

Foraging Behaviour of Adult Female Apennine Chamois in Relation to Seasonal Variation in Food Supply

Elisabetta BRUNO & Sandro LOVARI¹

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We tested the prediction that qualitative and quantitative seasonal variations of food resources influenced the foraging behaviour and efficiency of Apennine chamois, *Rupicapra pyrenaica ornata* (Neuman, 1899). In summer, when the abundance and diversity of food resources were greater, we found a greater rate of food intake and a reduced search for food, as well as lower aggressiveness, than in the autumn. Furthermore in summer the median group size of grazing chamois was greater than in the autumn, in accordance with the availability of rich, but concentrated, food resources in the former season. No seasonal difference in time devoted to foraging was found. Apparently, the Apennine chamois maximize food intake during summer to compensate for later shortages in the colder season.

[Istituto di Zoologia, Università di Parma, Parma, Italy, Present address of EB & SL: Zoologia e Anatomia Comparata, Dipartimento di Biologia Cellulare, Università di Camerino, Via F. Camerini n. 2, 62032 Camerino(MC), Italy]

1. INTRODUCTION

Ungulates modify their foraging in response to seasonal variations in local food resources, therefore their feeding behaviour may be used as an indirect, but effective indicator of forage quality and quantity (Owen-Smith, 1979). The food intake rate, together with the time devoted to foraging, determines the feeding efficiency of a herbivore (Owen-Smith, 1979). Moreover the food intake rate can provide an approximate indication of the quantity of ingested food.

Adult female Apennine chamois, *Rupicapra pyrenaica ornata* (Neumann, 1899), kids, yearlings of both sexes and a few subadult males live in Alpine meadows above 1700 m a.s.l. from June to December. In the cold season they move to lower, but very steep slopes, thickly covered with deciduous and coniferous forests (Lovari & Cosentino, 1986). Our observations were carried out in summer (when high quality food

¹ Requests for reprints should be sent to Sandro Lovari.

is available) and in autumn (with low quality food) to assess changes in the foraging behaviour of the chamois.

These ungulates live in mountain areas where food resources are markedly seasonal and where feeding may become extremely difficult in winter due to deep snow and other environmental constraints. Therefore, in the cold season their energetic loss is usually great, while food intake is often quite scarce (Knaus & Schröder, 1975).

In a previous paper we showed that foraging rate, alertness and spatial position during group grazing were not significantly different between young adult and older females (Bruno & Lovari, 1988).

Ferrari *et al.* (1988), in our same study area, showed that the late spring, summer and early autumn diets of females, kids and subadults depend mainly on the plant community *Festuco-Trifolietum thalii*. The chamois grazing selection keeps this vegetation type suitable to supply a protein rich diet in a seasonal period which corresponds to the lactation and the early weaning of the kids; the grazing frequency of *Leguminosae* leaves (whose proteins have a high digestibility) increases to the phenologic decrease of proteins in young leaves and flowers, from June to September. The composition of the diet shows monthly shifts conditioned by the grassland phenology and the grazing selection.

Intense food competition is likely to generate a disruptive effect on the feeding efficiency of flock members through a greater rate of aggressive interactions. In turn, it could be expected that the aggression level in relation to food competition will raise with the decreased forage quality and quantity.

In this study we tested the prediction that chamois adjust their foraging behaviour, in terms of time budget and feeding efficiency, to the decreasing quality and quantity of food resources from summer to autumn, detected by Ferrari *et al.* (1988) in our study area. One could predict that in summer chamois obtain enough nutrients to ensure their survival later, when their food supply is less abundant (autumn) to poor (winter). As the winter ranges of chamois are in rugged, very steep and forested terrain (Lovari & Cosentino, 1986), where watching them at close range — or even at all — may often be impossible, we restricted our study to a comparison between summer and autumn foraging behaviour.

2. STUDY AREA

The study area, in the Abruzzo National Park, Central Apennines, Italy, extended from 1750 m a.s.l. (the upper beech timberline) to 2249 m a.s.l. (Mt. Petroso) in the core of the chamois range in the park. The local climate is cold to temperate. Yearly rainfall averages

1600—1700 mm in the higher altitudes. The ground is snow-covered from November to June. Normally the snow is less than 2 m deep. In shaded areas it can last till July or even August.

3. METHODS

Data were recorded on a sample of seventeen 4—13 year old females and one 18 year old individual, from 15 September to 12 November 1985 and on the same sample (apart from one female seriously crippled in the meantime) from 15 July to 15 August 1986. The chamois were individually recognizable by a coloured plastic ear tag.

