



Original Investigation

Effects of livestock and non-native mouflon on use of high-elevation pastures by Alpine chamois

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ABSTRACT

Interspecific interference among livestock, native and non-native large herbivores is a key management and conservation issue, and little is known about its dynamics and implications. We investigated whether native Alpine chamois (*Rupicapra r. rupicapra*) modify their spatial distribution when non-native mouflon *Ovis orientalis musimon* and livestock (domestic sheep *Ovis aries*, and domestic goats *Capra hircus*) inhabit the same areas in the Alpine meadows of Italian Eastern Alps. We walked 5 hiking trails (5.0 ± 0.1 km) at dawn, twice a month during summers 2007 and 2008. During these surveys, we located each group of free-ranging ungulates (chamois, mouflon, and livestock). We also estimated the quality of meadows, finding that forage availability increased linearly as the distance from rocks (i.e., chamois refuges) increased. We predicted that the linear distance between chamois groups and rocks would depend on the co-presence of livestock and mouflon groups. Our results showed that chamois were more likely to be observed in areas with low food availability, but safer (i.e., closer to the rocks), whenever the nearest livestock group was larger and closer, especially if the shepherd's dog was present. Avoidance of the best feeding patches by the wild species is presumably due to spatial interference (e.g. visual and acoustic disturbance) and/or predation risk perception caused by the presence of shepherd's dogs. Similarly, the larger was the nearest group of mouflon, the closer to rocks was located the chamois group. Interestingly, mouflon group vicinity induced chamois to move closer to rocks only if mouflon rams were within the group. This suggests that physical displacement of the smaller species (i.e. chamois) is likely to occur to avoid direct disturbance of larger mouflon rams. Our study clearly showed how a native herbivorous species adjusts its spatial distribution and decreases the likelihood of using areas with higher food availability when livestock and/or a non-native species co-occur.

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Introduction

Animals are expected to adjust their spatial use depending on resource requirements (MacArthur, 1972). Spatial use, however, can be influenced by interspecific interference (Putman, 1996), predation risk (Mysterud et al., 1999) and anthropogenic factors (Herrero et al., 1996). Interspecific interactions may lead to lower density or even to the complete displacement of one competitor from its preferred habitats (Gordon and Illius, 1989; Forsyth and Hickling, 1998; Latham, 1999). In regards to large herbivores, the study of interspecific interactions is particularly important if native

ungulates coexist with non-native species or free-ranging livestock (Vázquez, 2002; La Morgia and Bassano, 2009). While native sympatric species commonly show a low degree of interaction, as a consequence of niche differentiation (Hartnett et al., 1997), the introduction of non-native wildlife species may drastically unbalance the structure of the herbivore community (Vázquez, 2002). The co-presence of domestic ungulates along with non-native ungulates leads to further complications, with obvious concerns for the conservation of native ungulates, possibly endangered by such cumulative effects.

Previous studies on the interaction between wildlife and livestock suggest that spatial segregation is likely to occur because of direct competition (e.g. Coe et al., 2001; Kie, 1996). Other studies clearly showed that diet overlap occurs between wild and domestic ruminants (e.g., Mysterud, 2000; Mussa et al., 2003). Free-ranging cattle (*Bos taurus*), domestic sheep (*Ovis aries*) and domestic goats (*Capra hircus*) within summer grazing areas can affect the spatial distribution of wild ungulates and modify their activity budgets

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and diet (Kie et al., 1991; Kie, 1996; Mattiello et al., 2002; Brown et al., 2010). Moreover, livestock, being often locally abundant and artificially kept at high densities by supplementary feeding, are potentially competitors for wild ungulates (Latham, 1999). In addition, the need to minimize endoparasite uptake from faeces may also play a role in driving spatial behaviour of wild ungulates (Fankhauser et al., 2008). The contest for space and food among competitors could have negative consequences on the population dynamics of native species (Forsyth and Hickling, 1998; Forsyth, 2000; Mishra et al., 2004), particularly in mountainous areas where ungulates face seasonal nutritional bottlenecks. For example, in autumn adult males of Alpine chamois (*Rupicapra r. rupicapra*) trade feeding activities for mating ones and fat reserves decline fast (Forsyth et al., 2005; Willis and Ingold, 2007; Garel et al., 2011). Afterwards, winter rigours exert severe constraints on the survival of both male and female chamois (Bocci et al., 2010). Females, in particular, which have depleted fat reserves during harsh winters, may face high energetic demands for birth and lactation in spring (Ofstedal, 1984). Thus, summer may be considered the most important season for food intake and consequent body growth, and the presence of livestock and non-native ungulates may affect the achievement of a good condition.

