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Ecological drivers of group size in female Alpine chamois, *Rupicapra rupicapra*

Abstract: In large mammalian herbivores, an increase in herd size not only reduces predation risk but also energy intake. As a consequence, the size of the groups made up by herbivores is often assumed to be the outcome of a trade-off depending on local predation risk and food availability. We studied Alpine chamois (*Rupicapra rupicapra*) group size in a 3660 ha wide area (central-Eastern Alps, Italy) where mouflon (*Ovis gmelinii*) were also present. We walked seven hiking trails (spanning a total of 33.9 km) in a high-elevation environment every 15 days from May to October in 2007–2009, and located all the groups of free-ranging ungulates within our study site. We analyzed the size variation in female groups with kids of Alpine chamois in relation to (i) forage availability (as estimated using the normalized difference vegetation index); (ii) distance from safe areas; (iii) presence of potential competitor species (i.e., mouflon); and (iv) environmental variables (elevation, slope exposure). We found that forage availability was one of the most important drivers of group size patterns. Larger groups were found in meadows with higher productivity, whereas smaller groups were located in lower quality meadows in sheltered areas, indicating how the female group size may be the outcome of both resource availability and predation risk avoidance. Interestingly, proximity of a mouflon group was able to modify the size of Alpine chamois female groups, especially if the nearest mouflon group was concurrently close and inclusive of a higher percentage of rams.

Keywords: forage quality; group size; *Ovis gmelinii*; *Rupicapra rupicapra*; shelter area.

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Introduction

It is often accepted that large mammalian herbivores make up groups whose size is a trade-off between the benefits of predation avoidance, i.e., benefits provided by shared vigilance and dilution of risk (Dehn 1990, Hunter and Skinner 1998, Childress and Lung 2003, Manor and Saltz 2003) and the costs of feeding competition (Jarman 1974, Kie 1999). The “many eyes” hypothesis (Pulliam 1973) and the “safety in numbers” hypothesis (Cresswell 1994) assume that vigilance serves the main function of detecting predators (Frid 1997, Beauchamp 2003, 2007), thus promoting the aggregation in large groups. The latter is also supported by the “herd defensive behaviour” hypothesis, i.e., all the females in the herd gather tightly around the kids, sheltering them under their bellies, as was observed in *Ovis canadensis* Shaw, 1841 (Geist 1971), *Ovis gmelinii ophion* Blyth, 1841 (Hadjisterkotis 1990), and *Rupicapra rupicapra* Linnaeus, 1758 (Bertolino 2003). Conversely, as Fritz and De Garine-Wichatitsky (1996) reported in the impala (*Aepyceros melampus* Lichtenstein, 1812), the perception of the resource by individuals in a group is strongly affected by the number of individuals foraging together. The trade-off between food availability and safety was reported to be influenced also by the habitat structure (Isvaran 2007) and may ultimately affect population performance (McNamara and Houston 1987). Thus, it is important, in light of conservation efforts, to understand the factors influencing the foraging activity and safety-related behaviours. In particular, it can be useful to identify the processes that can shape the variation in group size, analysing the costs and benefits of group living in different ecological contexts.

Among ungulates, the occurrence of larger groups in open grasslands has been extensively documented (Jarman 1974, Shankar Raman 1997, Isvaran 2007). Habitat selection should ensure access to abundant, high-quality forage (Zweifel-Schielly et al. 2008), especially over the months before the limiting season and during the female reproductive period. This requirement is particularly true in the case of species living in a mountain area that have to face nutritional bottlenecks, i.e., the winter season, and in which a delay in kids’ growth might affect their survival rate during the following winter (Clutton-Brock et al.

1989), ultimately influencing population performance (Gaillard et al. 1998, 2000, Raithel et al. 2007). Moreover, in a rugged mountain area, the selection of foraging sites could also be influenced, among other factors, by habitat structure, i.e., by the effects of more severe daily temperature range promoted by aspect and elevation (Crête and Courtois 1997). Living in better sites can contribute to an early development of young and guarantee a greater survival rate (e.g., Gaillard et al. 1997).

