Université de Sherbrooke, Département de biologie, Sherbrooke, Québec

Group Choice by Subadult Bighorn Rams: Trade-offs between Foraging Efficiency and Predator Avoidance

Kathreen E. Ruckstuhl & Marco Festa-Bianchet

Abstract

In addition to sexual segregation, many social ungulates show varying degrees of age segregation, especially among males. We investigated factors affecting group choice by subadult male bighorn sheep, using census data collected between 1982 and 1998 in a marked population. We examined whether group composition varied with population size and structure. Changes in total population size were correlated with the number of yearling males and yearling females, but not with the size of other sex-age classes. In years of high population size, female groups were larger than in years of low population size, while mixed sex-age and subadult groups showed a nonsignificant trend in the same direction. Typical group sizes of bachelor groups and the occurrence of mixed or bachelor groups were not affected by population size. When there were few subadult males in the population, groups of subadult males were less frequent than in years with many subadult males in the population, but the typical group size did not change. Subadult males were rarely seen in peer groups, and switched from female groups in spring to bachelor groups in autumn. An individual's choice of group type is affected by its body mass, but also by the availability of enough potential group mates to provide sufficient predator-detection efficiency.

Corresponding author: K. E. Ruckstuhl, Department of Zoology, LARG, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK. E-mail: kruckstuhl@hotmail.com

Introduction

Many animals form temporary groups when migrating, breeding or searching for food, while others live in fluid or stable groups all year round (Alexander 1974; Wrangham & Rubenstein 1986; Avery 1994; Christal et al. 1998). Predation risk is thought to be one of the selective pressures leading to

gregariousness (Hamilton 1971). Regardless of the reasons for group formation, to maintain cohesion, group members must synchronize behaviors (Jarman 1974; Rook & Penning 1991; Agesuma 1995). In sexually dimorphic ungulates, the sexes are often segregated outside the rut (Main et al. 1996), but young males usually stay in female groups for one to several years before they switch to adult male groups (known as bachelor groups) (Festa-Bianchet 1991). In female groups, young males may enjoy reduced predation risk (detection and dilution effects; Dehn 1990), but they may also face a trade-off between behaving according to the optimal time budget for their body size and the need to be synchronous with the rest of the group. Young growing animals may need more food than adults to complete body growth (Robbins 1993), and foraging behavior that maximizes body growth may only be optimized in groups composed of same sex and age peers (Ruckstuhl 1999), therefore, subadult males may form subadult groups. Groups of subadult males have been reported in chamois (*Rupicapra rupicapra*) (Krämer 1969), ibex (*Capra ibex*) (Villaret & Bon 1995), and mouflon (*Ovis gmelini*) (Bon et al. 1993; Cransac et al. 1998). In these species, the formation of subadult male groups was not caused by eviction from female groups by territorial, harem-holding males, as was observed in impala (*Aepyceros melampus*) (Estes 1991). Subadult males appeared to prefer the company of other young males, and freely left and rejoined whichever groups they chose (Cransac et al. 1998). Young impala females were also reported to prefer to form peer groups (Murray 1981). Social preference may therefore be established early in life and persists into adulthood (Bon 1991; Bon & Campan 1996; Villaret & Bon 1998). What drives this preference for peer groups is largely unknown. While Villaret & Bon (1998) interpreted social preferences in young males as a means to practice fighting skills, establish dominance hierarchies and increase social bonding, Ruckstuhl (1999) argued that specific sex–age groups form because sex–age peers have similar optimal activity patterns. Synchrony in peer groups would therefore be facilitated compared with mixed groups (Ruckstuhl 1999). In sexually dimorphic ungulates, young males are larger than adult females but smaller than adult males (Festa-Bianchet et al. 1996; Cransac & Hewison 1997). Because body mass affects foraging behavior of ruminants (Mysterud 1998), young males may optimize their foraging behavior, particularly the duration of bouts of feeding and ruminating, by forming peer groups.