In regard to the alpine environment, it is still unknown whether Alpine chamois could have limited access to the best foraging sites as a consequence of the co-presence of non-native mouflon (*Ovis orientalis musimon*) and free-ranging livestock. The introduction of mouflon in the Alps began in 1962 and the Alpine population in Italy is now around 5500 individuals (in all the Alps about 16,500 individuals – Carnevali et al., 2009; Apollonio et al., 2010). So far, the effects of these introductions have been poorly investigated. Studies conducted in the Pyrenees suggested that Pyrenean chamois (*Rupicapra p. pyrenaica*) were displaced by the presence of non-native mouflon (Gonzalez, 1984, 1986). Similarly, a marked spatial segregation was recorded between Pyrenean chamois and livestock in Spain and France (Berdoucou, 1986; García-González et al., 1990) and between Cantabrian chamois (*Rupicapra pyrenaica parva*) and livestock in Spain (Rebollo et al., 1993). The present study investigates the interference of livestock and non-native mouflon on the spatial distribution of native Alpine chamois. We predicted that the access by Alpine chamois to the best summer foraging sites could be negatively affected by the presence of mouflon and livestock. We also predicted that the presence of shepherd's dogs guarding livestock could further enhance physical displacement, as a response to direct harassment and predation risk perception.

Material and methods

Study area

The study was conducted in a 45.5 km² wide area of the Southern slope of the Brenta Massif (46°05' N; 10°50' E), Trento Province, Central-Eastern Alps, Italy (Fig. 1). Elevation ranged from 950 to 2850 m a.s.l. (mean elevation 2005 m a.s.l.). Observations were carried out in grassland meadows above the tree line (2000 m a.s.l., 12% rocks and 88% meadows), where blue moor grass (*Sesleria albicans*) and carnation grass (*Carex firma*) were dominant (Adamello Brenta Nature Park – official data). The extension of all meadow patches ($n=69$) was 40.04 km², the mean patch size was 1.86 (SE, ± 0.23) km² and the mean distance between near patches was 87 (SE, ± 63) m. These areas were commonly used in summer by Alpine chamois (12 animals/km², estimated by block count censuses in early summer; Fig. 2), mouflon (introduced by hunting associations in the 1970s, 4.5 animals/km², estimated by block count censuses in early summer; Fig. 2), and large flocks of domestic sheep and domestic goats (variable number from year to