Among the factors that can also modify the behaviour and spatial distribution of the native species is the recent introduction of a potential competitor, particularly when the non-native species is more massively horned and heavier than the native one. Indeed, physical displacement can be a central mechanism of interaction, especially between two species with highly overlapping habitat use (Latham et al. 1999) in a limited environment. In fact, whereas native sympatric species commonly show low degrees of interaction as a consequence of niche separation and resource partitioning (Hartnett et al. 1997), the introduction of non-native species can dramatically change the previous set-up of the herbivore community and lead to competition (Chapman et al. 1993, Vázquez 2002).

We used the Alpine chamois (*Rupicapra rupicapra*) as a model species and studied the size of its groups in a rugged mountain area of the central-Eastern Alps (Italy) where the non-native mouflon (*Ovis gmelinii* Blyth, 1841) was also present. In particular, we considered groups of females with kids from May to October during the study period. This is a crucial period for kids, which should be provided with an abundant food intake thanks to better milk quality and later through direct access to high-quality meadows. At the same time, the newborn and kids are vulnerable to predation by golden eagles (*Aquila chrysaetos*) (Glutz Von Blotzheim et al. 1971, Ferrario et al. 1985, Haller 1996). Nebel et al. (1996) observed that kids of Pyrenean chamois (*Rupicapra pyrenaica* Bonaparte, 1845) represented over 80% of the prey biomass of golden eagles during the predator's breeding season. Whereas adult chamois are heavy and protected by horns, kids are more vulnerable to predation (Krämer 1969, Knaus and Schröder 1983, Haller 1996). Bertolino (2003) reported the observation of herd defensive behaviour as an attempt to prevent a golden eagle from preying on kids. Moreover, Hamel and Côté (2009) reported for mountain goats (*Oreamnos americanus* de Blainville, 1816) a similar maternal defensive behaviour and offspring reactions to avian predator are also consistent with anti-predatory defence reported against terrestrial predators (e.g., Lingle et al. 2005). Terrestrial predators such as wolves (*Canis lupus* Linnaeus, 1758), lynxes (*Lynx lynx* Linnaeus, 1758), and brown bears (*Ursus arctos* Linnaeus, 1758) can

be effective, too, even if the use of steep, rocky areas can reduce their impact on the ungulate community (see e.g., Gazzola et al. 2005). These species have disappeared from many areas within the distribution range of *Rupicapra* spp. However, according to Byers (1997), formerly present predators can be at the origin of behavioural adaptations that herbivores still exhibit.

We analyzed the size variation in female groups with kids of Alpine chamois, in relation to the effects of (I) quality of meadows, (II) distance from safe areas, (III) presence of mouflon, and (IV) variables related to the physical environment (elevation, slope exposure).

Specifically, the aim of this study was to test the following four hypotheses:

- H₁: We predicted that larger female groups should be found in meadows with higher productivity, showing how the female group size may be the outcome of forage availability. Feeding in the best foraging sites may lead to a high food intake and a proper body growth in summer (Festa-Bianchet and Côté 2008).
- H₂: According to predation risk avoidance, we predicted that large groups could keep at a greater distance from safety areas than smaller ones, especially in the presence of vulnerable offspring (Festa-Bianchet 1988a).
- H₃: As mouflon may negatively interact with native chamois (Gonzalez 1984, 1986, Bertolino et al. 2009, Chirichella et al. 2013), we expected chamois to make up larger groups when mouflon are present to avoid being displaced by them.
- H₄: Given that environmental variables (i.e., elevation and aspect) could have an impact on the microclimatic characteristics, compromising the survival of young ungulates in mountain ranges through a delay in growth (Festa-Bianchet 1988b, Clutton-Brock et al. 1989, Festa-Bianchet and Jorgenson 1998, Grignolio et al. 2007), we assumed that female chamois preferred areas facilitating thermoregulation in kids, and predicted that low elevation and southern exposure should promote the formation of larger groups.

