

## Reproductive parameters, kidney fat index, and grazing activity relationships between the sexes in Cantabrian chamois *Rupicapra pyrenaica parva*

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Reproductive parameters, kidney fat index and grazing activity of both sexes of Cantabrian chamois *Rupicapra pyrenaica parva* (Cabrera, 1910) in relation to age, season and year are presented and compared with those of other chamois subspecies and cervids. Females younger than three years old had not ovulated. Ovulated ovaries were significantly heavier than non-ovulated ovaries in March–April, and these differences remained until the following rutting season. All pregnant females carried a single foetus. A significant decrease in the percentage of parous females was found in 3–11 years age class (94%) compared with > 11 years (50%). There were no differences in the kidney fat index (KFI) between age classes for either of the sexes throughout the study period. Females showed a significant higher KFI in August–October 1993 than in August–October 1992, coinciding with a significantly greater abundance of grass in 1993. Throughout the year KFI in females showed less fluctuations than in males. Males began the rutting season with a significant KFI three times higher than did females. However, by the spring, the KFI of the males had fallen to half of that of the females. In March–April pregnant females showed a significantly higher KFI than non-pregnant or late-conception adult females. Feeding activity of females and sward height throughout the year were inversely related. Females grazed more actively than males in the summer, rut and spring, except in winter where no differences in feeding activity between sexes were found. The differences in the KFI and feeding activity are discussed in relation to the parental investment and the sexual dimorphism-body size theory.

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*Key words:* *Rupicapra pyrenaica parva*, body condition, reproductive parameters, fecundity, age, grazing activity

### Introduction

The study of temporal variation in physiological condition allows an understanding of the animals adaptation to its environment (Riney 1982). For example, the response of both sexes to environmental change can be different (Anderson *et*

*al.* 1972, Mitchell *et al.* 1976, Medin and Anderson 1979) and this influences the mortality rate (Clutton-Brock *et al.* 1982). In polygynous ungulates in which sexual body weight differences can exceed 30% (Nowak 1991), differences in habitat and food resources used have been explained by physiological responses of both sexes which are related to body size (Demment 1982, Illius and Gordon 1987, Beier and McCullough 1990, Main *et al.* 1996). Additionally, the response to the environment can vary between age classes (Houssin *et al.* 1993), reproductive status (Mitchell *et al.* 1976, Clutton-Brock 1982, Huot 1989), individuals (Dusek 1987), or can reflect seasonal, annual and geographical differences (Mitchell *et al.* 1976, Medin and Anderson 1979, Dusek 1987, Sæther and Gravem 1988, Storch 1989).

Cantabrian chamois *Rupicapra pyrenaica parva* (Cabrera, 1910) is a subspecies present at the western part of the distribution area for the genus (Cantabrian mountains, northern Spain), where it constitutes an isolated population. The most recent population size estimation was carried out in 1995 with densities comprised of between 2.1–22.4 animals/km<sup>2</sup>, the figures are: 12,400 individuals in the Cantabrian East range (Asturias 7300, León 4500 and Cantabria 600), 1000 individuals in the Cantabrian West range (Somiedo, Quirós and Lena districts), and some small and scattered populations in Los Ancares leoneses and Muniellos districts, with approximately 200 individuals. Presently the population size is decreasing due to outbreak of scabies (unpublished reports from Principado de Asturias, Junta de Castilla y León, y Cantabria). Although the management regulations are different among provinces, the hunting harvest varies from 5–10% per annum in the different areas. The Cantabrian chamois selects areas with cliffs and very steep slopes with different aspects, subalpine meadows, general habitat diversity and isolation (Pérez-Barbería 1994a). Throughout the year chamois make seasonal altitudinal displacements conditioned by snow fall, these displacements are short planimetric distances (1–2 km) because the steep slopes of the Cantabrian mountains offer a wide altitudinal range throughout all of its landscape. In summer chamois occupy open mountain areas (mainly above 1000 m) out of the range of other ungulates (red deer, roe deer), and only occasionally do they share their habitat with livestock (goats, cattle and horses), although they seldom graze together (Pérez-Barbería 1994a). Although the Cantabrian chamois is a popular game species, published information on reproductive parameters and body condition is not available.