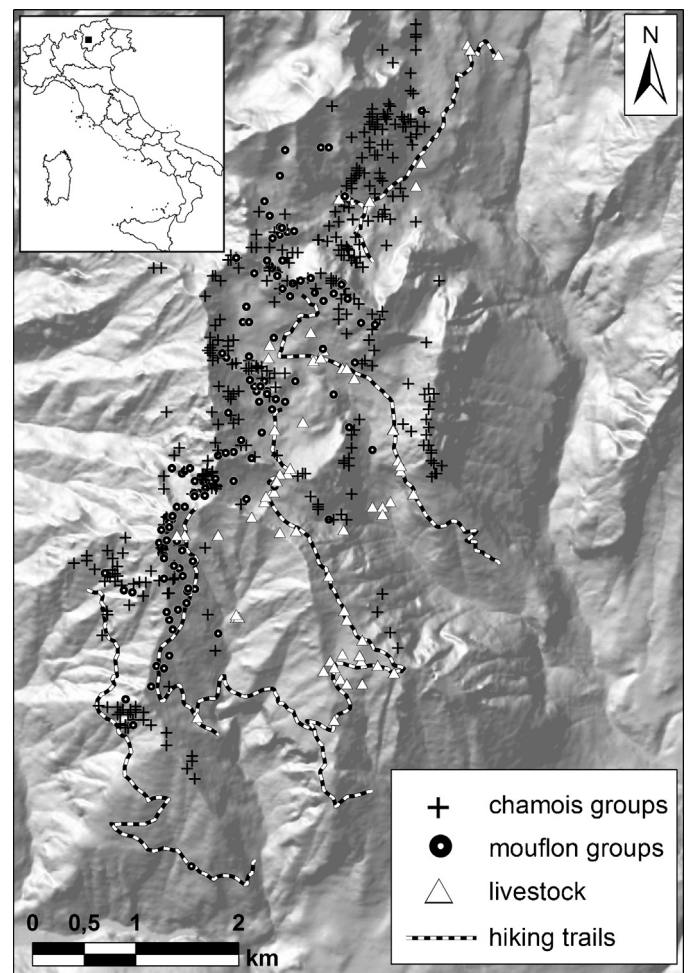


Fig. 1. Digital elevation model of the 45.50 km² wide study site of the Brenta Massif (46°05' N; 10°50' E), Eastern Italian Alps. Locations of ungulate groups (chamois, mouflon, livestock) observed from 5 hiking trails walked during summers 2007–2008 were reported on the map.

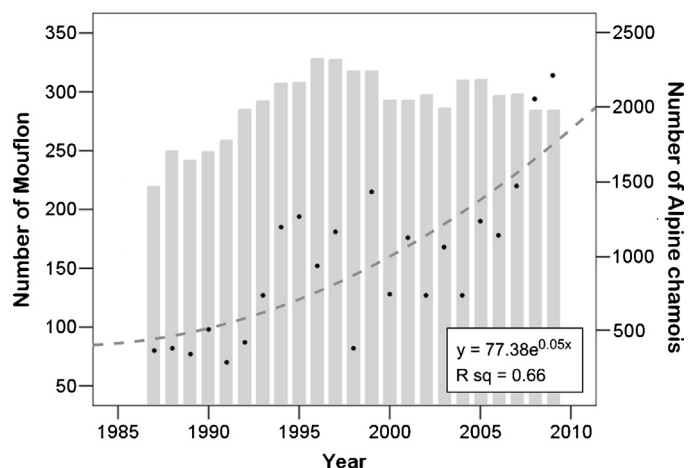


Fig. 2. Increase of mouflon population estimates (black dots, dotted regression line, regression equation and R^2) recorded from 1987 to 2009 for the 45.50 km² wide study site of the Brenta Massif, Eastern Italian Alps. Background grey bars represent Alpine chamois population estimates for the same period in the SE sector of the Brenta Massif. Population estimates were obtained with block count census for both species (Trento Province – official data).

Table 1
Parameter estimates, standard errors (SE), 95% Confidence Intervals (CIs) and *t*-test of the General Linear Model explaining the variability of normalized green index ($\arcsin(\sqrt{\text{green index}/100})$) as a function of the linear distance from rocks (\log_e -transformed). Data were recorded in 18 randomly selected meadows (1 every 1.5 km²) of the study site in the Eastern Alps, Italy.

Parameter	Estimate	SE	95% CIs		<i>t</i>	<i>p</i>
			Lower	Upper		
Intercept	1.354	0.050	1.256	1.452	27.197	<0.001
\log_e -distance from rocks	−0.001	0.009	−0.019	0.017	−0.132	0.895

year: about 800 heads in 2007 and 1200 in 2008) often guarded by shepherds and their dogs. Livestock was not provided with salt and artificial forage. Red deer (*Cervus elaphus*, 1 animal/km², estimated by spotlight counts in spring; Trento Province – official data) and roe deer (*Capreolus capreolus*, 8 animals/km², estimated by spotlight counts in spring; Trento Province – official data) were abundant, but were never observed in the Alpine meadows during our study.

Potential terrestrial predators were represented by a small and yet stable population of brown bear (*Ursus arctos*) and a few lynx (*Lynx lynx*) (Groff et al., 2009). Among birds of prey, the golden eagle (*Aquila chrysaetos*; Pedrini et al., 2005) was the only one which may prey upon chamois kids in their first weeks of life.

In the whole study area, hunting with rifles was allowed from mid-September to mid-December.