Materials and methods

Study area

The present study was conducted in a 3660 ha wide area in the Presanella Massif (46°14'N; 10°45'E), central-Eastern

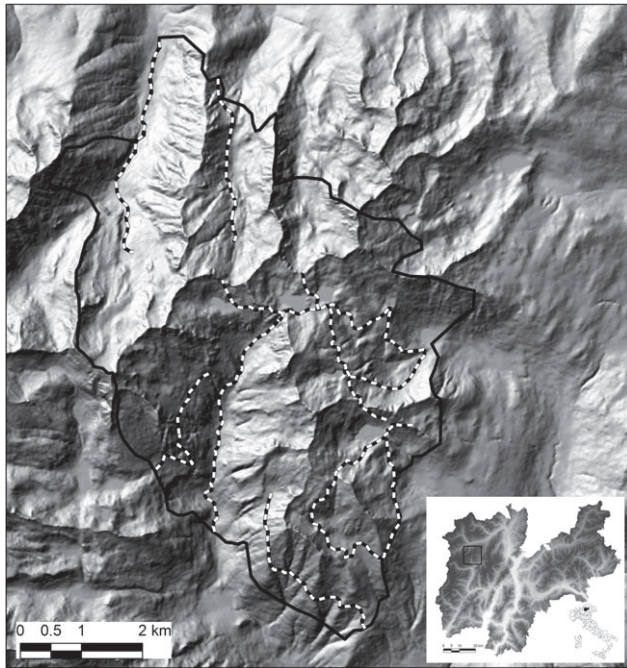


Figure 1 Digital elevation model of the 3660 ha study area, and its location (black square) in the Trento Province (Eastern Italian Alps, Italy). Black and white lines represent the seven hiking trails (33.9 km) that were walked once every 15 days from May to October (2007–2009).

Alps, Trento, Italy (Figure 1). Elevation of the area ranged from 1350 to 2950 m a.s.l. (mean: 2222 m). Direct observations were performed above the tree line (2000 m a.s.l.), where primary grasslands were typically composed by meadows of *Festuca scabriculmis* and *Carex curvula* (Adamello Brenta Park, official data). These areas were commonly used from May to October by Alpine chamois (13.7 individuals/100 ha; kids/adult females=0.73) and mouflon (introduced by hunting associations in the 1970s, 2 individuals/100 ha). Red deer (*Cervus elaphus* Linnaeus, 1758) and roe deer (*Capreolus capreolus* Linnaeus, 1758) were also abundant, although they more commonly used areas below the tree line. During the study period, neither domestic livestock nor free-ranging dogs were present in the places surveyed. We had no evidence of predation by the only large carnivore in the area, the brown bear, whereas the golden eagle preyed especially upon kids and lambs in their first weeks of life. Adamello Brenta Nature Park (and the surrounding area) is permanently occupied by pairs of this species (Pedrini et al. 2005). Within the Alpine chain, golden eagle nests are usually just below the top of the tree line, i.e., below the main hunting areas (Haller 1996, Haller and Sackl 1997), and the main foraging habitats include Alpine grassland (Haller 1996).

Data collection and analysis

From May to October in 2007–2009, we walked seven hiking trails (33.9 km, Figure 1) once every 15 days. Observations were conducted during the first 4 h after sunrise when the activity of wild ungulates was the highest (Cederlund 1989, Green and Bear 1990, Aublet et al. 2009). During each survey, we recorded and mapped all the groups of free-ranging ungulates using a 10×50 binocular, a 60× telescope, a Global Positioning System device, a hand compass, and a rangefinder. Individuals of each group of chamois and mouflon were assigned to age-sex classes following previous studies (for mouflon, see Ciuti et al. 2008, Pipia et al. 2009; for chamois, see Gerard and Richard-Hansen 1992, Herrero et al. 2002).