Group choice, however, is unlikely to depend only upon foraging efficiency. Predator avoidance may increase with group size: Risenhoover & Bailey (1985a, b) found that in mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*), a minimum group size of five was required to significantly decrease vigilance and increase individual feeding rate. Feeding rate seemed highest and vigilance lowest in groups of 20 individuals. Therefore, in small populations the need to reduce predation risk by forming large groups may override the need to optimize foraging behavior by forming peer groups. In some cases there may simply not be enough peers in the population to form a group. Consequently, both a population's size and its sex–age composition may affect the occurrence of different types of groups.

We investigated whether or not the number of subadult males in a population affects the occurrence of subadult male groups, and examined how group choice by subadults varied according to season and population size. The study animals were Rocky Mountain bighorn sheep in a population whose size and sex–age composition varied widely over time, because of changes in disease prevalence and predation pressure. Males and females were segregated outside the rut (Ruckstuhl 1998). Ruckstuhl (1999) found that males aged 2 and 3 yr switched among bachelor and female groups, synchronizing their activity with other group members and therefore possibly paying a cost when in groups that did not share their optimal time budget.

Because predator detection and dilution effects increase with group size, we predicted that subadult males, adult males and females would form groups of their own only when they were sufficiently numerous in the population, otherwise they would form mixed age and sex groups. Neither intra- nor inter-sexual aggression influence group choice in bighorn sheep (Geist 1971). The lack of density-dependence in population dynamics (Festa-Bianchet et al. 1998) suggests that food was not limited in our study population, therefore we did not expect that competition would affect group formation.

Methods

Habitat and Study Species

The Sheep River Wildlife Sanctuary lies in the foothills of the Rocky Mountains in south-western Alberta (50°N, 114°W; elevation 1420–1740 m). It includes open south-facing slopes and grassy meadows, intermixed with aspen (*Populus tremuloides*) copses and coniferous forest (Boag & Wishart 1982). Since 1981, almost all bighorn sheep have been individually marked with plastic ear tags (Festa-Bianchet 1991). Females and males used the same foraging areas in the sanctuary (Ruckstuhl & Festa-Bianchet 1998). Bighorn sheep made some use of the wildlife sanctuary year-round, although ewes migrated to alpine areas about 12 km to the west in May to lamb. Ewes were in alpine areas most of the time until late summer (Festa-Bianchet 1986a; Ruckstuhl & Festa-Bianchet 1998). Rams often used low foothill areas east of the sanctuary (Ruckstuhl 1998).

To sample group composition, the sanctuary (53 km^2) was censused once per week from Apr. to Oct. The locations, time of day, ID, age, and sex of each sheep seen were noted. Census efficiency in the sanctuary was very high, for example in winter we found, on average, 97% of the marked ewes during each census (Festa-Bianchet 1986b). From weekly censuses we knew how many individuals of a given sex–age class were in the population during a given month or year. We considered four group types: (1) females with lambs, yearlings, and with or without subadult males; (2) subadult males (2–3 yr-old-males); (3) mixed-sex-age; and (4) bachelor groups (adult male groups with or without subadult males). Lambs remained with their mothers until Nov. or later and were not included in the analysis. Solitary

sheep were also noted. The same individuals were observed repeatedly, in different or in the same groups. Many sheep were seen once a week throughout most of the Apr.–Oct. period. Although some of our analyses are affected by pseudo-replication (Machlis et al. 1985; Leger & Didrichsons 1994), in most cases we used yearly averages for statistical comparisons. Because we were interested in the ontogeny of individual behavior with age, we deliberately made repeated observations of the same individuals.

Data Analyses

We limited our analyses to weekly censuses performed in spring (Apr. and May, just before lambing) and fall (Sep. and Oct., just before weaning of lambs), when most sheep were in the Wildlife Sanctuary (Festa-Bianchet 1986a; Festa-Bianchet 1986b), in 1982–87 and 1994–98. Females were considered adult at 2 yr old and males from the age of 4 yr. Females achieve about 85% of asymptotic mass and can have lambs as 2 yr-olds, while males do not reach 85% of asymptotic mass until 4 yr old (Festa-Bianchet et al. 1996).