Data collection and analyses

From 15 June to 15 September of two consecutive years (2007–2008), we walked the same 5 hiking trails (5.0 km ± 0.1, total = 25 km) once every 15 days to locate each group of ungulates above the tree line (2000 m a.s.l.). Observations were conducted during the first 4 h after sunrise when the activity of wild and domestic ungulates was the highest (Cederlund, 1989; Green and Bear, 1990; Shi et al., 2006; Aublet et al., 2009). During each survey, all groups of free-ranging ungulates were located using binoculars 10 × 42 (Swarovski SLC-WB), and a 60 × 80 telescope (Swarovski ATS-80-HD). We considered a group as a variable number of individuals that were spatially associated (i.e., distance of two different groups higher than 50 m) and had a correlated behaviour (Parrish and Edelstein-Keshet, 1999; Krause and Ruxton, 2002). The size of each group and the presence of the shepherd's dogs were recorded. Free dogs, when present, were always accompanied by shepherds. Individuals of each group of mouflon or chamois were identified and classified by age and sex (for mouflon see Ciuti et al., 2008; for chamois see Herrero et al., 2002). Once a group was spotted, the observer's position was recorded using Global Positioning System (GPS) device (Garmin GPSMAP-60CSx). The distance of the group centroid and the angle measurement with respect to the North were measured using a rangefinder (Bushnell laser Elite 1500 – 7 × 26) and a hand compass (Ziel professional C90). Final coordinates of the centroid of each group as well as the distances among group centroids were calculated using of ArcGIS 9.3 (ESRI Inc., 1999–2008). This study was conducted at a local spatial scale (area extent = 45.50 km²; pixel size = 0.01 km²).

During the same period, once every 15 days, we estimated the forage availability of meadows using the greenness index (as reported by Carranza and Valencia, 1999) in 18 randomly selected sampling sites (1 sampling point every 1.5 km²; computed using Hawth's Tools for ArcGIS, Beyer, 2004). For each sampling site, we collected grass measurements along a linear transect at five sampling points, which were set every 10 m (total sampling points = 90). At each sampling point and in the area of approximately 1 m around it, we dropped four squares of 30 cm × 30 cm (total samplings: 360 every 15 days) and we estimated the following metrics: (i) grass cover: a visual estimate of the percentage of area covered by grass

within the square; (ii) green index: the leaf blades localized at the four corner tips of the square could be either green or brown. The green index was calculated as the number of tips touching green leaves (from 0 to 4) in proportion to the tips touching any leaf blade (0–4); and (iii) grass length: at the spot with most grass cover within the sampling square, we measured the length of the longest aerial part of the grass. These data have been shown to be correlated with forage quality and quantity (in terms of dry mass) (Carranza and Valencia, 1999).

We analyzed the variations in grass measurements as a function of the linear distance from the nearest rocks. We modelled both the normalized green index ($\arcsin(\sqrt{\text{green index}/100})$) and the forage availability (grass cover × grass length/100) of meadows by fitting two General Linear Models (GLMs) with normal distribution of errors. In both models, the \log_e -transformed linear distance from the nearest rocks was fitted as a covariate (Tables 1 and 2). Given that forage availability increased as the distance from rocks was higher (see “Results” section for details), we selected the linear distance (\log_e -transformed) of chamois groups from rocks as the dependent variable in our analyses. Distance of chamois groups from rocks was a variable that included at the same time food availability (i.e., higher food availability far from rocks) and security perception by chamois (i.e., safer areas close to rocks in mountain ungulates *sensu* Grignolio et al., 2007a). On the basis of these assumptions, we modelled how the linear distance of chamois groups from rocks was affected by the presence of other ungulate species (domestic ungulates and/or mouflon). To predict the distance of chamois groups from rocks we chose the following covariates: chamois group size (\log_e -transformed); percentage of rams within the nearest mouflon group; group size (\log_e -transformed) of the nearest mouflon group; distance (metres; \log_e -transformed) of the nearest mouflon group; group size (\log_e -transformed) of the nearest livestock flock; distance (metres; \log_e -transformed) of the nearest livestock flock; presence of the shepherds' dogs within the nearest livestock flock.

Among the environmental variables, we considered the slope of the terrain where the chamois group was observed (expressed within the 0–90° range; 0°: flat terrains; 90° rocky walls), its elevation (m a.s.l.) and its aspect (cos-mountainside, i.e., the expression of the mountain side exposure with respect to the North). The aspect, originally expressed within the 0–360° range, was cosine transformed, therefore assuming values from −1 (South facing slope) to 1 (North facing slope). We built a correlation matrix (Pearson correlation coefficient, r_p) with all the explanatory variables potentially able to predict the distance of chamois groups from rocks, so as to exclude collinearity issues. The correlation coefficient r_p was never higher than 0.7 (Sokal and Rohlf, 1995). All spatial data were calculated using ArcGIS 9.3 (ESRI Inc., 1999–2008). The fixed factors in the models were the shepherds' dogs presence within the nearest livestock flock (0 = dog absent, 1 = dog present), and the month of observation (June, July, August, September). We considered the hiking trail (sampling unit) repeated once every 15 days in different years (2007 and 2008) as a random factor in our mixed models to avoid pseudo-replication of data (Machlis et al., 1985). We used the Information-Theoretic (IT) approach based on Akaike information criterion corrected for small sample

Table 2

Parameter estimates, standard errors (SE), 95% Confidence Intervals (CIs) and *t*-test of the General Linear Model explaining the variability of forage availability (grass cover \times grass length/100) as a function of the linear distance from rocks (\log_e -transformed). Data were recorded in 18 randomly selected meadows (1 every 1.5 km²) of the study site in the Eastern Alps, Italy.