We examined how the number of adult females per group was affected by (I) forage quality and availability; (II) distance to and kind of safe areas; (III) presence of mouflon; and (IV) environmental and seasonal variables, elevation, aspect, and month of observation. The following variables were considered as potential predictors of the number of adult females per group during the May–October period:

(i) Forage quality and availability

We used the normalized difference vegetation index (NDVI), a satellite-based measurement collected by the National Aeronautics and Space Administration (Land Processes Distributed Active Archive Center, <https://lpdaac.usgs.gov>; United States Geological Survey–Earth Resources Observation and Science) as a proxy of forage quality and quantity (Reed et al. 1994, Griffith et al. 2002, Pettorelli et al. 2005) of the Alpine meadows used by each female chamois group. We considered the moderate resolution imaging spectroradiometer dataset (250 m resolution). We assigned the NDVI value of each plot assessed contextually to each survey (every 15 days) to the group located in it. Typical meadows covering the siliceous substrate inside the study area were homogeneous and dominated by *Festuca scabriculmis* and *Carex curvula* (Adamello Brenta Nature Park, official data). Thus, we considered a direct correlation between the NDVI values and productivity of meadows, i.e., higher values with greater biomass and greater levels of chlorophyll.

(ii) Distance and kind of safe areas

We calculated the log-transformed distance from the nearest rocks and from the tree line, the log-transformed perimeter/area of meadows, and the slope of the terrain (expressed within the 0–90° range, where 0° indicates flat terrains and 90° indicates rocky

walls) where the chamois group was observed to test the importance of close safe areas in shaping the female chamois group size. We also considered the month of observation as a fixed variable to control the potential effect of the vulnerability of kids.

(iii) Presence of non-native species

We calculated and associated to each female chamois group the log-transformed distance and the log-transformed group size of the nearest group of mouflon, and the percentage of rams within it.

(iv) Other environmental variables

We considered the elevation (in meters a.s.l.) and aspect of the terrain where the chamois group was observed. Aspect, initially expressed within the 0–360° range, was cosine transformed, thus assuming values ranging from -1 (south facing slopes) to 1 (north facing slopes), and subsequently sine transformed, assuming values from -1 (west facing slopes) to 1 (east facing slopes).

All spatial data were calculated using ArcGIS 9.3 (ESRI Inc. 1999–2008).

We built a correlation matrix (Pearson correlation coefficient, r_p) with all the explanatory variables potentially able to predict the size of female Alpine chamois groups so as to exclude collinearity issues. The correlation coefficient r_p was never higher than 0.7 (Sokal and Rohlf 1995). We then analysed the variation of log-transformed number of females per group by fitting a set of linear mixed effect models (LME) with the maximum likelihood (ML) method. The month of data collection was included in the models as a fixed factor, whereas the other predictor variables (listed above) were included as covariates. The hiking trail (sampling unit) repeated once every 15 days between May and October (from 2007 to 2009) was fitted as a random factor to avoid pseudo-replication of data (Machlis et al. 1985). We used the information-theoretic approach based on Akaike information criterion (AIC; Burnham et al. 2011, Symonds and Mousalli 2011) to select the best fitting model. The most complicated model considered included all the predictors listed above and their possible two-way interactions (total number of parameters: 25). The other models considered derived from the latter by simplification. 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. Statistical

analyses were performed using R version 2.13.1 (R Development Core Team 2011).

Results

From May to October in 2007–2009, we sighted a total of 1002 female chamois groups. The number of adult females within each group ranged from 1 to 25 (mean \pm SE: 5.86 ± 0.11), with no significant variation of mean group size between months when the latter factor was tested alone ($F_{5,996} = 0.615$, $p = 0.688$).