In this study we aim to explore, (i) descriptive features of luteal structures, uterus weight and its morphology, to give basic lines to assess the female reproductive status (pregnant and non-pregnant, nulliparous and parous) using uterus and ovaries, (ii) relationships between kidney fat index, sex, age and reproductive status, and (iii) development of kidney fat index throughout the year and between years in relation to the sward height and grazing activity. This information is discussed on data reported for other chamois subspecies and cervids.

## Material and methods

### Study area and sampling

During 1992 and 1993, 194 Cantabrian chamois (1992: 76 females and 31 males; 1993: 39 females and 11 males and 37 samples with some missing information) were collected from sport hunting and management culls in the Cantabrian Mountains (Asturias, northern Spain, details about the study area can be found in Pérez-Barbería *et al.* 1996a). Material collected from animals which died naturally provided some additional data. Sex and age were recorded for each individual, and jaws, kidneys and perinephric fat, uterus, foetuses and ovaries were collected. However, some samples presented unknown culling month or inaccurate age estimation, moreover in some animals the shot damaged uterus, ovaries or kidneys, therefore the sample size varies throughout the different analyses in this study.

### Age estimation and kidney fat index

Age was estimated either by counting horn growth segments (Pérez-Barbería *et al.* 1996b), using cementum growth lines of the first permanent incisor (Pérez-Barbería and Fernández-López 1996) or with jaw tooth-row eruption and wear methods (Pérez-Barbería 1994b, Pérez-Barbería and Mutuberria 1996) depending on the type of sample available. For the kidney fat index (KFI) the ages were pooled into three age classes, 2–6, 7–11 and > 11 years.

KFI was estimated using a modification of the Riney index (Anderson *et al.* 1972, Thomas *et al.* 1989, Holand 1992), which uses the pooled weight of two kidneys ( $K$ ) and the pooled weight of the perinephric fat ( $P$ ), where  $KFI = 100P/K$ . The tunica fibrosa was included in the weight of the kidney. Using KFI with the pooled weight of both kidneys compensates for differences between the weight of the two kidneys and their perinephric fat (Anderson *et al.* 1972). When a kidney was missing or damaged, KFI was calculated with the available kidney. Kidney weight is introduced in the KFI in order to place animals of different sizes on a comparable basis (Riney 1982). However, Batcheler and Clarke (1970) and Dauphiné (1975) pointed out that kidney weight varied with season thus distorting the KFI. In our data set differences in kidney weight (ie mean of both kidneys) were not found between the sampling periods for either sex ( $p = 0.476$ ,  $p = 0.204$ , females and males respectively), therefore we have considered KFI without adjustment between periods, as suggested by Dauphiné (1975).

### Reproduction measurements

Females culled between March–April were judged parous if a foetus was present or the ovaries contained corpora lutea. In this period presence of corpora lutea (CL) in absence of a foetus indicated a recent abortion. Females collected between August and October were considered to have been parous in the previous calving season if a corpus rubrum (CR) was present (Langvatn 1992a). Prior to May (ie calving season), non-parous females were characterised by the absence of foetuses or corpora lutea. After the calving season, non-parous females were characterised by the absence of corpora rubra. Reproductive cycles that occurred earlier than the previous calving season were not considered. Ovaries were fixed in formalin and sliced sagittally into approximately 1 mm sections for macroscopic examination (Langvatn 1992a). Although macroscopic examination does not allow accurate identification of all ovarian structures, it can be used to detect corpora lutea and corpora rubra associated with parturition during the preceding 5–6 months in red deer (Langvatn 1992a), mule deer – *Odocoileus hemionus* (Medin and Anderson 1979) and Cantabrian chamois (Rolf Langvatn pers. comm.). The ovaries and the uterus were weighed ( $\pm 0.1$  g) separately prior to fixation. The uterus was removed from each female, separated from the vagina at the cervix and dissected longitudinally to check for the presence of foetuses. The texture, colour and thickness of the uterus wall from non-pregnant females was examined in order to assess the reproductive status (parous or nulliparous).