In mid-Sep. in the Ram Mountain population, about 200 km north of Sheep River, 3-yr-old males weigh about 86 kg, 15 kg more than the average adult female but about 20 kg less than adult (5 + yr) males (Festa-Bianchet et al. 1996). The years 1988–93 were omitted from most analyses because sheep were not censused every week, but were included in analyses of correlation between population size and the sizes of different age–sex classes (Tables 1 and 2). Non-parametric statistics were used when data were either not normally distributed or

Table 1: Population size and number of adult males, females and subadults present in the Sheep River Wildlife Sanctuary from 1982 to 1998[a]

Year	Males	Females	3YM	2YM	1YM	1YF	SUBM	TOTP	POPS
1982	32	49	1	10	9	8	11	140	High
1983	28	48	3	9	9	8	21	144	High
1984	24	50	11	9	13	10	20	147	High
1985	43	53	0	4	10	5	4	153	High
1986	31	49	0	5	2	3	5	107	Low
1987	29	46	4	1	3	6	5	99	Low
1988	26	44	2	3	8	5	5	99	Low
1990	19	50	3	7	14	6	10	118	High
1991	15	54	9	5	15	7	14	118	High
1994	23	41	7	2	3	3	9	97	Low
1995	27	42	7	2	4	6	9	95	Low
1996	31	40	3	2	4	4	5	93	Low
1997	22	39	10	3	5	10	13	98	Low
1998	30	38	4	4	12	8	8	110	High

[a] 3YM = 3-yr-old males, 2YM = 2-yr-old males, 1YM = yearling males, 1YF = yearling females, SUBM = subadult (2–3 years-old) males, TOTP = total population size, POPS = population size.

Table 2: Correlation of yearly population size and the size of different sex–age classes of bighorn sheep at Sheep River 1982–98. n1 = 7 low density years and n2 = 7 high density years (see Table 1 (POPS and TOTP)). Significant p-values are given in italics

Sex-age-class	Auto-correlation coefficient	Correlation coefficient (Spearman)	p
Yearling females	0.11	0.56	*<0.05*
Yearling males	0.30	0.77	*<0.001*
2-year-old males	0.06	0.39	0.16
3-year-old males	−0.06	0.12	0.68
Adult females	0.19	0.20	0.48
Adult males	0.15	0.05	0.88

sample size was small. The occurrence of each group type was calculated as the percentage of observations of that group type over the total of all groups observed in a year. In the results we report the occurrence of different sex–age groups, but for statistical analyses the data were standardized to remove year effects. The standardized frequency of each group type for year (i) was $Sf_i = ((x_i - x)/sd_x)$, where x_i is the total frequency of a particular group type in year i; x is the average frequency of that group of all years, and sd_x is the standard deviation of the frequency of a group type in year i.

The effect of population size on the proportion of different group types and of typical group sizes (Jarman 1982) was analysed using Mann–Whitney U-tests (Siegel & Castellan 1988). We also used U-tests to determine whether yearly changes in size of a given sex–age class affected the frequency of occurrence of different group types.

Because 95–100% of the study animals were marked, each year we knew the total number of sheep and the size of each sex–age class (Table 1). We divided the study period into years of high and low population size according to whether the number of sheep was more or less than the average for all years. The number of individuals/year belonging to each sex-age-class was also classified as high or low, depending on whether it was above or below the average for all years.

We tested for a correlation between total population size and the size of different sex–age classes using Spearman rank correlation coefficients over the year of the study (Siegel & Castellan 1988). If necessary, variables were standardized and auto-correlation of temporal data evaluated using SPSS (Norusis 1993). Animal-centered group size (or typical group size) is a better measure than average group size of the social environment experienced by the average individual (Jarman 1982). For example, if 99 individuals were together and one was solitary, the average group size would be 50, but almost all individuals would experience a large group size. Typical group sizes were calculated for each group type as:

$$\bar{g} = \sum_{i=1}^{N} g_i^2 \Big/ \sum_{i=1}^{N} g_i$$

where $\bar{g}$ = typical group size, and g_i = group size of ith group.