Parameter	Estimate	SE	95% CIs		<i>t</i>	<i>p</i>
			Lower	Upper		
Intercept	59.124	27.765	4.705	113.543	2.129	0.034
\log_e -distance from rocks	25.019	4.827	15.559	34.480	5.183	<0.001

size (AICc; Burnham and Anderson, 2002; Symonds and Mousalli, 2011) to select the best fitting model. Akaike's weights w_i for each i model were computed. The effect of each variable (i.e., parameter estimation) included in a confidence set of models with $w_i > 0.05$ and $\sum_{i=1}^n w_i > 0.9$ was obtained via model averaging in an AICc framework (Burnham and Anderson, 2002; Symonds and Mousalli, 2011). We estimated R^2 following Magee (1990) to describe the way models fitted the observed data as follows: $R^2 = 1 - \exp(-2/n(\log L_M - \log L_0))$, where n is the number of observations, $\log L_M$ is the standard log-likelihood of the model (which includes fixed and random effects) and $\log L_0$ is the standard log-likelihood of the intercept-only model. All means are reported with standard errors and all medians are reported with interquartiles. Statistical analyses were performed using R version 2.13.1 (R Development Core Team 2011).

Results

Forage availability as a function of the distance from rocks

The green index of meadows did not change as the distance from rocks increased (Table 1, Fig. 3). However, forage availability increased as the distance from rocks increased (Table 2, Fig. 3).

Predicting the distance of chamois groups from rocks

During summer 2007 and 2008, 567 chamois groups (median group size: 9; $Q_1 = 3$, $Q_3 = 11$), 157 mouflon groups (median group size: 13; $Q_1 = 4$, $Q_3 = 21$), and 62 livestock flocks (mixed domestic goats and domestic sheep; median group size: 310; $Q_1 = 98$, $Q_3 = 618$) were observed in our study area.

The final set of LME models predicting the distance of chamois groups from rocks is reported in Table 3. The probability of the most parsimonious LME model (AICc = 1554; $R^2 = 0.41$) to be the most approximating model was 77%. We thus considered a confidence set of two models with a cumulative Akaike weight equal to 0.90 ($\sum_{i=1}^2 w_i = 0.90$; Table 3). Parameter estimation was obtained via model averaging (Table 4).

Chamois were closer to rocks if a dog was present within the nearest livestock flock (distance of chamois from rocks: dog present: 250.4 ± 66.0 m; dog absent: 378.3 ± 64.2 m). Chamois groups were usually more distant from rocks in June (472.9 ± 72.3 m) than during the rest of the summer (July–September: 356.4 ± 29.4 m) (Table 4).

Chamois in smaller groups stayed closer to rocks (Table 4). The distance of chamois groups from rocks decreased if the nearest group of mouflon was larger or included a higher percentage of rams (Table 4). The distance of the nearest mouflon group did