Observations on foraging efficiency and on time budgets were done continuously by the focal animal technique (Altmann, 1974) from 8:00 to 17:00 hours in autumn and from 06:00 to 19:00 hours in summer, for a total of 135 animal-hours. On the other hand, whenever possible, data on group size and on activity rhythms were collected on groups of chamois, for a total of 51 group-hours.

Data were recorded directly onto check-sheets (cf. Hinde, 1973). We used a beeping timer which generated a tone at 1 or 5 minute intervals to record duration measures, a manual counter for frequency measures and 8×30 Zeiss binoculars, when necessary. We watched the chamois at a minimum distance of 30 m, being careful to minimize disturbance. In our area the chamois are habituated to the presence of tourists and can be approached up to 30 m without eliciting any detectable alarm response (Lovari & Cederna, unpublished data).

Activity rhythms. Activities were classified as feeding, lying down and other (inclusive of all remaining activities). We ranked 3 age classes: kids, yearlings, adults. Every 30 minutes we recorded group size and the number of chamois grazing, lying down or engaged in other activities (other) per age class.

We used the conventional definition of a "group" (Krämer, 1969; Berducou & Bousses, 1985) as at least 3 animals staying in sight and less than 40 m apart from each other at the time of observation.

Time budget. Feeding, ruminating or other activities of each tagged individual were recorded every 5 minutes, for 1 hour. Different chamois were observed throughout the day-time, on each day of data recording.

Foraging efficiency. The parameters used to measure foraging efficiency were the following:

(1) Number of bites of grass/minute; a bite was identified by a distinct jerking motion of the head (cf. Seip & Bunnell, 1985). This parameter has been used as an indirect measure of food intake rate, e.g. Murton *et al.* (1971) for *Columba palumbus* Linnaeus, 1758; Greig *et al.* 1983) for *Larus argentatus* Pontoppidan, 1763, Seip & Bunnell (1985) for *Ovis dalli stonei* Allen, 1912; Renecker & Hduson (1985) for *Alces alces* (Linnaeus, 1758).

(2) Number of steps for food searching/minute; the head is oriented towards the ground and kept below the withers. This parameter is a measure of food searching activity, an index of food dispersion and foraging continuity, e.g. Murton *et al.* (1971) for *Columba palumbus*; Jennings & Evans (1980) for *Sturnus vulgaris* Linnaeus, 1758; Greig *et al.* (1983) for *Larus argentatus*; Risenhoover & Bailey (1985) for *Oreamnos americanus* (Blainville, 1816).

(3) Number of steps caused by social interactions/minute; dominance displays and threats cause the focal animal to move. It is a measure of feeding discontinuity because of aggressive interactions during foraging in a group.

(4) Number of head-lifts/minute; the head is kept above the withers (cf. Lipetz & Bekoff, 1982). It is a measure of alertness rate, e.g. Lipetz & Bekoff (1982) for *Antilocapra*

americana (Ord, 1815); Underwood (1982) for African *Antilopinae*; Sullivan (1984) for *Picoides pubescens* Linnaeus, 1766; Alados (1985) for *Capra pyrenaica* Schinz, 1838; Risenhoover & Bailey (1985) for *Oreamnos americanus*.

4. RESULTS

4.1. Group Size

Groups were significantly larger in the warm season than in autumn ($T=25$, $N=16$, $p=0.05$, 2-tailed Wilcoxon T-test) (Fig. 1).