### Food availability

To compare the abundance of grass between 1992 and 1993, the sward height (Illius 1986) on six fenced areas (between 5–20 ha) situated in Quirós area (Cantabrian Mountains, altitude 1700 m) in the altitude range occupied by the chamois was used. Sward height measurements were made at the end of June, before the plots were grazed by livestock. The mean height of grass in each plot was calculated from 80 sample points using a sward stick. Although these values only show the abundance of grass at the end of June, we consider them valuable indices to compare annual changes in the abundance of grass, since they were highly correlated with mean annual values of sward height, calculated bi-monthly throughout the year, in other lower altitude ranges in Asturias ( $r_p = 0.89$ ,  $n = 6$ ,  $p = 0.018$ ). To analyse the changes of grass abundance throughout the year, sward height was recorded monthly (from March 1993 to March 1994) in three plots (between 105 and 500 m<sup>2</sup>, altitude range 1540–1640 m) situated in the middle of the Cantabrian chamois distribution range (Caso, Asturias). The mean sward height in each plot was estimated using between 36 and 170 sample points.

### Grazing activity

Between March 1993 and February 1994 the diurnal grazing activity of chamois was recorded each fortnight during two days, using the scan-sampling method (Martin and Bateson 1993). The activity of all visible animals was recorded at the end of 15 minute intervals. An animal was judged to be involved in "feeding activity" if it was eating or its head was lower than its shoulders and the muzzle close to the ground. The percentage of animals feeding at the end of a 15 minute interval represents one sample. Degrees of freedom were calculated on the number of these samples (Martin and Bateson 1993). Samples were pooled into the following periods to compare the time spent in grazing activity throughout the year and between sexes: summer, August–October; rutting season, November; winter, December–March; spring, April–July.

### Statistical analysis

Ovulation frequencies and the number of parous females in each age class were compared using chi-square test. Sampling appropriateness clearly suffers from bias generated by hunting and culling variables. This results in widely different sample size in which each cell contains an incompletable set of factor combinations (ie periods, sexes and/or age class). We have conducted a nonbalanced analysis of variance on  $\log_e$ -transformed KFI variable with the following design: Y + M + Mc + A + YM + YMc + YA + YMA + YMcA + S + SY + SM + SMc + SA + SMY + SMcY + SMYA + SMcYA, where four main effects: A – age class, S – sex, Y – year, and M – month and interactions to the fourth order were considered. Month effect was considered as a continuous variable in a regression approach, including it as two lower order polynomial terms, linear (M) and quadratic (Mc), in order to assess the best response of this factor (Mead *et al.* 1993). A hierarchical decomposition of the sums of squares was used, each term was adjusted only for the terms that precede it in the design, the sums of squares in the model add up to the total sum of squares (Norušis 1990). Homogeneity of variance was verified using Cochran's C test ( $p = 0.293$ ) and by inspection of the normal plot of residuals. After the omnibus analysis of variance some one-way analyses of variance were performed to compare the KFI between sexes in some particular seasons. Homogeneity of variance was verified in all cases ( $p \geq 0.473$ ).

The Student test for paired-samples was used to compare the weight of right and left ovaries. When uterus weight was compared between parous non-pregnant and nulliparous females, the age effect on uterus weight was removed using the standard residuals of the linear regression uterus weight (y) against age (x). Grass abundance comparisons between years were conducted using Wilcoxon matched-pairs signed-ranks test (Siegel 1956), and Kruskal-Wallis single factor analysis and Student-Newman-Keuls (SNK) non-parametric multiple comparison test was used to compare the sward height among seasons (with  $\alpha = 0.05$  in all cases, Zar 1984). SPSS/PC+ (v. 5.0.1) software package was used for the statistical analysis (Norušis 1990).

## Results

### Ovaries and uterus analysis

Within a pair of ovaries from the same animal, ovaries with CL were heavier than ovaries without CL in March–April (Paired-sample *t*-test:  $t = 13.42$ ,  $df = 14$ ,  $p < 0.001$ ), and similarly, ovaries with CR were also heavier than ovaries without CR in August–October ( $t = 4.80$ ,  $df = 62$ ,  $p < 0.0001$ , 6 missing values). Significant differences also resulted under unpaired ovaries analysis (Table 1).

