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ORIGINAL PAPER

# Males are faster foragers than females: intersexual differences of foraging behaviour in the Apennine chamois

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**Abstract** Availability of food resources and individual characteristics can influence foraging behaviour, which can differ between males and females, leading to different patterns of food/habitat selection. In dimorphic species, females are usually more selective in food choice, show greater bite rates and spend more time foraging than males. We evaluated sexual differences in foraging behaviour in Apennine chamois *Rupicapra pyrenaica ornata*, during the warm season, before the rut. Both sexes selected nutritious vegetation patches and spent a comparable amount of time feeding. However, males had a significantly greater feeding intensity (bite rate) and a lower search effort for feeding (step rate), as well as they spent more time lying down than females. Females selected foraging sites closer to refuge areas than males. In chamois, sexual size dimorphism is seasonal, being negligible in winter–spring, but increasing to 30–40 % in autumn. Our results suggest that males enhance their energy and mass gain by increasing their food intake rate during the warm season, to face the costs of the mating season (November). Conversely, females seem to prioritize a fine-scale selection of vegetation and the protection of offspring. A great food intake rate of males in the warm season could have developed as a behavioural adaptation leading herbivores to the evolutionary transition from year-round monomorphism to permanent dimorphism, through seasonal dimorphism.

**Keywords** Foraging behaviour · Sexual size dimorphism · Bite rate · Ungulates · Chamois

## Introduction

Foraging behaviour is influenced by quantity, quality, accessibility and dispersion of food resources (Macdonald 1983; Spalinger and Hobbs 1992; Sih and Christiansen 2001; Heuermann et al. 2011) and by individual characteristics, e.g. age, sex, reproductive status and body size (Clutton-Brock et al. 1982; Gross et al. 1995; Ruckstuhl et al. 2003; Heuermann et al. 2011). Foraging behaviour can be different in the two sexes (e.g. birds: Le Valliant et al. 2013; marsupials: Newsome 1980; ungulates: Ruckstuhl et al. 2003; carnivores: McDonald et al. 2000; pinnipeds: Beck et al. 2007; primates: Gautier-Hion 1980). In dimorphic animal species, sexual differences of foraging behaviour may depend on metabolism, sex-specific reproductive requirements or competition avoidance between sexes (e.g. Reynolds 1972; Newsome 1980; von Schantz and Nilsson 1981; Gross et al. 1995; Ruckstuhl et al. 2003; Beck et al. 2007). In turn, different patterns of spacing may occur between males and females (e.g. Ruckstuhl and Neuhaus 2000, 2002).

Food intake depends upon the time spent feeding, the quantity and quality of food ingested and the rate at which an individual crops and ingests forage (Spalinger and Hobbs 1992; Gross et al. 1995; Wilmshurst et al. 1999; Heuermann et al. 2011; St. Louis and Cotè 2012). Herbivores adjust their foraging and resting behaviour according to their energy requirements, e.g. modifying the time spent foraging (Clutton-Brock et al. 1982; Pelletier 2005; Willisch and Ingold 2007) and the bite rate (Ruckstuhl et al. 2003; Hamel and Côté

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2009). Furthermore, foraging behaviour and relative energy requirements should be influenced by body size (Jarman 1974; Demment and Van Soest 1985; Illius and Gordon 1987). Smaller animals have higher metabolic rates/body mass unit, greater energetic requirements/body mass unit, as well as a faster turnover rate of food in their gut than larger ones (Demment and Van Soest 1985; Illius and Gordon 1992).

Sexual size dimorphism (SSD) is widespread in polygynous mammals, with males usually larger than females mainly because of male competition for mating rights (Ralls 1977; Pérez-Barberìa et al. 2002). In ungulates, it has been suggested that SSD determines differences in foraging behaviour between males and females. Most likely, digestive efficiency differs between sexes, with males being more efficient than females (Van Soest 1994; Pérez-Barberìa et al. 2008). In addition, between late pregnancy and nursing, energy requirements of females are increased by costs imposed by maternal care. There are several mechanisms which females can adopt to compensate for their relatively lower digestive efficiency and greater energy demands imposed by pregnancy/lactation. Females usually spend a longer time foraging than males (Clutton-Brock et al. 1982; Ruckstuhl 1998; Neuhaus and Ruckstuhl 2002a; Ruckstuhl and Neuhaus 2002; Pérez-Barbería et al. 2007). Females could show greater chewing rates (Gross et al. 1995; Moquin et al. 2010) or bite rates than males, especially when nursing/weaning of offspring occur, which are potential mechanisms for individuals to compensate for morphological differences or energy needs (captive Nubian ibex *Capra ibex*: Gross et al. 1995; Alpine ibex: Neuhaus and Ruckstuhl 2002a; Mountain bighorn sheep *Ovis canadensis*: Ruckstuhl et al. 2003; but see Pérez-Barbería et al. 2007, who showed no sexual differences in bite rate of Soay sheep *Ovis aries*, in a 2.3 ha "experimental arena"). Females could also be more selective than males (Pérez-Barbería et al. 2007), spending more time moving while foraging (Ruckstuhl 1998) or showing a greater step rate (Komers et al. 1993) than males. Thus, the foraging behaviour of female ungulates tends to maximize the intake rate of high-quality food, to enhance their digestion rate and to meet great energy requirements determined by maternal care (Ruckstuhl et al. 2003).