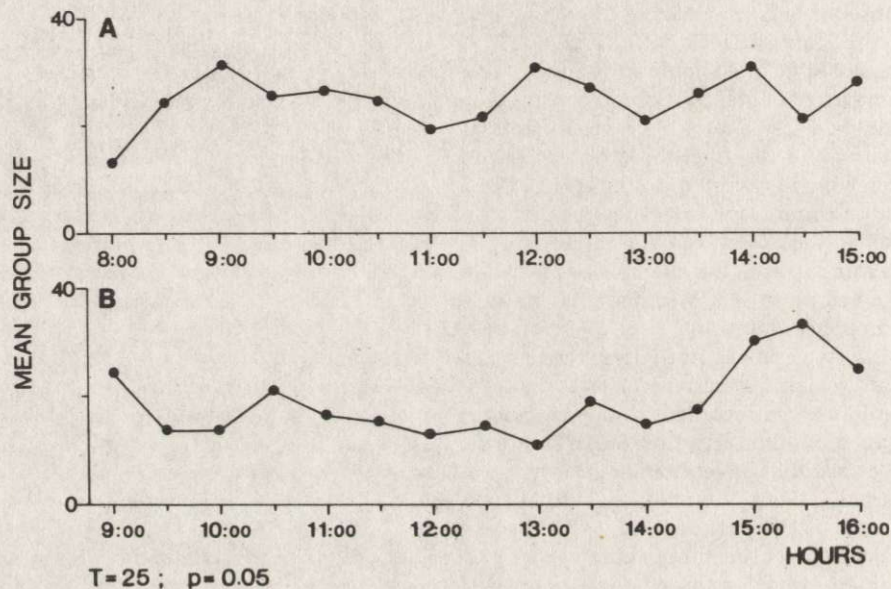


Fig. 1. Day-time variation of median group size. A=summer; B=autumn.

4.2. Activity Rhythms

The rhythms of feeding had at least two peaks in the autumn (Fig. 2-G), whereas at least three peaks were found in the summer (Fig. 3-G).

Both in summer and in autumn, significant correlations were shown between grazing kids, yearlings and adults, as well as between these same age classes at lying down (Table 1, Fig. 2-3). On the contrary, no significant correlation was shown between kids, yearlings and adults engaged in activities unrelated to feeding (other) (Table 1, Figs 2-3) either in summer or in autumn.

Finally, the comparison made on activity rhythms of the adults did not show any significant correlation between summer and autumn. The same result occurred for kid activity rhythms (Table 2). We could

Table 1

Sperman Rank Correlation Coefficients (r_s values) comparing the activity rhythms of kids (K), yearlings (Y), adults (A). N=15. (Data based on time spent in different activities by different age classes during scans every 30 minutes).

Age class	Summer			Autumn		
	Feeding	Lying down	Other	Feeding	Lying down	Other
K:A	0.688**	0.762**	0.016 NS	0.773***	0.784***	0.482 NS
Y:A	—	—	—	0.816***	0.893***	0.465 NS
K:Y	—	—	—	0.726*	0.667**	0.304 NS

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS — not significant.

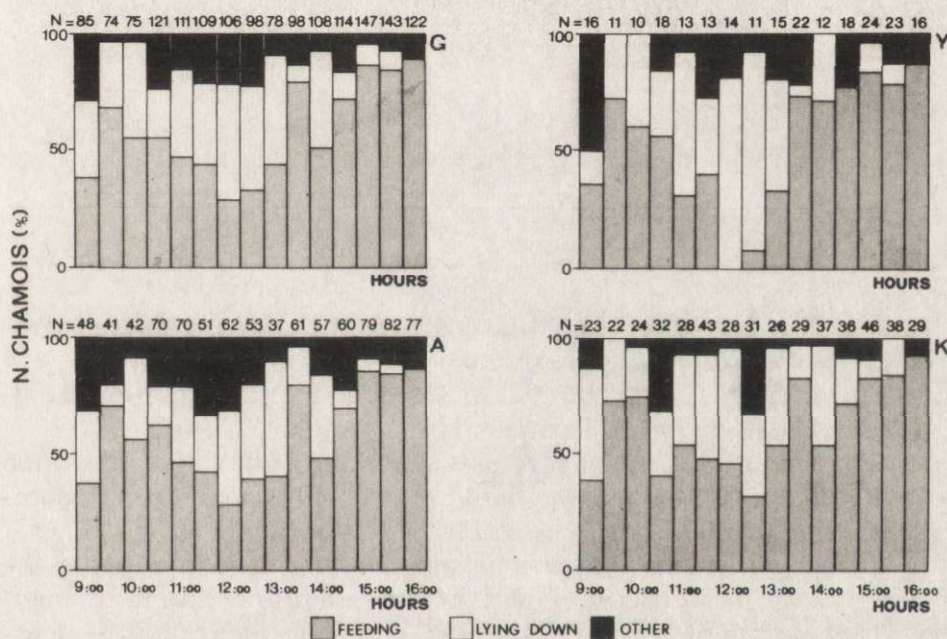


Fig. 2. Day-time activity rhythms (feeding, lying down, other) in autumn. G=group; A=adults; Y=yearlings; K=kids. (Data based on time spent in different activities by different age classes during scans every 30 minutes).

not collect enough data on the yearlings in summer because of their apparent scarcity in that season in the open Alpine meadows.