Table 1. Comparison of unpaired ovary weights (g) of Cantabrian chamois at different reproductive stages (Cantabrian Mountains, northern Spain). CL – corpus luteum, CR – corpus rubrum, presence or absence of CR or CL in ovaries is indicated with “+” or “-”. Presence of CL was considered between March–April; presence of CR was considered between August–October. Reproduction stages previous to last calving season were not considered. <sup>1</sup>The weight of ovaries with CL is compared with the weight of ovaries without CL. <sup>2</sup>The weight of ovaries with CR is compared with the weight of ovaries without CR.

CL	CR	Mean	SD	<i>n</i>	df	<i>F</i>	<i>p</i>
+		1.7	0.38	15			
-		0.5	0.19	166	1.176	323.6	0.0001 <sup>1</sup>
	+	0.5	0.19	69			
	-	0.4	0.16	79	1.146	13.7	0.0003 <sup>2</sup>

Mean uterus weight in parous non-pregnant females was higher than in nulliparous females (parous non-pregnant: mean = 20.8, SD = 5.40,  $n = 61$ ; nulliparous:  $9.4 \pm 2.12$ ,  $n = 4$ ; Mann-Whitney test:  $Z = -3.330$ ,  $p < 0.001$ ). This difference remained when the uterus weight was controlled for age ( $Z = -3.031$ ,  $p < 0.002$ ). Uterus morphology aided the distinction between nulliparous and parous females. The external appearance of a parous uterus was dark with transverse bands and well developed cornua. The uterus was also well vascularised and presented thick walls. The nulliparous uterus was paler and smoother. The cornua were smaller and thinner and the myometrium was thinner, smoother and less vascularised.

### Reproductive status

Significant differences in the percentage of parous females were found when 11 age class was compared with 3–11 age class (percentage of parous females 50 and 94%,  $n = 6$  and  $n = 51$ , respectively;  $\chi^2 = 6.90$ ,  $df = 1$ ,  $p = 0.009$ ). No data for 3 years class were available, and sample size of age classes 1 and 2 years with reproductive information was small ( $n = 2$  and  $n = 3$  respectively), these five females had not ovulated. The percentage of parous females older than 3 years was 90.4%. All pregnant females carried a single foetus ( $n = 15$ ).

## Kidney fat index

Significant differences were found in two main factors, year and sex, two two-factor interactions, sex  $\times$  year and sex  $\times$  month, and two three-factor interactions, sex  $\times$  month  $\times$  year and sex  $\times$  quadratic month  $\times$  year (Table 2). The three-factor interaction which included the quadratic month term had a similar effect in comparison with the month linear term (Table 2). There were no significant four-factor interactions. KFI was not affected by the age class effect (Table 2). The seasonal effect of the KFI on sex varied between years (Fig 1). Throughout the two years females maintained a relatively less annual variation of KFI in comparison with males (coefficient of variation, 1992: female - CV = 18.10, male - CV = 29.52; 1993: female - CV = 14.51, male - CV = 17.36). The following interpretation of the KFI trends should be considered with caution due to the large gaps between some of the sampling periods. The KFI development pattern of males throughout 1992 showed a minimum value at the end of spring following a large increase during summer with a maximum at the end of summer (Fig. 1). In 1993 the KFI was higher in the two sexes (females: 1992 vs 1993 =

Table 2. Analysis of variance for the kidney fat index (KFI) of Cantabrian chamois (Cantabrian mountains, northern Spain). Four main factors and interactions until fourth order are considered. Main factors: variation between years, 1992 and 1993 (year); variation between months (month: linear effect of months; month-c: quadratic effect of month, both effect were considered as continuous variables); variation between age classes (age) and between sexes (sex).