If SSD influences foraging behaviour, we would expect that males and females show different patterns of foraging even when both sexes have great energy requirements, but different body mass. To date, sexual differences of foraging behaviour have been investigated mainly in species showing SSD all year long (e.g. Gross et al. 1995; Neuhaus and Ruckstuhl 2002a; Ruckstuhl et al. 2003). Information is scarce for weakly/seasonally dimorphic species (but see Neuhaus and Ruckstuhl 2002b; Ruckstuhl and Neuhaus 2009, for monomorphic ungulates). In chamois *Rupicapra* spp., SSD is seasonal (Crampe et al. 1997; Pérez-Barberia et al. 1998; Garel et al. 2009; Rughetti and Festa-Bianchet 2011). In northern chamois *Rupicapra rupicapra*, SSD is negligible in winter–spring, but males are *c.* 30–40 % heavier than females, in autumn (mid-September to November; Garel et al. 2009; Rughetti and Festa-Bianchet 2011). Besides, chamois show little sexual dimorphism in skeletal size (*c.* 5 %, Rughetti and Festa-Bianchet 2011), horn length (e.g. Lovari and Scala 1984; Rughetti and Festa-Bianchet 2011) and body morphology (Couturier 1938; Lovari 1985). Thus, males gain weight quickly, throughout summer–early autumn, which should allow them to increase their ability in intrasexual competition for partners, which occurs in November (in Europe, *R. rupicapra*, Krämer 1969; von Hardenberg et al. 2000; *R. pyrenaica*, Lovari and Locati 1991; Pérez-Barberia et al. 1998). At the same time, females should increase their intake of nutritious vegetation in spring–summer–early autumn (*R. pyrenaica*: Ferrari et al. 1988; Bruno and Lovari 1989), when nursing/weaning occurs. If so, we could expect that, in summer–autumn, both sexes have great energy requirements and tend to maximize their food intake, when high-quality food resources are available (Ferrari et al. 1988). If sexual differences of foraging behaviour are influenced by SSD, we may expect that male and female chamois follow the pattern observed for dimorphic species.

We analysed sexual differences in foraging behaviour (bite rate, step rate, vigilance rate, selection of feeding site, activity budget) in Apennine chamois *R. pyrenaica ornata*. We have tested the predictions that females (1) show greater bite and step rates, (2) spend more time feeding, (3) select high-quality food patches with respect to males. We also predicted that (4) females are more vigilant than males, because of presence of offspring.

## Materials and methods

### Study area

Our study area was located in the core of the distribution range of the Apennine chamois, in Abruzzo, Lazio and Molise National Park (ALMNP, central Apennines), upper Val di Rose (65 ha, mean altitude: 1,850 m a.s.l), above the treeline (mixed beech *Fagus sylvatica* forests, *c.* 1,700–1,800 m a.s.l.) up to the top of M. Sterpi d'Alto and M. Boccanera (1,966 and 1,982 m a.s.l, respectively).

Bioclimatically, the area lies in the temperate oceanic bioclimate, lower orotemperate thermotype, lower/upper humid ombrotype (Pesaresi et al. 2014). Snow cover lasts from late November to May–June (Bruno and Lovari 1989).

Vegetation is a complex mosaic of mesic and dry grasslands, respectively, dominated by palatable graminoids (35.5 %) and unpalatable tall grass *Brachypodium genuense* (24.9 %), and patches dominated by clover *Trifolium thalii* (15.2 %; see Supplementary online material). These plant communities are in vegetative activity from mid-June to late August and enter the senescence phase in September (Puppi Branzi et al. 1994). Rocks and screes with sparse vegetation are also present (24.4 %).

Our study area was used by at least 85, 82 and 73 chamois, in 2010, 2011 and 2012, respectively (31–39 adult females/year and 9–16 adult males/year). The area was used also by red deer (mean density in ALMNP=5.0 deer/100 ha; mean density in the core range of chamois=14.3 deer/100 ha, in 2010; Latini 2010). Roe deer *Capreolus capreolus* and wild boar *Sus scrofa* also occurred in the ALMNP, but they only visited the upper grasslands occasionally. The wolf *Canis lupus*, the brown bear *Ursus arctos* and the golden eagle *Aquila chrysaetos* were also present.