4. 3. Time Budget

The seasonal comparison made on the time budget of adult females showed neither statistically significant correlations (Sperman Rank Correlation test), nor statistically significant differences (2-tailed Wilcoxon T-test).

Table 2
Sperman Rank Correlations Coefficients (r_s values) on seasonal comparisons of adults (A) and kids (K) activity rhythms. N=15. (Data computed as in Table 1).

Summer vs. Autumn	Feeding	Lying down	Other
A	-0.421 NS	0.599*	-0.404 NS
K	-0.116 NS	0.347 NS	0.000 NS

* $p < 0.01$; NS - not significant.

Table 3
Seasonal comparisons (N=14, 2-tailed Wilcoxon T-test) made on foraging efficiency parameters (individual means).

Parameter/minute	Individual means		T values
	Summer	Autumn	
N bites of grass	33.20	23.42	1*
N steps for food searching	3.54	4.40	26 NS
N steps caused by social interactions	0.24	0.72	9*
N head lifts	0.62	0.63	51 NS

* $p < 0.01$; NS - not significant.

4. 4. Foraging Efficiency

Seasonal comparisons made on foraging efficiency parameters provided the following results (individual means) (Table 3):

(1) The number of bites/minute (*i.e.* the food intake rate) proved significantly much greater in summer than in autumn.

(2) The number of steps for food searching/minute (*i.e.* the food searching activity measure) appeared greater in autumn than in summer, but the difference was not statistically significant.

(3) The number of steps caused by social interactions/minute (*i.e.* the feeding discontinuity measure) was greater in autumn than in summer.

(4) The number of head lifts/minute (*i.e.* the alertness activity measure) did not vary seasonally.

To compensate for data dispersion, individual variances (instead of means) were also used for the same seasonal comparisons. Previous results were confirmed; just one fell from significant to nearly significant, *i.e.* the number of steps caused by social interactions.

5. DISCUSSION

Our prediction that chamois adjust their feeding behaviour to the seasonal variation of food resources so as to maximize their food intake rate was supported. In particular, it was found that:

(a) the largest groups occurred in summer, which is congruent with what was observed by Lovari & Cosentino (1986). This may happen

because in summer: (1) food resources are abundant and concentrated (same study area; see Ferrari *et al.*, 1988), therefore the chamois gather to feed on the Alpine meadows; (2) food competition is reduced because of the greater food availability (*cf.* also Clutton-Brock *et al.*, 1982, for *Cervus elaphus* Linnaeus, 1758). On the other hand, wolf predation on chamois seems rare in the same area (Lovari, 1984: 106) and it is unlikely that it underlies group formation.

(b) Feeding rhythms and group size had parallel day-time variations; feeding and lying down were correlated between age classes making up the feeding herds. Activities such as moving, resting, mainte-

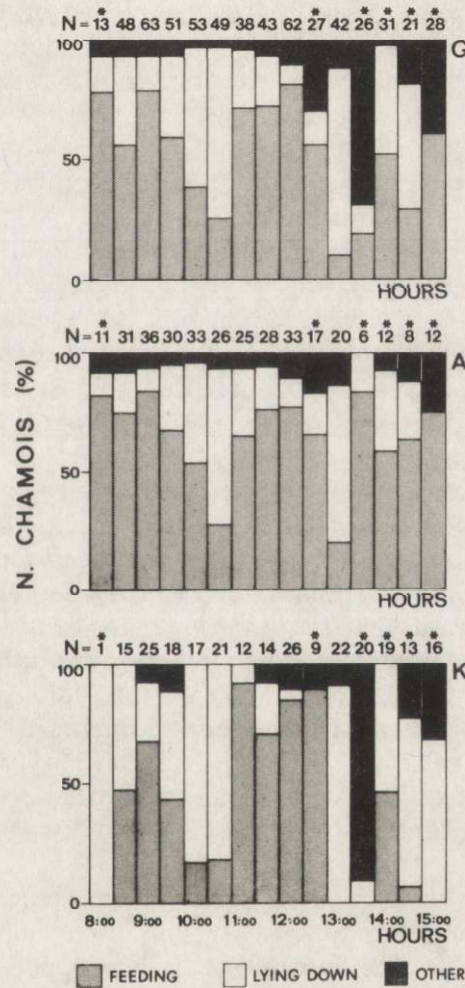


Fig. 3. Day-time activity rhythms (feeding, lying down, other) in summer. (Abbreviations and data computation as in Fig. 2). Data on yearlings were not extensive enough to include in the diagram (*cf.* sect. 4.2). Asterisks indicate data collected in one day.

nance behaviour (*i.e.* other) were not correlated; this suggests different age-dependent requirements for such activities.