Source of variation	df	MS	F	p
Year	1	20.39	54.03	< 0.0005
Month	1	0.16	0.43	0.513
Age	2	0.74	1.95	0.149
Month-c	1	0.00	0.00	0.947
Year $\times$ month	1	0.59	1.55	0.217
Year $\times$ month-c	1	1.03	2.74	0.102
Year $\times$ age	2	0.10	0.26	0.774
Sex $\times$ month $\times$ year	2	0.29	0.77	0.467
Sex $\times$ month-c $\times$ year	2	0.35	0.93	0.400
Sex	1	2.48	6.58	0.013
Sex $\times$ year	1	11.08	29.36	< 0.0005
Sex $\times$ month	1	1.63	4.31	0.042
Sex $\times$ month-c	1	0.13	0.33	0.567
Sex $\times$ age	2	0.40	1.07	0.349
Sex $\times$ month $\times$ year	1	2.40	6.37	0.014
Sex $\times$ month-c $\times$ year	1	2.92	7.74	0.007
Sex $\times$ month $\times$ year $\times$ age	1	0.03	0.07	0.790
Sex $\times$ month-c $\times$ year $\times$ age	1	0.04	0.11	0.747
Residual	68	0.38		
Total	91	0.79		

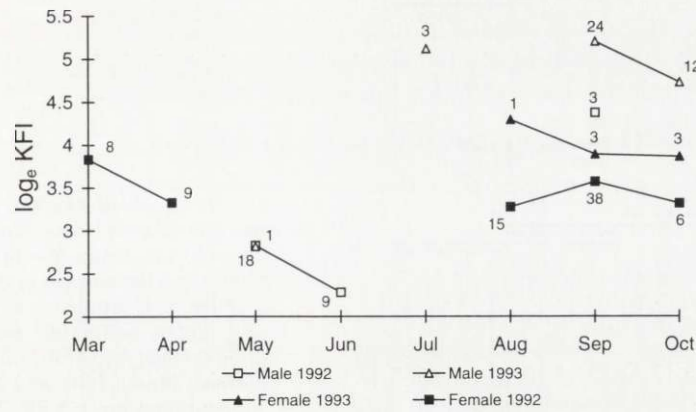


Fig. 1. Annual trends of the kidney fat index (KFI) for the two sexes in Cantabrian chamois throughout two years (1992, 1993) in the Cantabrian mountains (Asturias, Spain). Sample size is shown close to the symbols.

$3.49 \pm 0.632$  vs  $3.91 \pm 0.568$ ,  $F_{1,113} = 12.36$ ,  $p = 0.0006$ ; males: 1992 vs 1993 =  $2.82 \pm 0.831$  vs  $4.72 \pm 0.819$ ,  $F_{1,36} = 33.37$ ,  $p < 0.00005$ ). In spite of the small sample size of males in 1993, the data suggests a similar general pattern of development of KFI to the preceding year, but with an earlier strong increase in KFI at the end of spring in comparison with 1992, and maintaining similar values during summer until October (Fig. 1). The data indicates that between September–October (both years pooled) KFI of males was higher than those of females (female: mean =  $3.69 \pm 0.618$ ; male: mean =  $4.77 \pm 0.621$ ;  $F_{1,87} = 24.59$ ,  $p < 0.0005$ , Fig. 1).

#### Grazing activity and sward height

Females spent a smaller proportion of their feeding time in the summer than in winter or spring (Kruskal-Wallis test:  $\chi^2 = 19.51$ ,  $df = 3$ ,  $p = 0.0002$ , Fig. 2b). Male feeding activity was significantly lower during the rut than in summer, winter or spring. In winter, male grazing activity was higher than in the other seasons (Kruskal-Wallis test:  $\chi^2 = 36.64$ ,  $df = 3$ ,  $p < 0.0001$ , Fig. 2).

Females showed higher feeding activity than males in the summer, rut and spring (Mann-Whitney test:  $U = 2264$ ,  $p = 0.002$ ;  $U = 300$ ,  $p = 0.0001$ ,  $U = 4675$ ,  $p < 0.0001$ , respectively; Fig. 2). Winter feeding activity did not differ between sexes ( $U = 7739.5$ ,  $p = 0.119$ ). An inverse trend between abundance of grass and time spent feeding was observed, but was only significant in females ( $r_s = -1.0$ ,  $p < 0.001$ ; Fig. 2).