## Bite rate, step rate and vigilance rate

Behavioural observations were conducted from dawn to dusk (2010–2012, mid-July to late August and mid-September first, 10 days of November, before the mating season; Bruno and Lovari 1989). Apennine chamois were spotted from vantage points, at a distance of 30–200 m. In our study area, chamois are habituated to tourists and can be approached up to 30 m without eliciting any alarm response (Cederna and Lovari 1985).

The bite rate/step rate of adult female chamois (>3 years old; Lovari 1985; cf. Bruno and Lovari 1989) was recorded through continuous focal animal sampling (Altmann 1974). Observations started when the sex of the focal individual was assessed, by observing either his “brush” of hair under the abdomen (male sex) or her udder (female sex), through 10×50 binoculars and/or 20–60× spotting scopes (Lovari 1985). On summer–early autumn, sexes are usually spatially segregated (cf. Shank 1985; Lovari and Cosentino 1986; our unpublished data), which reduces further the risk of wrong assignation of sex. We made any effort to concentrate our observations on females with offspring (i.e. 62–73 %/year of the total number of females). Old females without kid-at-heel are often solitary, separate from the main herds (Lovari and Cosentino 1986): we avoided collecting data on them. Observations were carried out in 10-min bouts, divided by 1-min sampling intervals (Ruckstuhl et al. 2003). Each 1-min focal sample was followed by an interval of 10 s, to record data onto a checksheet (Bruno and Lovari 1989; Ruckstuhl et al. 2003). We recorded (1) number of bites to grass per minute (bite rate, an index of food intake rate: Bruno and Lovari 1989; Ruckstuhl et al. 2003; Hamel and Côté 2009): a bite was identified by a distinct jerking motion of the head (Bruno and Lovari 1989); (2) number of steps for food searching per minute (step rate, an index of food selection, food dispersion and foraging continuity: Bruno and Lovari 1989; Neuhaus and Ruckstuhl 2002a, b): a “foraging step” is defined as a forward movement of one of the forelegs, with the head close to the ground (Bruno and Lovari 1989). We also recorded the number of head lifts per minute (see below), as an index of alertness and discontinuity of foraging (Bruno and Lovari 1989; Ruckstuhl et al. 2003). When necessary, 10×50 binoculars and 20–60× spotting scopes were used to allow for the visibility of chamois mouth movements. For each sampling event, we recorded group size and structure (cf. Bruno and Lovari 1989). We also estimated the proportion of rock cover around the focal animal (0–25, 25.1–50, >50 %) in a radius of five times the body length of an adult Apennine chamois (i.e. 5 m ca.), to compare bite/step rates of chamois between areas with different rock cover. The geographic location of the focal animal was mapped with a GPS device, after it left the area. Locations were overlain on the vegetation map of our study area, to assess the type of vegetation (vegetation with *T. thalii*; palatable graminoids; other patches) grazed by the focal animal. We carried out short-term (10 min/ind) observation bouts on different individuals, to reduce pseudoreplication of data. Daily movements of female chamois herds were constant and predictable, allowing us to follow them during our observation bouts. We recorded data on individuals who could temporarily be distinguished by their respective positions on the slope (Frid 1997). Small morphological differences (Lovari 1980) that were visible at close range decreased the probability of recording data from the same individual more than once daily. Care was taken to distribute observations homogeneously among all times of the day and all sectors of our study area, to circumvent pseudoreplication.

We recorded 818 sampling bouts of foraging adult Apennine chamois (females: $n$=581; males: $n$=237), for a total of 125 observation hours and 20 min. Observation bouts were discarded when the focal animal moved off and disappeared from sight after less than 5 min. We estimated the differences in the bite rate and step rate of males and females, through generalized linear mixed models, with Poisson errors (Crawley 2007). The number of bites (or the number of steps) in 1-min sampling intervals were fitted as response variables. In global models, we fitted sex, season (summer: July–August; autumn: September–November, cf. Bruno and Lovari 1989), vegetation type (patches dominated by *T. thalii*; patches with palatable graminoids; other vegetation patches), rock cover, year and the two-way interactions between sex and season and vegetation type, as explanatory variables.

We compared the vigilance rate of males and females through generalized linear mixed models with Poisson errors (Crawley 2007). The number of head lifts in 1-min sampling intervals was fitted as response variables. In global models, we fitted sex, season, group size, group type (unisexual vs. mixed-sex groups), year and the two-way interactions between sex and season, group size, group type and year in global models.