Table 1 shows the 10 best LME models predicting the log-number of adult females per group. We performed parameter estimates only for the model with the lowest AIC value (AIC=789.82, $R^2=0.42$; Table 1). The most parsimonious LME model included variables such as forage quality and availability (NDVI), distance and kind of safe areas, and presence of mouflon groups. The model included only one 2-way interaction (log-distance from the nearest mouflon group \times male percentage within the nearest mouflon group, Table 1). Neither the elevation and aspect of the terrain where the chamois group was observed nor the month of observation was found to affect the number of adult females per group (Table 1).

Female chamois groups were larger when the forage quality and quantity were higher (Pearson correlation with log-number of adult females within each group: $r_p = 0.547$, $p < 0.001$; $n = 1002$). With respect to the variables related to the distance and kind of safe areas, smaller female chamois groups were located on steeper slopes, closer to the rocks and to the tree line, and grazing on meadows with irregular shape, i.e., with a higher ratio between perimeter and area (Table 2). The presence of mouflon groups was also found to affect female chamois group size: the closer the mouflon group, the larger the female chamois group size; likewise, the higher the percentage of rams within the nearest mouflon group, the larger the female chamois group size (Table 2). Finally, female chamois group size was affected by the interaction of these two variables: a female chamois group of a given size kept at a greater distance from the nearest mouflon group when rams were present and this distance was reported to be proportional to the percentage of rams (Table 2).

Discussion

The group size of females with kids was found to be stable throughout the birth, lactation, and weaning periods.

Table 1 The 10 best linear mixed-effect models explaining the variation of the (log-transformed) number of Alpine chamois adult females per group.

Forage quality and availability NDVI		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Safety areas	log-Distance from rocks	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	log-Distance from tree line	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Slope	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	log-Perimeter/area of meadows	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	log-Distance from rocks×log-Distance from tree line	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	log-Distance from rocks×log-Perimeter/area of meadows	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Presence of mouflon	log-Distance from tree line×log-Perimeter/area of meadows	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Month of observation	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	log-Distance from mouflon	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	log-Mouflon group size	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Males within mouflon group (%)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	log-Distance from mouflon×log-Mouflon group size	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Environmental variables	log-Distance from mouflon×Males within mouflon group (%)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	log-Mouflon group size×Males within mouflon group (%)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Elevation	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	cos-Aspect (N-S)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	sin-Aspect (E-O)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
AIC		804.180	803.591	803.416	800.036	799.458	798.494	798.478	797.372	796.526	789.823						
ΔAIC		14.357	13.768	13.539	10.213	9.635	8.671	8.655	7.549	6.703	0						

Each column represents a single model. [x=terms included in a model, AIC=Akaike information criterion value; ΔAIC=difference in the AIC value between a given model and the most parsimonious model (i.e., lowest AIC)]. See the text for details on model selection and on explanatory variables.

Table 2 Parameter estimates (β), standard errors (SE), and 95% Confidence Intervals (CIs) of the best model (AIC=789.823; $R^2=0.42$; see Table 1) explaining the variation of the (log-transformed) number of Alpine chamois adult females per group.

Parameter	β	SE	CIs	
			Lower	Upper
Intercept	0.420	0.171	0.085	0.755
NDVI	0.728	0.043	0.644	0.812
log-Distance from rocks	0.233	0.010	0.213	0.253
log-Distance from tree line	0.060	0.010	0.040	0.080
Slope	-0.005	0.001	-0.007	-0.003
log-Perimeter/area of meadows	-0.113	0.017	-0.146	-0.080
log-Distance from mouflon	-0.174	0.024	-0.221	-0.127
Males within mouflon group (%)	0.240	0.054	0.134	0.346
log-Distance from mouflon \times Males within mouflon group (%)	-1.030	0.263	-1.545	-0.515

This finding could presumably be related to (i) the vulnerability of kids throughout the monitoring period (from May to October); (ii) the social behaviour of females that aggregate while reaching areas above the tree line (i.e., our monitoring areas) after birth period (Krämer 1969); and (iii) the end of data collection, set before the rutting period, occurring in November (Schröder 1971). As a matter of fact, for both Alpine and Pyrenean chamois, mother and kid remain very close to one another during the first six months of the kid's life, i.e., far beyond the end of lactation at the end of August (Richard-Hansen and Campan 1992, Ruckstuhl and Ingold 1999).