Sward height was taller in 1993 than in 1992 (Wilcoxon matched-pairs signed-ranks test:  $Z = 2.201$ ,  $p = 0.028$ ). Sward height differed among seasons

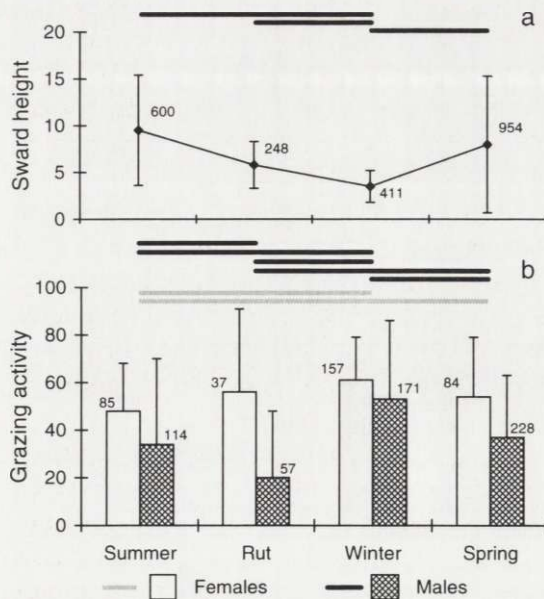


Fig. 2. (a) Sward height (cm) throughout one year (March 1993 – March 1994) in an area of Cantabrian Mountains (Asturias, Spain). (b) Percentage of diurnal grazing activity of Cantabrian chamois females and males, estimated using scan-sampling method (see Material and methods), between March 1993 and February 1994. Vertical lines are  $\pm 1$  SD. The ends of the horizontal lines indicate periods which differ significantly (Student-Newman-Keuls non-parametric multiple comparison test,  $\alpha = 0.05$ ).

(Kruskal-Wallis test:  $\chi^2 = 395.964$ ,  $df = 4$ ,  $p < 0.0001$ ), being shorter in winter than in other seasons. In summer sward height was taller than in other seasons, Fig. 2.

## Discussion

### Reproductive status

In Alpine chamois *Rupicapra rupicapra* populations, females often are sexually mature at 18 months of age (Couturier 1938), but there is great inter-population variation in age at maturity. The percentage of parous females at 2 years of age has been reported to be 63.3% (Houssin *et al.* 1993), 95% (Boillot and Perrin 1986 in Houssin *et al.* 1993) and 66.7% (Couturier 1988 in Houssin *et al.* 1993). In New Zealand parous females at 8 months of age are not rare (Alpine chamois – Bauer 1985). Stable chamois populations show later maturation than colonising ones (Bauer 1985). Ovulated animals were not found in our five females between 1-2 years old. This finding was supported by visual observations between August 1991 and March 1993 in a population of approximately 170 individuals (Caso, Asturias), in which no 2 year-old females were observed accompanied by kids. However more information is clearly necessary on the 2 and 3 years age classes.

The percentage of parous females older than 3 years (90.4%) was similar to that reported by other authors in Alpine chamois (92.5% Houssin *et al.* 1993, 80.4–91.4% Storch 1989). These authors found no evidence of decrease of fertility in relation to age up to 14 years, but the number of animals studied aging 13–14



years was small. Reimers (1983) pointed out that breeding performance remains unchanged throughout life in reindeer, although Clutton-Brock (1984) found a decline in the oldest age classes in red deer. Our results show a decrease of fertility in age classes over 11 year old, but this was not accompanied by a reduction in the kidney fat index as might have been expected. It is possible that fertility is only affected in very poor body condition. Besides, without knowing the body condition of the animals prior to the rut, it is questionable to relate the condition of the animals to reproduction of the previous year. From the samples collected between March–April ( $n = 17$ ), only one non-pregnant female showed a big CL, suggesting a recent abortion. Foetal losses during pregnancy seem rare in chamois, as in red deer (R. Langvatn, pers. comm.) and reindeer (Reimers 1983). Probably, the main cause of a non-pregnant status in Cantabrian chamois is the failure to conceive, as it has been suggested by Reimers (1983) in reindeer.