The identity of the focal animal observed in 10 1-min sampling intervals, date and time of the day (divided by 1-h intervals) were fitted as random effects (random intercept) in all models, to control for the effect of repeated measures in 1-min sampling intervals, recorded within the same 10-min observation bout, in different days and at the same times of the day. Minimum adequate models were estimated by removing the least significant term at each step, starting from the highest level of interactions, until the elimination of terms caused a significant increase in the residual deviance (Crawley 2007). *F* deletion tests were used to assess the significance of changes in residual deviance (Crawley 2007: 325). Statistical analyses were conducted through the R 3.0.2 software, nlme package (R Development Core Team 2013).

### Activity budget

From dawn to dusk, activities of chamois were recorded (feeding; lying; other activities, e.g. moving, interacting, etc., Bruno and Lovari 1989) at 30-min intervals. Individuals whose sex could not be assessed were not included in the analyses. Sexual differences in activity budget were assessed seasonally. Absolute frequencies of sightings of individuals feeding, lying or involved in other activities were compared between sexes through *G*-tests (Sokal and Rohlf 1995).

### Selection of vegetation type

We assessed the selection of vegetation type by foraging chamois through the comparison of locations of focal individuals (see the "Bite rate, step rate and vigilance rate" section) with the vegetation map of our study area. For each sex, selection of vegetation type was assessed through selection ratios and Bonferroni confidence intervals:

$$w_i = o_i/\pi_i$$

where: $o_i$=number of observations in the habitat $i$/total number of observations; $\pi_i$ ($i$=1,…, $M$)=extent of habitat $i$/total study area (Manly et al. 2002).

Confidence intervals were estimated through the following formula:

$$w_i \pm z_{\alpha/2}\mathrm{se}(w_i)$$

where se $(w_i)=\sqrt{[o_i\ (1-o_i)/u\pi_i^2]}$, with $u$=total number of observations/habitat $i$ (Manly et al. 2002); $\alpha=0.05$; $z_{\alpha/2}$ is the critical value of the standard normal distribution corresponding to an upper tail area of alpha/2. Intervals overlapping 1 indicate habitats used proportionally to availability. Intervals with the lower limit >1 indicate selection, whereas those with the upper limit <1 indicate avoidance (Manly et al. 2002). We considered the following habitats: veg. with *T. thalii*; palatable graminoids; unpalatable graminoids; rocks. Selection of vegetation type was also compared between sexes, through generalized linear mixed models with binomial errors (Crawley 2007). Locations of focal males and females (females: 1; males: 0) were fitted as response variables. In global models, we fitted habitat, season, distance from cliffs (i.e. escape terrain for chamois, e.g. Shank 1985; cf. Caro et al. 2004, for mountain ungulates), slope, elevation, aspect, year and the two-way interactions habitat × season and group size × distance from cliffs, as explanatory variables. Date and time of the day were entered as random effects (random intercept). Distance from cliffs, slope, elevation and aspect were derived through GIS analyses (ArcGIS 9.3, ESRI©). No multicollinearity occurred ($r_s<|0.6|$, Green 1979) between continuous explanatory variables. Model selection procedures were carried out as described above (Crawley 2007).

## Results

### Bite rate, step rate and vigilance rate

In contrast to our prediction 1, irrespective from the season, chamois males showed a significantly greater bite rate and a significantly lower step rate than females (Fig. 1; Tables 1 and 2). The bite rate was significantly greater in summer than in autumn; in patches with *T. thalii* than in other patches; in areas with a low extent of rock cover than in patches with >25.0 % of rock cover and in 2012 than in 2010–2011 (Table 1). The final model for step rate included also the significant effects of vegetation, rock cover and year (Table 2).

The vigilance rate tended to be greater in females than in males, decreased with increasing group size, was greater in areas with >50 % rock cover than in other patches and in 2010 than in 2011–2012 (Table 3).

### Activity budget

We collected 1,739 sightings of chamois groups (solitary females, female groups or females with offspring: 28.8 %; solitary males or male groups: 51.3 %; mixed-sex groups: 19.9 %). Feeding was the main activity of both sexes (Table 4). In summer of all the 3 years, activity budget differed significantly between sexes (*G*-test: $G$=8.734–41.099; $df$=2; $P$<0.05). In autumn, activity budget differed between sexes in 2010 ($G$=16.606; $df$=2; $P$<0.001), but not in 2011–2012 ($G$=1.691–4.026; $df$=2; $P$>0.05). These differences occurred because of a different proportion of sightings of individuals lying/in other activities, between sexes (Table 5). Pooling lying/other activities, activity budget did not differ significantly between sexes ($G$=0.395–1.766; $df$=1; $P$>0.05). Thus, in contrast with our prediction 2, males and females spent a