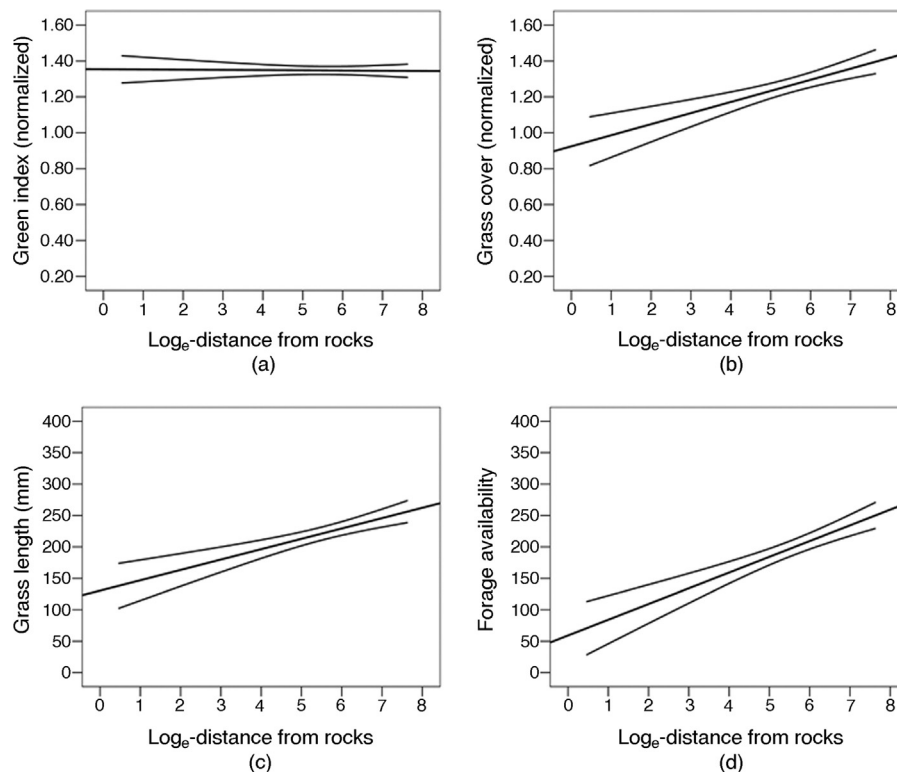


Fig. 3. Variation of green index (a), grass cover (b), grass length (c), and forage availability (grass cover \times grass length/100) (d) as a function of the linear distance from rocks (\log_e -transformed, in metres). Data were recorded in 18 meadows of the study area, Eastern Alps, Italy. Linear regression lines (with 95% Confidence Intervals) are reported on each graph.

Table 3

Selection of Linear Mixed Effect Models predicting the variability of the linear distance of chamois' groups from rocks (\log_e -transformed, in metres) in the Eastern Alps, Italy (2007–2008). Each column represents a single model. [x=terms included in a model. AICc=Akaike information criterion value corrected for small sample size; Δ AICc=difference in the AICc value between a given model and the most parsimonious model (i.e., lowest AICc); w_i Akaike weight]. Parameters were calculated via model averaging of the top two ranked models (in bold; $\sum_{i=1}^2 w_i = 0.90$) and reported in Table 4 see the text for details on explanatory variables.

Shepherds' dogs presence	x	x	x	x	x	x	x	x	x	x	x
Month	x	x	x	x	x	x	x	x	x	x	x
\log_e -chamois group size	x	x	x	x	x	x	x	x	x	x	x
Rams within mouflon group (%)	x	x	x	x	x	x	x	x	x	x	x
\log_e -mouflon group size	x	x	x	x	x	x	x	x	x	x	x
\log_e -distance from mouflon group	x	x	x	x	x	x	x	x	x	x	x
\log_e -livestock group size	x	x	x	x	x	x	x	x	x	x	x
\log_e -distance from livestock group	x	x	x	x	x	x	x	x	x	x	x
Slope	x	x	x	x	x	x	x	x	x	x	x
Elevation	x	x	x	x	x	x	x	x	x	x	x
Aspect	x	x	x	x	x	x	x	x	x	x	x
\log_e -mouflon group size \times rams within mouflon group (%)	x	x	x	x	x	x	x	x	x	x	x
\log_e -distance from mouflon group \times rams within mouflon group (%)	x	x	x	x	x	x	x	x	x	x	x
\log_e -distance from mouflon group \times \log_e -mouflon group size	x	x	x	x	x	x	x	x	x	x	x
\log_e -distance from livestock group \times \log_e -livestock group size	x	x	x	x	x	x	x	x	x	x	x
\log_e -distance from livestock group \times shepherds' dogs presence	x	x	x	x	x	x	x	x	x	x	x
\log_e -livestock group size \times shepherds' dogs presence	x	x	x	x	x	x	x	x	x	x	x
\log_e -distance from livestock group \times \log_e -chamois group size	x	x	x	x	x	x	x	x	x	x	x
AICc	1577.6	1569.1	1568.8	1565.0	1563.1	1561.6	1560.5	1560.2	1557.5	1554.0	
Δ AICc	23.6	15.1	14.8	11.0	9.1	6.9	6.5	6.2	3.5	0	
Akaike weight w_i	0.0000	0.0004	0.0005	0.0031	0.0081	0.0243	0.0297	0.0345	0.1331	0.7662	

not affect the distance of chamois from rocks (Table 4). However, chamois groups were more likely to be closer to rocks if the nearest mouflon group was concurrently closer and inclusive of a higher percentage of mouflon rams (2-way interaction, Table 4). Chamois were more likely to be closer to rocks when the nearest livestock flock was larger or closer (Table 4). Finally, chamois were more likely to be more distant from rocks when located in steeper terrains (Table 4).