We tested the effect of the total number of sheep on typical group sizes within each group type with a Kruskal–Wallis test (Siegel & Castellan 1988). To test whether subadults showed a preference for a specific group type depending on season and population size, we divided the number of groups including subadults by the average number of subadults present in these groups. We therefore calculated the relative number of subadults/group instead of the absolute number, because the number of subadults varied greatly between years. We then tested any differences in preference according to population size with a Kruskal–Wallis test and preference depending on season with Mann–Whitney U-tests. Multiple comparisons of nonparametric data were done using U-tests with Bonferroni-adjusted p-values. Medians are given with minima, maxima and 95% confidence intervals (CI). Unless otherwise stated, sample sizes (yearly averages) of five vs. six for high- and low-density years are compared.

Results

Solitary Sheep

Solitary sheep were rare (104 out of 3104 observations). There was no difference in the proportion of solitary sheep in years of high (median $= 7.5\%$, min. $= 3.6\%$, max. $= 9.8\%$, CI $= 4.0$–10.2%, n $= 5$ yr) or low (median $= 7.7\%$, min. $= 4.0\%$, max. $= 14.5\%$, CI $= 4.4$–13.3%, n $= 6$ yr) population size (Mann–Whitney U $= 20$, p $= 0.56$). A median of eight (min. $= 1$, max. $= 18$, CI $= 2$–14) solitary sheep/census yr were observed when population size was low and eight (min. $= 6$, max. $= 17$, CI $= 5$–17) when it was high. On average, solitary sheep joined a group within 1 ± 1 d of when they were first sighted alone. Focal animal observations (Ruckstuhl 1998) revealed that 90% of all solitary sheep seen were in the process of switching from one group to another within the same day.

Dynamics of Group Formation

We censused 1256 groups during years of low population size and 1734 groups in years of high population size. The total number of sheep in the population each year was correlated with the number of yearling males and yearling females, but not with the number of individuals of any other sex–age class (Table 2).

Population size did not affect the occurrence of subadult male groups (U $= 20$, p $= 0.56$, test on standardized frequencies; years of low population size, median $= 2.6\%$, min. $= 0\%$, max. $= 3.3\%$, CI $= 0.66$–3.44%, n $= 5$; years of high population size, median $= 3.7\%$, min. $= 0.7\%$, max. $= 8.3\%$, CI $= 0.81$–7.87%, n $= 6$). There were no more subadult males present in years of low than of high population size (U $= 13$, p $= 0.16$, Table 1). However, we saw more subadult male groups in years with many subadult males than in years with few subadult males (U $= 4$, p < 0.05) (Fig. 1). Subadult males were seen much more often in
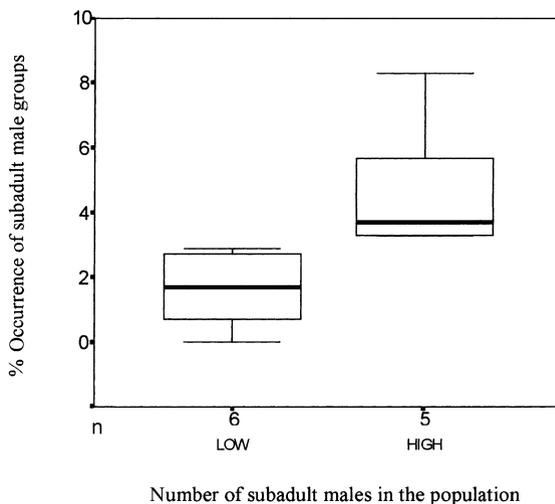
Fig. 1: The per cent occurrence of groups of subadult male bighorn sheep in year with low or high numbers of 2-yr-old males in the Sheep River population; n = number of years. The number of 2-year-old males in the population is reported in Table 1. The median, minimum, maximum and interquartile range are shown

female (44.6 ± 10.2% of all observations of groups with subadult males, n = 271) or bachelor groups (45.7 + 7.3% of all observations, n = 280) than in groups of their own (6.4 ± 5.6% of all observations, n = 38) (Kruskal–Wallis $\chi^2 = 21.36$, p < 0.001).