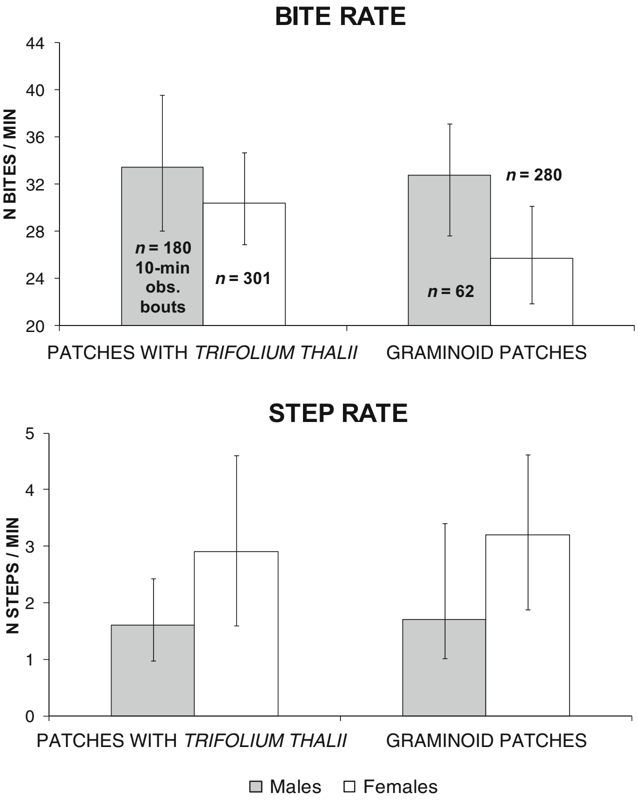

**Fig. 1** Foraging behaviour of adult female and male Apennine chamois: sexual differences in bite rate (*up*) and step rate (*down*). Medians± interquartile ranges are shown

comparable percentage of time foraging, while, especially in summer, the former spent a greater percentage of time lying down than the latter did (Table 4).

## Selection of vegetation type

Both sexes selected vegetation with *T. thalii* and avoided foraging in patches with unpalatable graminoids and rocks, in both season (Fig. 2). Patches with palatable graminoids were generally used for foraging according to their availability by both sexes, but for summer, when females selected them (Fig. 2). In contrast to our prediction 3, the selection of vegetation type did not differ between males and females either in summer or in autumn (GLM, contrast variable: palatable graminoids; patches with *T. thalii*: $B=-0.349$, SE=0.344; $P=0.310$; patches with rocks: $B=-0.623$; SE=1.056; $P=0.555$). Females foraged at a significantly lower distance from cliffs (median distance: 13.6 m, interquartile range (IQR): 6.8–31.5 m, females; median: 55.0 m, IQR: 23.7–75.9 m, males) and in significantly larger groups than males (median group size: 15 individuals, IQR: 9–24, females; median: 5 individuals, IQR: 2–7, males; Table 5). In particular, group size decreased with distance from rocks (Spearman's rho=−0.260, $P<0.001$) and this relationship seemed to be stronger for males than females, although $r^2$ values were very low (males: $r^2=0.028$; females: $r^2=0.012$).

**Table 1** Variables affecting the bite rate of adult Apennine chamois, estimated through generalized linear mixed models with Poisson errors ($N=818$ 10-min observation bouts for a total of 7,514 1-min intervals)

| Variable | *B* | SE | *P* |
|---|---|---|---|
| Sex (males) | 0.173 | 0.011 | <0.001 |
| Season (summer) | 0.164 | 0.033 | <0.001 |
| Vegetation (patches with *Trifolium thalii*) | 0.034 | 0.012 | 0.003 |
| Rock cover (25–50 %) | −0.038 | 0.010 | <0.001 |
| Rock cover (>50 %) | −0.134 | 0.012 | <0.001 |
| Year (2011) | 0.068 | 0.039 | 0.079 |
| Year (2012) | 0.272 | 0.039 | <0.001 |
| Intercept | 3.145 | 0.032 | <0.001 |

**Table 2** Variables affecting the step rate of adult Apennine chamois, estimated through generalized linear mixed models with Poisson errors ($N=818$ 10-min observation bouts for a total of 7,514 1-min intervals)

| Variable | *B* | SE | *P* |
|---|---|---|---|
| Sex (males) | −0.454 | 0.054 | <0.001 |
| Vegetation (patches with *T. thalii*) | −0.111 | 0.053 | 0.036 |
| Rock cover (25–50 %) | −0.084 | 0.040 | 0.036 |
| Rock cover (>50 %) | 0.392 | 0.049 | <0.001 |
| Year (2011) | −0.107 | 0.091 | 0.243 |
| Year (2012) | 0.195 | 0.092 | 0.033 |
| Intercept | 1.030 | 0.079 | <0.001 |

