with what has been observed in Soay sheep and ibex where females have significantly higher bite rates than males (Pérez-Barbería and Gordon 1999a; Neuhaus and Ruckstuhl 2002). Note that bite rate may greatly vary according to the type and height of the grass (see Orr et al. 1997; Pérez-Barbería and Gordon 1999a; Ruckstuhl et al. 2003). At present, we have no clear idea about the mechanisms implicated in the differences in activities between mixed-sex and unisex groups.

The level of between-group synchrony observed was close to zero, indicating that the timing of the activity of the sheep during the experiments involved mechanisms other than photoperiod timing or external synchronizing factors such as moving the animals before each trial. Maier and White (1998) reported similar results by comparing between-group and within-group synchrony in caribou (*Rangifer tarandus granti*). Our findings indicate a strong social effect mediated by visual contact on the activity of individuals in single-sex and mixed-sex groups, as revealed by high levels of within-group synchrony. This has already been found in groups of domestic and wild sheep as well as in muskoxen and red deer (Rook and Penning 1991; Côté et al. 1997; Conradt 1998b).

In contrast to what was found in bighorn sheep or red deer (Conradt 1998b; Ruckstuhl 1998) but in accordance with a study of Alpine ibex (Ruckstuhl and Neuhaus 2001), the activity synchrony in our animals was much higher in male than in female groups. This occurred despite the fact that females almost never engaged in play-like or agonistic-like interactions. These types of interactions were more frequent in male groups, suggesting that it is not a factor impairing synchrony. On the contrary, the observed social interactions may facilitate group synchronization. The question of why the synchrony differed between male and female groups remains unclear and needs further investigation. However, our results suggest that the inter-individual variability in the time spent resting was greater among females than males. A higher variability in the activity budget may weaken the degree of activity synchrony within groups containing females. Previous studies have reported lower activity synchrony in mixed-sex groups in several species (Conradt 1998b; Ruckstuhl 1998; Ruckstuhl and Neuhaus 2001). We have no clear indication that the activities of the males were more affected by the presence of the opposite sex than were the activities of the females, although the difference in activity synchrony between single-sex and mixed-sex groups tended to be larger in males. We also observed that the synchrony in mixed-sex pairs tended to be lower than in single-sex pairs. This suggests that activity synchronization is more difficult to achieve between individuals within mixed-sex groups although sexual differences in the activity budget tended to be smaller within mixed-sex groups than among single-sex groups. The interactions initiated by males towards females may be a factor contributing to the lower synchrony observed in mixed-sex groups.

Whether the difference in synchrony between individuals in mixed-sex groups and single-sex groups can by itself mediate group splitting in sheep is unclear. Conradt and Roper (2000) have suggested that the difference in synchronization may explain 35% of social segregation. Our study was not designed to assess the effect of asynchrony on group splitting. However, the difference in synchrony between female and mixed-sex groups is moderate, and it seems to be insufficient to induce splitting in mixed-sex groups of merino sheep (see Michelena et al. 2004). This does not mean that the activity budget hypothesis, or at least the assumption that increasing dimorphism in body mass is correlated with differences in activity budget, is unfounded. However, Yearsley and Javier Perez-Barberia (2005) concluded that the difference in the time spent active and the scale of dimorphism between sexes must be beyond the range found in current segregating ungulate populations to generate social segregation. On the other hand, if the difference in activity budget and synchrony is not high enough to induce group splitting on its own, it could be a contributing factor, together with other social (level of inter-sex attraction) or ecological factors (habitat patchiness) (Bon and Campan 1996). Sheep, in particular males, are very gregarious. The deficit of synchrony may be high enough to increase the splitting probability of mixed-sex groups in species where inter-sex attraction is lower than intra-sex attraction. Other behavioural differences – for example, in movement rate, speed or dispersal (Dubois et al. 1993; Bon et al. 2005) – could also be involved in group fission, even if movements represent a small part of the activity budget. Note also

that large differences in activity budget can be observed between individuals that are strongly associated, as occur in groups containing both young or sub-adults and females. This means that activity synchrony may be a factor of cohesion without being a necessary condition for individuals to remain in the same group. Our analyses should be extended by considering other parameters – for example the distance and orientation between individuals – to assess the characteristics and consequences of group composition on group dynamics.

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