There were more subadult males in bachelor groups than in female groups in spring and autumn (Table 3). Hence, subadult males were seen much more often in male than in female groups ($\chi^2 = 10.61$, p < 0.001).

Subadult males generally switched from adult female to bachelor groups from spring to autumn (Table 3). There were more subadult males in male groups

Table 3: Sightings of subadult males and mean number seen in either male or female group in spring or autumn (1982–87 and 1994–98). The number of groups observed is reported in brackets

	Sightings of subadult males		Mean number in group in spring[a]	Mean number group in autumn
	Spring	Autumn		
Female groups	367 (151)	280 (120)	2.43 ± 0.14	2.33 ± 0.14
Bachelor groups	427 (126)	457 (154)	3.39 ± 0.25	2.97 ± 0.16
Total/statistics	794 (277)	737 (274)	Z = −2.64, p < 0.01	Z = −2.63, p < 0.01

[a] Z = Mann–Whitney U-test value for the comparison of mean numbers of subadults in female or male groups.

Table 4: Mean number of subadult bighorn sheep males observed in male or female group in spring and autumn of 1982–87 and 1994–98. Years were ranked as either high or low population size according to whether the total number of sheep in the population was more or less than the long-term average. Number in brackets represent the number of groups observed

	Spring	Autumn
Female groups at high population size	2.04 ± 0.41 (26)	1.64 ± 0.15 (45)
Male groups at high population size	4.91 ± 0.54 (46)	3.42 ± 0.30 (62)
Female groups at low population size	2.51 ± 0.41 (125)	2.75 ± 0.18 (75)
Male groups at low population size	2.51 ± 0.19 (80)	2.67 ± 0.17 (92)

Table 5: Typical group size for bighorn sheep in different group types in years of high and low population size at Sheep River. The p-values showing significant differences between high- and low-density years are given in italics; n = number of groups

Group type	Low density	High density	Z	p	n
Female	23.0 ± 2.8	39.1 ± 4.9	−2.24	p < 0.05	767
Subadult male	3.8 ± 1.0	6.2 ± 0.6	−1.66	p = 0.09	38
Mixed sex-age	44.3 ± 6.6	57.2 ± 5.5	−1.74	p = 0.08	145
Bachelor	14.2 ± 1.6	12.9 ± 2.2	−0.46	p = 0.67	387

than in female groups in years of high population size (U = 252.5, p < 0.001 for spring, U = 652.5, p < 0.001 for fall), but not in years of low population size (U = 4911, p = 0.82 in spring, U = 3321.5 p = 0.67 in the autumn) (Table 4).

There was no difference in the occurrence of female groups in years of high or low population size (U = 14, p = 0.25; high population median = 63.8%, min. = 49.2%, max. = 65.7%, CI = 50.3–68.5%, n = 5; low population median = 51.3%, min. = 42.1%, max. = 64.1%, CI = 41.9–62.6%, n = 6). Contrary to our expectations, mixed groups were no more common at low than at high population size (U = 10, p = 0.43). Mixed groups accounted for 11.2 ± 2.3% of all sightings in low-density years and 8.6 ± 0.4% in high-density years.

Typical group sizes of bachelor groups did not differ according to population size, while subadult or mixed groups tended (nonsignificantly) to be larger in years of high than of low population size (Table 5). The typical size of female groups was larger in years of high population than in years of low population (Table 5).

Discussion

The goal of this study was to determine how group choice by subadult bighorn males is affected by population size and by the availability of potential group mates. Our study confirmed that Rocky Mountain bighorn sheep are very gregarious: the very small number of solitary individuals observed did not depend on population size and most solitary sheep were moving from one group to

another. In contrast, desert bighorn sheep in the south-western USA are often alone or in groups of two or three, although groups of nine are most common (Monson & Sumner 1980). Such small group sizes likely reflect the sparse distribution of food in desert habitats and were uncommon in our study population.