## Discussion

Sexual differences in foraging behaviour of dimorphic ungulates have been linked to differences of metabolic/energetic requirements related to body size (Demment and Van Soest 1985; Illius and Gordon 1992; Van Soest 1994). Male and

**Table 3** Variables affecting the alertness rate of adult Apennine chamois, estimated through generalized linear mixed models with Poisson errors ($N=818$ 10-min observation bouts for a total of 7,514 1-min intervals)

| Variable | *B* | SE | *P* |
|---|---|---|---|
| Sex (males) | −0.142 | 0.073 | 0.053 |
| Group size | −0.021 | 0.003 | <0.001 |
| Rock cover (25–50 %) | 0.094 | 0.067 | 0.163 |
| Rock cover (>50 %) | 0.254 | 0.087 | 0.002 |
| Year (2011) | −0.424 | 0.110 | <0.001 |
| Year (2012) | −0.251 | 0.110 | 0.023 |
| Intercept | −0.804 | 0.099 | <0.001 |

**Table 4** Activity budget of adult male and female Apennine chamois: number of sightings of individuals at feeding, lying or in other activities

| Season | Sightings | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Feeding | | | | Lying | | | | Other activities | | | |
| | Males | | Females | | Males | | Females | | Males | | Females | |
| | *N* | % | *N* | % | *N* | % | *N* | % | *N* | % | *N* | % |
| Summer | 912 | 63 | 1,796 | 60 | 439 | 30 | 769 | 26 | 95 | 7 | 408 | 14 |
| Autumn | 1,175 | 62 | 2,094 | 63 | 503 | 27 | 690 | 21 | 203 | 11 | 525 | 16 |

female Apennine chamois did not match the pattern observed in permanently dimorphic or monomorphic ungulates (e.g. Gross et al. 1995; Neuhaus and Ruckstuhl 2002a; Ruckstuhl et al. 2003; Ruckstuhl and Neuhaus 2009; Pérez-Barbería et al. 2007). The two sexes spent a comparable amount of time feeding and they grazed in the same habitat with nutritious food patches (short, i.e. <10 cm tall, forb patches dominated by *T. thalii*), with different tactics. Females favoured a fine-scale selection of nutritious vegetation (cf. Ferrari et al. 1988). Males showed a significantly greater bite rate than females, and they spent more time lying down (cf. Ruckstuhl 1998; Neuhaus and Ruckstuhl 2002a). Females were also more vigilant than males (cf. San José et al. 1996; Childress and Lung 2003). During the warm season, both female and male chamois should have great energetic requirements, as the former nurse their offspring, while the latter quickly increase their body weight before the mating season (Garel et al. 2009; Rughetti and Festa-Bianchet 2011). In monomorphic plain zebras *Equus caballus*, lactating females showed a greater bite rate than males (Neuhaus and Ruckstuhl 2002b). Our results suggest that energy requirements related to life history strategies and reproduction costs play an important role in determining sexual differences of foraging behaviour, rather than only body size-related energy requirements. In turn, sexual differences of foraging behaviour may not only depend on the latter, but they could also be influenced by energetic requirements imposed by life histories of the two sexes per se.

To our knowledge, no study has shown a greater feeding intensity in male herbivores than in females (cf. Gross et al. 1995; Neuhaus and Ruckstuhl 2002a, b; Ruckstuhl et al. 2003; Ruckstuhl and Neuhaus 2009; Pérez-Barbería et al. 2007). Male chamois may have increased their food intake rate by increasing their bite rate. Although no data are available on sexual differences in rumen size, sexual differences in hind-foot length are negligible (*R. rupicapra*: *c.* 5 %, Rughetti and Festa-Bianchet 2011) and those of mandible features are even (*R. pyrenaica*: García-González and Barandalla 2002), suggesting a very low skeletal dimorphism, probably including mouth size and shape. If so, bite size may be expected similar between sexes, when both of them feed on swards of approximately the same height (e.g. <10 cm tall: *T. thalii* and other forbs present in clover-dominated patches). Males showed a significantly greater bite rate than females, when both sexes foraged on the same vegetation patches, and both sexes spent a comparable amount of time foraging. If so, both

**Table 5** Sexual differences in the selection of foraging sites, in adult Apennine chamois, estimated through generalized linear mixed models with binomial errors (1: females; 0: males)

| Variable | *B* | SE | *P* |
|---|---|---|---|
| Distance to cliffs | −0.076 | 0.010 | <0.001 |
| Group size | 0.160 | 0.036 | <0.001 |
| Distance to cliffs × group size | 0.004 | 0.001 | <0.001 |
| Intercept | 1.134 | 0.504 | 0.024 |