Our study shows that female group size in Alpine chamois was significantly affected by the productivity of meadows. We found larger groups in meadows with higher forage quality and availability. In contrast, smaller female chamois groups were located in low-quality meadows but closer to safe areas, i.e., closer to the rocks and to the tree line, typical refuge areas for Alpine chamois (Bögel and Härer 2002). In addition, both the slope of terrain and the irregular shape of meadows negatively affected group size. Chamois took advantage of steeper terrains that can be considered safer than flatter terrains (Grignolio et al. 2007). Moreover, potential escape routes are more numerous in areas with irregular shapes where the centre of the meadow is closer to a safe area. Accordingly, female group size seems to be a response to forage availability, i.e., better foraging sites attract greater numbers of females, and/or intra-competition effect (i.e., better foraging sites support greater numbers of females), as well as to predation risk.

Our findings are consistent with those obtained by other authors. Molvar and Bowyer (1994) reported that Alaskan moose (*Alces alces gigas* Linnaeus, 1758) group size increases with distance to cover. Moreover, Festa-Bianchet and Côté (2008) reported that in areas where mountain goats make greater use of precipitous

cliffs, they should form much smaller groups than those observed in the open tundra of Caw Ridge (northwest of Grande Cache, Alberta), owing to a combination of smaller foraging areas and lower predation risk. However, it should be noted that the results reported by these authors and those obtained in the present study might also be a simple consequence of group instability and mobility. In many ruminant species including the chamois (Pépin and Gerard 2008), groups are mobile entities often fusing and splitting up. According to Barrette (1991) and Gerard et al. (2002), this instability makes mean group size sensitive to any increase in local population density and/or the distance at which individuals can see one another because increase in these parameters enhances the probability of group fusion. In this regard, group mobility might further lead to gradients of mean group size between open meadows where visibility is high, and forests or rocky areas where visibility is reduced.

Contest for space and food among potential competitors can negatively affect the 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. A remarkable overlap has been reported in the Alps between the diets of chamois and mouflon, both species being mainly grass eaters during the growing season (Bertolino et al. 2009; see also García-González and Cuartas 1996 for the Pyrenean chamois). Moreover, as reported by Gonzalez (1984, 1986) in the Pyrenees, and by Chirichella et al. (2013) in a mountain massif adjacent to the present study area, mouflon tend to modify the spatial distribution of chamois. There is no evidence of direct aggression or chasing of chamois by mouflon, but spatial displacement of the former by the latter clearly occurs. In the present study, the size of female chamois groups was positively affected by the presence of mouflon: the closer the nearest

mouflon group, the larger the female chamois group size. Moreover, the presence of mouflon rams seemed to induce chamois to form larger groups, possibly because rams are heavier and more massively horned than chamois (Pérez-Barbería et al. 1996, LeBlanc et al. 2001). Accordingly, hypothesis H₃ seems to be correct: female groups of Alpine chamois may aggregate to avoid spatial displacement by mouflon, especially by rams. However, following the mechanistic arguments of Barrette (1991) and Gerard et al. (2002), it might alternatively be argued that larger chamois groups are a simple consequence of displacement by mouflon, provided that displacement of a chamois group often makes it encounter another chamois group.

Finally, our findings show that the female chamois group size was not influenced by environmental variables, such as elevation and aspect of the terrain, where chamois groups were observed. This result suggests that, in contrast to what Pépin and Gerard (2008) found in the Pyrenean chamois, female Alpine chamois are not especially attracted by warmer locations in the growing season.

Our study showed how the group size of this herbivorous species can be modified by different ecological processes. Considering and monitoring these processes in a crucial period for kids should help to better understand and foresee annual population recruitment, an important conservation issue for a native ungulate exposed to human interventions (mainly hunting) and seasonal nutritional bottlenecks.

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