We predicted that in years with high sheep numbers, sheep would not only segregate by sex but also by age. Bon (1991) argued that subadult males of sexually dimorphic ungulates prefer peer groups because there they can practice fighting skills and establish dominance hierarchies, which are important determinants of reproductive success. Geist (1968) showed that bighorn sheep females and subadults tend to interact with sheep of similar body size and Ruckstuhl (1999) suggested that individuals of similar body size may form groups of their own to optimize time budgets and foraging efficiency. Social preferences and differences in optimal time budgets, however, are not the only criteria affecting group selection by large herbivorous mammals: increased protection from predators appears to be the main reason for gregariousness (Hamilton 1971; Dehn 1990). It is therefore likely that different, sometimes conflicting, factors affect group choice in ungulates. Group membership in bighorn sheep is fluid and depends on the number of individuals within a given sex–age class as well as on the total number of sheep in the population. Changes in population size and composition during our study had a variety of causes, including a pneumonia epizootic in 1985–86 (Festa-Bianchet 1988) and cougar (*Puma concolor*) predation, mostly on females and lambs, in 1993–95 (Ross et al. 1997). In addition, levels of legal and illegal hunting (affecting almost exclusively adult males) varied widely among the year of the study. As a result, temporal changes in population size were not uniform among sex–age classes, giving us the opportunity to compare group dynamics with changes in overall population size as well as with changes in sex–age composition of the population.

As expected, groups of subadult males were larger and more common in years when many subadult males were present in the population, and smaller in years with few subadult males. Hence, the social tendency of young bighorn males is similar to that of young male ibex and mouflon (Bon & Campan 1989; Bon et al. 1993; Villaret & Bon 1995; Villaret & Bon 1998).

Subadult male groups, however, were rare. Subadult males were most often in either female or bachelor groups. The small number of subadult males could explain why subadult male groups were rare and ephemeral. Possibly, in most years there were not enough subadult males to form groups of sufficient size to provide adequate antipredator protection. Subadult males may chose safety over social preferences and optimal time budgets (Ruckstuhl 1999).

Risenhoover & Bailey (1985a) suggested that individual antipredator behaviors in bighorn sheep decline considerably as group size increased from one to 20, and that vigilance was lowest and feeding rate highest in groups of 20 or more sheep. Our study population included 20 subadult males only in 1984 (Table 1).

Subadult males increasingly preferred bachelor groups to female groups from spring to autumn, supporting the hypothesis that group choice may be affected by body size (Ruckstuhl 1998; Ruckstuhl 1999). As summer progresses, young males, particularly 3-yr-olds, become progressively larger than adult females (Festa-Bianchet et al. 1996). Two-year-old males, which are similar in body size to females, switched frequently between male and female groups but were more often with females in summer (Ruckstuhl 1998).

As population size increased, adult females formed larger groups rather than forming more groups of a similar size, while the number of rams in bachelor groups was unrelated to total population size. Females may prefer to form larger groups when numerous, or individual females still join a group even though it exceeds an optimal size (Ranta 1993; Rannala & Brown 1994; Parrish & Edelstein-Keshet 1999). Alternatively, there may be little difference in the fitness consequences of groups of 20 or of 60 animals (the largest groups observed in the study population). Typical group size of mixed sex-age groups tended to be larger in high population size years than in low population size years, possibly because there were more females in mixed groups. Mixed groups are unstable and often result from males joining a group of females to test female reproductive status. Therefore, mixed groups may be driven by male reproductive strategy rather than by foraging or antipredator behavior. Mixed groups mainly form during the pre-rut period (Geist 1971). Adult males and females are segregated for most of the nonbreeding period (Ruckstuhl 1998).

Our study shows that group choice in bighorn sheep is affected by the sex and age of each sheep but also by the sex–age composition of the population. To understand mammalian sociality, we must take into account changes in population size and structure. To uncover such trends in large mammals, long-term monitoring and individual identification are necessary.