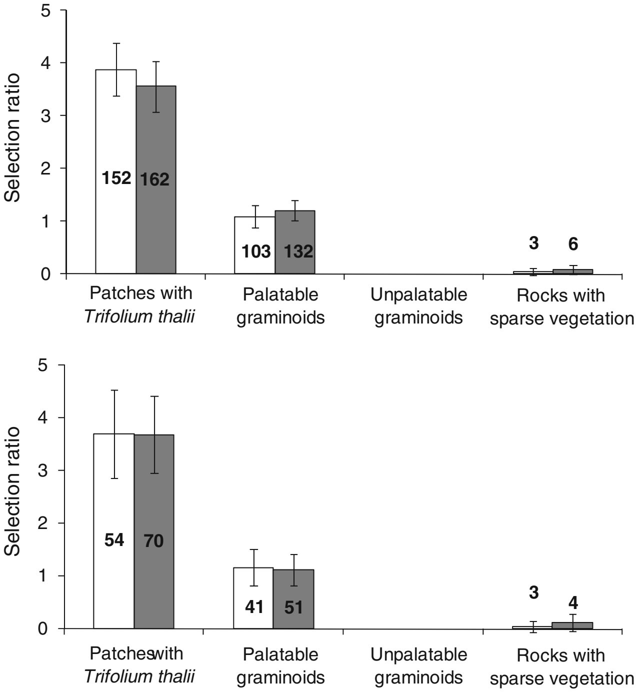

**Fig. 2** Selection of vegetation type for foraging, in female and male Apennine chamois, estimated through selection ratios and Bonferroni confidence intervals. *Within*/*above* the *bars*, sample sizes

the instantaneous and the daily food intake of males would be greater than those of females. Our results suggest that females were more selective, and they ingested food of a greater quality, than males. If so, sexual differences of foraging behaviour would not necessarily lead to differences in energetic intake, indicating that males and females meet their energy requirements through different tactics. Especially in summer, males also spent a longer time lying down than females, which may reflect a longer rumination time of the former than that of the latter (Ruckstuhl 1998; but see Moquin et al. 2010). If so, males could have processed a comparatively greater quantity of food or vegetation of a lower quality, with respect to females (e.g. Gross et al. 1995; Pérez-Barbería et al. 2007).

Why did male Apennine chamois show a greater bite rate than females? Male ungulates reduce heavily their food intake during the mating season, to concentrate on reproductive activities (e.g. Clutton-Brock et al. 1982; Pérez-Barberia et al. 1998; Apollonio and Di Vittorio 2004; Pelletier 2005; Willisch and Ingold 2007; but see Corlatti and Bassano 2014). In polygynous mammals, intrasexual competition for mating is strong between males and energy demanding (Darwin 1871; Yoccoz et al. 2002; Mysterud et al. 2005; Garel et al. 2011). Adult male Alpine chamois are heavier than females before the mating season, but sexual size dimorphism almost disappears in spring (Garel et al. 2009; Rughetti and Festa-Bianchet 2011), indicating a great energy cost for males, during the mating season. In Pyrenean chamois *R. pyrenaica pyrenaica*, no mass dimorphism was apparent during winter (Crampe et al. 1997). In Cantabrian chamois *R. pyrenaica parva*, at the beginning of rut, the kidney fat index of males was three times higher than that of females, but in the early spring, it was half that of females (Pérez-Barberia et al. 1998). These results suggest that SSD increases throughout summer–early autumn because of sexual differences in mass gain, which may involve fast accumulation of body fat and/or muscle tissue (Rughetti and Festa-Bianchet 2011). A conservative feeding tactic, based on both a high, nonselective at a fine scale, intake of nutritious vegetation and a long lying down time, should allow chamois males to accumulate fat and/or muscle tissue quickly during the short period of availability of high-quality food resources in alpine grasslands, and to enter the mating season in good body conditions. In turn, this strategy would allow males to overcome the costs of mating activities (Garel et al. 2011; Rughetti and Festa-Bianchet 2011) and reduce the cost of maintaining a large body weight during the winter (Corlatti et al. 2013). The latter would also be expected to increase winter survival: in sharp contrast to other polygynous ungulates (but see Toïgo et al. 2007, for Alpine ibex *C. ibex*), survival of male chamois equals that of females (Bocci et al. 2010; Corlatti et al. 2012).

In the warm season, both male and female chamois showed a marked preference for patches dominated by *T. thalii*. Plant species belonging to these food patches have been shown to have a greater nutritional value than those in graminoid-dominated patches and their leaves are protein-rich and important for weaning (Ferrari et al. 1988). Adult male chamois were suggested to use low-quality habitats (*R. pyrenaica*: Ferrari et al. 1988; *R. rupicapra*: Nesti et al. 2010; Unterthiner et al. 2012). Our data show that adult male Apennine chamois also selected habitats with nutritious food resources. Our data agree with recent findings on Alpine chamois males, reporting a high content of faecal proteins and a low content of fiber even when using poor habitats (Corlatti et al. 2013), suggesting that males actively select the best food resources.