Some authors have reported that non-lactating females are in better condition than lactating ones (red deer – Mitchell *et al.* 1976, Clutton-Brock *et al.* 1982, Clutton-Brock *et al.* 1983; reindeer – Huot 1989, Tyler 1992). Our results indicate that in March–April non-pregnant adult females or those having a late-conception presented lower kidney fat index than pregnant females. Although the pregnant females in this period were not subjected to the cost of lactation, since they were shot prior to lactation period, it would be expected that they show poorer condition than those of females which did not bear pregnancy costs during winter. However, as body condition prior to mating influences conception (Mitchell *et al.* 1976), it is to be expected that at the beginning of winter non-pregnant adult females or those having a late-conception were in poorer body condition than pregnant females. If winter hardship prevents pregnant and non-pregnant females improve their body condition, it is possible that at the end of winter pregnant females are still in better condition than non-pregnant females. Lactation seems to have an influence on the body condition of Cantabrian chamois females. Pérez-Barbería and Nores (1996) using the timing of moult as an indicator of body condition found that chamois females shed their winter coat later than non-breeding females.

Uterus weight and appearance can be useful in assessing reproductive status of females. Nulliparous females had uteri lighter than 10 g, and more slender than those of parous females. These characteristics have also been used to assess mature and immature age classes in red deer (Langvatn 1992b) and mule deer – *Odocoileus hemionus* (Anderson *et al.* 1974).

Ovary weight can be useful to assess the ovulation in the preceding calving season. Ovulated ovaries during March–April were three times heavier than non-ovulated ones. Although CR size has been shown to decrease after parturition (Langvatn 1992a), the differences in weight between ovulated and non-ovulated ovaries were very small but significant. However, the use of ovary weight to assess ovulation is only advisable before the parturition season (March–April) when the differences in weight between ovulated and non-ovulated are greater.

#### Kidney fat index

Kidney fat index, although widely used to estimate corporal condition in large mammals, has also received criticisms (Anderson *et al.* 1972, Hanks 1981, Van Vuren and Coblenz 1985, Dusek 1987, Holand 1992). Nevertheless, KFI has value as it allows measurements over a wide range of body condition and sampling is a relatively simple task in the field (Riney 1982).

Although the sample size was small and all seasons were not represented throughout the two years of this study, the results were consistent with the fat mobilization pattern described for other ungulates. The KFI of females showed a more stable pattern than did males throughout the year, as Medin and Anderson (1979) pointed out in mule deer. Males started the rutting season with a KFI almost 3-fold higher than that of females. However, KFI of males in spring was half that than those of females. Similar results have been obtained in other artiodactyls (impala – Hanks *et al.* 1976, red deer – Mitchell *et al.* 1976, mule deer – Anderson *et al.* 1972, Medin and Anderson 1979, white-tailed deer – Dusek 1987, Dusek *et al.* 1989, reindeer – Reimers and Ringberg 1983, Alpine chamois – Storch 1989).

There are several hypotheses to explain the differences in body condition between sexes throughout the year, all of them being not mutually excluding, (i) body condition reflects changes in consumption of energy throughout the year, (ii) body condition reflects gain of reserves in relation to quality and quantity of food resources. In the first hypothesis there are two main causes of differences in consumption of energy between sexes, breeding and lactation for female and rut for male (Clutton-Brock *et al.* 1982). Since before the rut only females bear the reproduction costs, this might explain why males had almost three times higher KFI than did females at the beginning of the rut. It is not easy to evaluate the parental costs in both sexes, since some costs such as risk of predation, energy consumed (increase of walking and running) and injuries during the rut in males, are difficult to estimate (Clutton-Brock 1991). At the beginning of the pregnancy the apparent female parental costs (protection and lactation of the last kid) are relatively low (Pérez-Barbería and Nores 1996), thus during pregnancy the female supports mainly the winter-effect on its fat reserves, however the male supports both rut and winter effects. Our data does not allow us to know if the differences found between sexes in the KFI in spring (KFI in male lower than female) are due to a higher rut-effect or winter-effect in males. If we assume that the rut-effect cannot be the unique cause of the differences in KFI between sexes in spring, then, the winter-effect should involve both sexes in a different way.