There are different potential costs of grouping, such as having to synchronize activities with other group members or foregoing antipredator protection to stay in a small peer group. We predict that a more complex social structure, with a considerable level of age segregation, in addition to sex segregation, will be found in ungulate populations that are larger than the one we studied, or that are subject to a much lower degree of predation risk.

Acknowledgements

Literature Cited

Agesuma, N. 1995: Foraging synchrony in a group of Yakushima Macaques (*Macaca fuscata yakui*). Folia Primatol. **64**, 167—179.

Alexander, R. D. 1974: The evolution of social behaviour. Annu. Rev. Ecol. Syst. **5**, 325—383.

Avery, M. L. 1994: Finding good food and avoiding bad food: does it help to associate with experienced flockmates? Anim. Behav. **48**, 1371—1378.

Boag, D. A. & Wishart, W. D. 1982: Distribution and abundance of terrestrial gastropods on a winter range of bighorn sheep in southwestern Alberta. Can. J. Zool. **60**, 2633—2640.

Bon, R. 1991: Social and spatial segregation of males and females in polygamous ungulates: proximate factors. Ongulé/Ungulates **1**, 195—198.

Bon, R. & Campan, R. 1989: Social tendencies of the Corsican mouflon (*Ovis ammon musimon*) in the Caroux-Espinouse Massif (south of France). Behav. Process. **19**, 57—78.

Bon, R. & Campan, R. 1996: Unexplained sexual segregation in polygamous ungulates: a defense of an ontogenetic approach. Behav. Proc. **38**, 131—154.

Bon, R., Dubois, M. & Maublanc, M. L. 1993: Does age influence between-rams companionship in mouflon (*Ovis gmelini*)? Rev. Ecol. Terre Vie **48**, 57—64.

Christal, J., Whitehead, H. & Lettevall, E. 1998: Sperm whale social units: variation and change. Can. J. Zool. **76**, 1431—1440.

Cransac, N. & Hewison, A. J. M. 1997: Seasonal use and selection of habitat by mouflon (*Ovis gmelini*): comparison of the sexes. Behav. Proc. **41**, 57—67.

Cransac, N., Gerard, J.-F., Maublanc, M.-L. & Pépin, D. 1998: An example of segregation between age and sex classes only weakly related to habitat use in mouflon sheep (*Ovis gmelini*). J. Zool. Lond. **244**, 371—378.

Dehn, M. M. 1990: Vigilance for predators: detection and dilution effects. Behav. Ecol. Sociobiol. **26**, 337—342.

Estes, R. D. 1991: The Behavior Guide to African Mammals. Including Hoofed Mammals, Carnivores, Primates. Univ. of California Press, Berkley.

Festa-Bianchet, M. 1986a: Seasonal dispersion of overlapping mountain sheep ewe groups. J. Wildl. Manage. **50**, 325—330.

Festa-Bianchet, M. 1986b: Site fidelity and seasonal range use by bighorn rams. Can. J. Zool. **64**, 2126—2132.

Festa-Bianchet, M. 1988: A pneumonia epizootic in bighorn sheep, with comments on preventive management. Bienn. Symp. N. Wild. Sheep Goat Counc. **6**, 66—76.

Festa-Bianchet, M. 1991: The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Anim. Behav. **42**, 71—82.

Festa-Bianchet, M., Jorgenson, J. T., King, W. J., Smith, K. G. & Wishart, W. D. 1996: The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. Can. J. Zool. **76**, 330—342.

Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J. T. 1998: Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. Am. Nat. **152**, 367—379.

Geist, V. 1968: On the interrelation of external appearance, social behaviour and social structure of mountain sheep. Z. Tierpsychol. **25**, 199—215.

Geist, V. 1971: Mountain Sheep. A Study in Behaviour and Evolution. Univ. of Chicago Press, Chicago.

Hamilton, W. D. 1971: Geometry for the selfish herd. J. Theor. Biol. **31**, 295—311.