In both male and female Apennine chamois, the bite rate was significantly greater in summer than in autumn (cf. Bruno and Lovari 1989, for adult female Apennine chamois) and was greater in patches dominated by *T. thalii* than in grasses. On mountains, vegetation quality tends to decrease from summer to autumn (Ferrari et al. 1988; Ruckstuhl et al. 2003; Moquin et al. 2010). For a given bite size, a decrease in vegetation quality would be expected to determine an increase of chewing time, thus a reduction of bite rate. Furthermore, the development of vegetation throughout the warm season should determine an increase of both sward height and vegetation biomass, thus a reduction of bite rate (e.g. Bruno and Lovari 1989; Wilmshurst et al. 1999; Ruckstuhl et al. 2003; Hamel and Côté 2009). In graminoids-dominated patches attended by chamois (*c.* >10 cm tall), the size of grasses is greater than that of forbs composing *T. thalii*-dominated patches (*c.* <10 cm tall), which could explain why the bite rate is greater in the latter than in the former.

Our data indicate that male and female chamois showed social segregation (cf. Shank 1985; Lovari and Cosentino 1986), but not habitat separation. Several hypotheses have been tested on determinants of sexual segregation in highly dimorphic ungulates (e.g. Conradt 1998; Ruckstuhl and Neuhaus 2000, 2002; Conradt et al. 2001; Mooring et al. 2005; Loe et al. 2006). Although we did not test its determinants, in Apennine chamois, sexual segregation may not be related to sexual differences in the selection of foraging habitat (“forage selection hypothesis”: Main et al. 1996; Ruckstuhl and Neuhaus 2000, 2002), as both males and females foraged preferentially in patches with the same vegetation type, even if they used different tactics. Especially in summer, males spent more time lying down than females, which militates against synchronization of their behavioural activities, likely leading to segregation (“activity budget hypothesis”: Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000, 2002). Females selected foraging sites close to cliffs, i.e. escape terrain for kids (see Caro et al. 2004, for a review; bighorn: Festa-Bianchet 1988; Alpine ibex: Grignolio et al. 2007; Alpine chamois: Nesti et al.

2010). It has been suggested that, in dimorphic ungulates, larger males should be less vulnerable to predation than females and their offspring; thus, the latter should prioritize searching for safe places from predators, whereas, for males, quality of nutrition will dominate in their habitat choice ("predation risk hypothesis": Main et al. 1996; Ruckstuhl and Neuhaus 2000, 2002).

Our results provide insights on the way SSD may have developed among herbivores. Wild sheep and goats show a remarkable sexual dimorphism, both at morphology and body size levels (Schaller 1977). Geist (1987) suggested that wild sheep and goats are an evolutionary progression out of the goat-antelopes, and that their differences are partly a result of the colonization of cold, seasonal climates. Among goat-antelopes, the warm climate "resource defenders" serow *Capricornis sumatraensis* and goral *Naemorhedus goral* are monomorphic, whereas males weigh *c*. twice as much as females all year long in the cold-adapted Rocky mountain goat *Oreamnos americanus* (Festa-Bianchet and Côté 2008). Chamois are intermediate in this evolutionary pathway, by increasing their SSD throughout summer–autumn, before the rut. Not only body size, but a wealth of phenotypic traits, e.g. the presence of a ruff, horns or antlers in males, as well as coat patterns may discriminate sexes in dimorphic species (Eisenberg 1981; Bradbury and Andersson 1987; for syntheses: Clutton-Brock 1989; Pérez-Barberìa et al. 2002). These phenotypic traits do not differ in chamois. Morphology and body size of highly dimorphic wild goats and sheep represent a further evolutionary step (Geist 1987). Species from extreme environments evolved later than those from warm climates, e.g. goat-antelopes (Geist 1985). Our data suggest that, in the warm months, male chamois gain body weight by increasing food intake rate, thus preparing to meet costs of the mating season (Garel et al. 2011; Rughetti and Festa-Bianchet 2011) and winter rigours. Achieving dominance for mating through increased body size should have primed this foraging adaptation (Garel et al. 2011; Rughetti and Festa-Bianchet 2011).

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FF planned the study, collected most of field data, worked out data and wrote the first draft; AC participated in data collection and analyses, in 2012; MC carried out vegetation and some GIS analyses; VP and GC participated in data collection, in 2012; SL supervised all the study, from its planning to writing up.

**Ethical standards** The experiments carried out complied with the current laws of Italy.

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