Discussion

Our study showed that chamois groups were more likely to be closer to rocks when the nearest group of mouflon was larger. Mouflon group vicinity induced chamois to move closer to rocks only if mouflon rams were within the group. Chamois groups were more likely to be closer to rocks when the nearest livestock flock was larger and closer, especially when shepherds' dogs were present. Foraging patches of our study area were dominated by *S. albicans* and *Carex firma* irrespective to distance from rocks; thus, forage abundance was our proxy for different states of the

same vegetation association, and chamois clearly had lower food availability when they moved closer to rocks.

Different ungulate species that co-evolved were hypothesized to have developed mechanisms to limit the degree of resources competition (Prins et al., 2006). When a non-native ungulate is introduced in a long-established ungulate community, however, resource partitioning is unlikely to occur (Latham, 1999). Darmon et al. (2012) showed that coexistence and spatial overlap between Alpine chamois and mouflon in the northern French Alps may be possible because resource partitioning occurs. In contrast, we observed that the distance of mouflon groups affect chamois to be closer to rocks if mouflon rams were within the group, implying that chamois used areas with lower food availability. According to feeding ecology, Bertolino et al. (2009) confirmed the mouflon being a grass feeder in Italian Western Alps. The scat analyses showed that also Alpine chamois can be considered a grass feeder during summer (García-González and Cuartas, 1996). In this season, a remarkable dietary overlap was thus observed in the Alps between these two species mainly based on a similar use of graminoids and dicotyledons (Bertolino et al., 2009).

Table 4

Averaged parameters ($\hat{\beta}$), standard errors ($\hat{se}(\hat{\beta})$), and 95% Confidence Intervals (CIs) estimated by model averaging for the top two linear mixed models ($\sum_{i=1}^2 w_i = 0.90$; see Table 3 predicting the variability of the distance of chamois groups from rocks (\log_e -transformed, in metres) in the Eastern Alps, Italy (2007–2008).

Predictors	$\hat{\beta}$	$\hat{se}(\hat{\beta})$	95% Confidence Intervals	
			Lower	Upper
Intercept	−2.153	1.196	−4.497	0.091
Shepherds' dogs _[absent]	1.870	0.368	1.149	2.591
Shepherds' dogs _[present]	0 ^a	—	—	—
Month _[June]	0.752	0.363	0.041	1.463
Month _[July]	0.014	0.305	−0.584	0.612
Month _[August]	−0.054	0.319	−0.679	0.571
Month _[September]	0 ^a	—	—	—
\log_e -chamois group size	0.018	0.004	0.010	0.026
Rams within mouflon group (%)	−7.805	2.245	−12.205	−3.405
\log_e -mouflon group size	−0.284	0.104	−0.488	−0.080
\log_e -distance from mouflon group	0.073	0.095	−0.113	0.259
\log_e -livestock group size	−0.272	0.058	−0.386	−0.158
\log_e -distance from livestock group	0.693	0.093	0.511	0.875
Slope	0.019	0.008	0.003	0.035
\log_e -distance from mouflon group \times rams within mouflon group (%)	1.169	0.361	0.461	1.877

^a This parameter is set to zero because it is redundant.