The feeding rhythms showed at least two peaks in autumn, whereas at least three peaks occurred in summer: we do not know whether in autumn night feeding would compensate for lower diurnal feeding, because the rough terrain and the limited visibility even on full-moon nights did not allow night observations. However we expect that feeding activity would be more regular in summer, when abundance and diversity of food resources are greater, and food selection is possible. Our findings are consistent with such an expectation. Regular feeding plays an important role in stabilizing the milieu of microorganisms in the rumen and maximizes digestive efficiency (van de Veen, 1979; Kay & Staines, 1981), especially when the food intake rate is high.

Summer feeding, lying down and other activities were not significantly correlated to the autumn ones. Changing environmental factors, such as photoperiod, ground and pasture conditions, are likely to influence the activity rhythms of the chamois.

(c) In summer, the chamois showed a higher rate of food intake and a non-significant trend towards less searching for food. In summer the energy loss (in terms of food searching activity, aggressive interactions over food and vigilance) was less and the level of food intake was greater than in autumn. As time spent in foraging was not different in the two seasons, it can be concluded that the chamois foraging behaviour was more efficient in summer.

The rate of aggressive interactions during foraging was higher in autumn. Feeding competition can be expected to increase when food is scanty. Discontinuous feeding, therefore decreased foraging efficiency, could be the effect of the greater intra-group aggressive behaviour. However, other alternative hypotheses may also be possible, *e.g.* shorter rumen turnover time when chamois feed on low-quality forage.

We conclude that the foraging strategy of female Apennine chamois maximizes the energy and nutrient intake during the season offering greater food resources, to compensate for periods with a poor food supply such as autumn and even more so winter, when the Apennine chamois move to and feed in forested slopes at lower altitudes (Lovari & Cosentino, 1986).

Ferrari's *et al.* (1988) and our findings are not consistent with some theoretical models of optimal foraging (*e.g.* Schoener, 1971; Pulliam, 1974) which implicitly assume that food resources are of equal value and that natural selection maximizes caloric intake. Such models predict that an animal can only expand its diet to include progressively less preferred, *i.e.* usually less nutrient, items.

On the other hand, according to Owen-Smith & Novellie (1982), as food availability declines, an optimal foraging ungulate should widen its acceptance range initially, because energy becomes the critical factor on which diet is optimized, but, when the nutrient intake falls below maintenance demands, a quantitative narrowing of the diet should occur in favour of the most limiting nutrients. Ferrari's *et al.* (1988) and our data fit well in the latter prediction of this model. The Apennine chamois exhibited only a quantitative decrease of their diet as the poor season advanced. This suggests that chamois are limited more by the quality than by the quantity of food. They tend to compensate for the lower autumnal food intake rate by increasing the grazing frequency of Leguminosae leaves (*cf.* Ferrari *et al.* 1988 and sect. 1, this paper) and especially by maximizing the summer food intake. During the early growing season, the plant phenological stage (a factor affecting the availability of nutrient contents) is important for dietary optimization (Westoby, 1978). Therefore, the summer feeding, rather than the autumn one, is likely to influence the winter survival of female chamois.

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Elisabetta BRUNO i Sandro LOVARI

ŻEROWANIE SAMIC KOZICY W ZALEŻNOŚCI OD SEZONOWYCH ZMIAN
ZASOBNOŚCI POKARMU W APENINACH

Streszczenie

Sprawdzano hipotezę, że sezonowe zmiany jakości i ilości pokarmu wpływają na zachowania pokarmowe i efektywność żerowania kozic *Rupicapra pyrenaica ornata* (Neu-

man, 1899) w Apeninach. Latem, gdy większa jest dostępność i różnorodność pokarmu, tempo jego pobierania (mierzone liczbą zgryzów na minutę) było wyższe niż jesienią. Poszukiwanie pokarmu, mierzone liczbą kroków na minutę, było latem mniej intensywne. Agresywność kozic (wyrażona liczbą kroków spowodowanych interakcjami socjalnymi na minutę) była znacznie niższa latem. Jesienią malała liczebność grup żerujących kozic.

Nie wykryto natomiast różnic w czasie żerowania. Kozice prawdopodobnie maksymalizują tempo pobierania pokarmu latem, rekompensując jego przyszły niedobór w zimnym sezonie.