Jarman, P. 1982: Prospects for interspecific comparison in sociobiology. In: Current Problems in Sociobiology (King's College Sociobiology Group, eds). Cambridge Univ. Press, Cambridge, pp. 323—342.

Jarman, P. J. 1974: The social organisation of antelope in relation to their ecology. Behaviour **48**, 215—267.

Krämer, A. 1969: Soziale Organisation und Sozialverhalten einer Gemspopulation (*Rupicapra rupicapra*) der Alpen. Z. Tierpsychol. **26**, 889—964.

Leger, D. W. & Didrichsons, I. A. 1994: An assessment of data pooling and some alternatives. Anim. Behav. **48,** 823—832.

Machlis, L., Dodd, P. W. D., Fentress, R. & Fentress, J. C. 1985: The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z. Tierpsychol. **68,** 201—214.

Main, M. B., Weckerly, F. W. & Bleich, V. C. 1996: Sexual segregation in ungulates: new directions for research. J. Mammal. **77,** 449—461.

Mysterud, A. 1998: The relative roles of body size and feeding type on activity time of temperate ruminants. Oecologia **113,** 442—446.

Monson, G. & Sumner, L. 1980: The Desert Bighorn. Its Life History, Ecology and Management. Univ. of Arizona Press, Tucson.

Murray, M. G. 1981: Structure of association in impala, *Aepyceros melampus.* Behav. Ecol. Sociobiol. **9,** 23—33.

Norusis, M. J. 1993: SPSS for Windows. SPSS Inc., Chicago.

Parrish, J. K. & Edelstein-Keshet 1999: Complexity, pattern, and evolutionary trade-offs in animal aggregation. Science **284,** 99—101.

Rannala, B. H. & Brown, C. R. 1994: Relatedness and conflict over optimal group size. TREE **9,** 117—119.

Ranta, E. 1993: There is no optimal foraging group size. Anim. Behav. **46,** 1032—1035.

Risenhoover, K. L. & Bailey, J. A. 1985a: Foraging ecology of mountain sheep: implications for habitat management. J.Wildl. Manage. **49,** 797—804.

Risenhoover, K. L. & Bailey, J. A. 1985b: Relationships between group size, feeding time, and agonistic behavior of mountain goats. Can. J. Zool. **63,** 2501—2506.

Robbins, C. T. 1993: Wildlife Feeding and Nutrition, 2nd edn. Academic Press, New York.

Rook, A. J. & Penning, P. D. 1991: Synchronisation of eating, ruminating and idling activity by grazing sheep. Appl. Anim. Behav. Sci. **32,** 157—166.

Ross, P. I. Jalkotzy, M. G. & Festa-Bianchet, M. 1997: Cougar predation on bighorn sheep in southwestern Alberta during winter. Can. J. Zool. **74,** 771—775.

Ruckstuhl, K. E. 1999: To synchronise or not to synchronise: a dilemma in young bighorn males? Behaviour **136,** 805—818.

Ruckstuhl, K. E. 1998: Foraging behaviour and sexual segregation in bighorn sheep. Anim. Behav. **56,** 99—106.

Ruckstuhl, K. E. & Festa-Bianchet, M. 1998: Do reproductive status and lamb gender affect the foraging behavior of bighorn ewes? Ethology **104,** 941—954.

Siegel, S. & Castellan, N. J. 1988: Nonparametric Statistics for the Behavioral Sciences, 2nd edn. McGraw-Hill, Inc. New York.

Villaret, J. C. & Bon, R. 1995: Social and spatial segregation in Alpine Ibex (*Capra ibex*) in Bargy, French Alps. Ethology. **101,** 291—300.

Villaret, J.-C. & Bon, R. 1998: Sociality and relationships in Alpine ibex (*Capra ibex*). Rev. Ecol. Terre Vie **53,** 153—170.

Wrangham, R. W. & Rubenstein, D. I. 1986: Social evolution in birds and mammals. In: Ecological Aspects of Social Evolution in Birds and Mammals (Rubenstein D. J. & Wrangham, R. W., eds). Princeton Univ. Press, Princeton, pp. 452—471.