In our study-site the mouflon group size and mostly the composition of the nearest mouflon group forced chamois to use meadows closer to rocks. Chamois spatial distribution was strongly affected by the presence of rams in mouflon groups, suggesting that physical displacement is likely to occur when the latter are present. Mouflon rams are massively horned and heavier than chamois of both sexes, and they might be considered as potential competitors (see Pérez-Barbería et al., 1996 for *Rupicapra pyrenaica parva* and LeBlanc et al., 2001 for *Ovis canadensis*). Notwithstanding, there is no evidence of direct aggression or chasing of Alpine chamois by mouflon and further studies are needed to understand the mechanism of interaction between these species. Larger ungulate species sometimes prevail over smaller ones (Berger and Cunningham, 1998; Ferretti et al., 2011), especially when the coexistence of the two populations is quite recent, as suggested by findings on Himalayan thar (*Hemitragus jemlahicus*) and Alpine chamois in New Zealand (Forsyth and Hickling, 1998). Parkes and Forsyth (2008) showed that the diets of these two species strongly overlapped and the presence of thar modified chamois diet. Moreover, in regard to behavioural patterns, the two species showed signs of mutual intolerance and the effect of disturbance caused by interspecific encounters was sometimes pronounced on chamois (Forsyth and Clarke, 2001). A similar mechanism may be operating between Alpine chamois and mouflon in our study area. On the other hand, there are examples of smaller grazing ungulates apparently displacing larger ones (e.g., Nugent et al., 1987; Wray, 1992). Danilkin (1996) showed that the co-presence of sika deer (*Cervus nippon*) and roe deer entailed a change in population trends, with the latter showing a decline in population size after the former was introduced. In our study site mouflon population steadily increased, while the native species, after an increase in the 1980s and 1990s, recorded a stationary density in the last few years. However, these densities were collected on a large scale, whereas eventual displacements could have taken place at a very localized scale.

The co-presence of livestock was found to influence the distribution and behaviour of native ungulates (Kie, 1996; Coe et al., 2001; Brown et al., 2010), as the latter can be forced to move from the areas occupied by livestock to avoid visual and acoustic disturbance (Mattiello et al., 2002). No case of mixed groups with other ungulate species (wild or domestic) was reported for Alpine chamois. Diet overlap between domestic sheep and chamois is another source of interaction (Berdoucou, 1986; García-González et al., 1990; Rebollo et al., 1993; La Morgia and Bassano, 2009). In a recent study on Iberian ibex (*Capra pyrenaica*) in central Spain, the presence of a potential competitor (i.e., the domestic goat *Capra hircus* in extensive grazing system) forced ibex to select suboptimal habitats (Acevedo et al., 2007). Also, pronghorn (*Antilocapra americana*) was shown to avoid areas grazed by sheep during winter until spring regrowth occurred (Clary and Beale, 1983). Fankhauser et al. (2008) suggested that avoidance of feeding patches by the wild species should not only be interpreted in terms of interference, but should also be considered under the aspect of infection risk perception (Van der Wal et al., 2000; Ezenva, 2004). Livestock faeces odour may mediate the strength of this reaction (e.g., Aoyama et al., 1994). Similarly, our results showed that chamois selected foraging areas near rocks when livestock were closer and their group size was larger. Ruttimann et al. (2008) reported that all the encounters between chamois and domestic sheep only occurred when the latter moved into areas previously occupied by the former. On such occasions, when the number of domestic sheep was larger, chamois would usually show some signs of intolerance or leave the area. Kie et al. (1991) demonstrated that cattle competed with female mule deer (*Odocoileus hemionus*), particularly at high stocking rates, thus supporting our result on the impact of the increasing size of livestock flocks in forcing chamois groups to move from areas with higher forage abundance. Finally, in our study case, the presence

of the shepherd's dogs guarding the livestock also seemed to force chamois to stay closer to rocks. Also, the association between flocks and shepherd's dogs may account for greater responses to the presence of livestock groups in terms of distance. Lenth et al. (2008) reported that the presence of domestic dogs along recreational trails was correlated with altered patterns of habitat utilization by several ungulate species, but are needed to understand the effect of free-ranging dogs guarding livestock on the spatial behaviour of wild ungulates.

Alpine chamois in larger aggregations or in steeper terrain increased their probability to be more distant from rocks. As Molvar and Bowyer (1994) reported for Alaskan moose (*Alces alces gigas*), the group size was positively correlated with distance from cover, suggesting that social grouping is an adaptation to increased risk perception. Chamois took advantage of better foraging opportunities when they used steeper terrains, which are safer than flatter terrains for mountain ungulates (Grignolio et al., 2007b). Chamois groups were generally closer to rocks from July on, when the use of more shadowed areas (close to rocks) could be strategic to get relief from high summer temperatures (Aublet et al., 2009).

Our study clearly showed how a native herbivorous species adjusts its spatial distribution and decreases the likelihood of using areas with higher food availability when livestock and/or a non-native species co-occur. The contest for space and food among potential competitors could negatively affect long-term population dynamics of native species (Forsyth and Hickling, 1998; Forsyth, 2000; Mishra et al., 2004), particularly in mountainous areas where ungulates face seasonal nutritional bottlenecks.

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