Sexual dimorphism-body size theory might relate to the differences in the KFI between sexes during winter, when food resources are scarce and its quality is low. Some authors have pointed out that (i) males have larger body-size and they are more efficient at using abundant low quality forage due to their larger ruminoreticular volume which results in their more efficient conversion of fibre into energy (Demment 1982), (ii) males are also less selective feeders due to their

higher absolute metabolic requirements (Beier and McCullough 1990), and (iii) males are less efficient at grazing on scarce resources due to allometric differences in bite size (Illius and Gordon 1987). During winter, when the pastures in chamois Cantabrian area are scarce (Pérez-Barbería *et al.* 1997), the combine effect of the larger bite size relative to body size in female (Illius and Gordon 1987) and the non difference in grazing activity between sexes could explain why females show higher KFI than males.

However the use of the sexual dimorphism-body size theory in this way is open to discussion, since the sexual dimorphism-body size theory has been used to explain the sexual segregation in polygynous ungulates (Main *et al.* 1996), on the basis that males appear to use poorer-quality habitat (Clutton-Brock *et al.* 1982). However Bleich *et al.* (1997) have refuted this idea, since they found that mature males of mountain sheep (*Ovis canadensis*) obtain higher quality diets than do females, based on values for faecal crude protein.

The sex  $\times$  month  $\times$  year interaction points out that food resource variation across the seasons and years influences, in a different way, the condition of the sexes. In the present study, inter-annual changes of abundance of grass reflected differences in the KFI in the two sexes. Anderson *et al.* (1972) suggested that high values of KFI in autumn could be due to high levels of available resources during late spring and summer. Our results agree with this hypothesis. Pasture availability reached its peak in July and during the end of the summer and autumn the food available decreased due to livestock grazing activity (Pérez-Barbería *et al.* 1997). However, chamois were in the best condition in autumn. In addition, the food quality influences this pattern. In this area, crude protein in the pasture increases in spring and autumn and decreases in summer, and in winter it reaches the lowest values (Pérez-Barbería *et al.* 1997). Differences in the KFI between years have also been related to the annual rainfall, mean browse yields and snow depth (Anderson *et al.* 1972, Medin and Anderson 1979, Sæther and Gravem 1988), and the previous year rainfall has also been shown to affect horn growth, which is another body condition predictor (Spanish ibex – Fandos 1991, Cantabrian chamois – Pérez-Barbería *et al.* 1996b).

We did not find any relationship between age and the KFI, probably due to the small sample size in the youngest and oldest age classes. Storch (1989) found the yearling age class in poorer condition than adult animals. In white-tailed deer, Dusek *et al.* (1989) found no differences among female age classes over 1 year of age. On the other hand, Tyler (1992) reported an inverse relation between condition and age in reindeer. Perhaps these contradictory results are due to different environmental conditions or differences in the sample size of the old age classes. In our population old chamois were in good condition.

#### Food availability and grazing activity

Males entered the rutting season with approximately three times higher KFI than did females, despite the higher grazing activity exhibited by females during

spring and summer. Perhaps lactation costs are the cause by which the grazing activity increase did not revert in fat accumulation to the same rate as in males. This idea has been supported by studies which showed higher KFI of non-lactating females than lactating females (Mitchell *et al.* 1976, Clutton-Brock *et al.* 1983, Huot 1989, Tyler 1992). In our study although breeding and non-breeding females were pooled for sexual comparisons, the sexual differences in KFI were clear. The lowest levels of grazing activity in males were obtained during the rut. Reimers and Ringberg (1983) suggested that the loss of condition in reindeer males was mainly attributed to less feeding activity in conjunction with the increase of locomotion activity during the rutting season. An inverse trend between food availability and time spent in feeding was observed in females. Males followed the same trend except during the rut. Nevertheless this increase in grazing activity was not enough to maintain a good condition throughout the winter. This is consistent with the results of Reimers and Ringberg (1983) and Bruno and Lovari (1989), the former found a decrease in the food intake during winter, and the latter in autumn in relation to summer. In the present study, the time spent in feeding activity by both sexes tended to be at maximum during winter, presumably to compensate for the lack of food and the low quality of the pastures (Pérez-Barbería *et al.* 1997). In fact, in winter the time spent feeding by chamois was the highest throughout the year, and no sex differences were observed.

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