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Reproductive payoffs of territoriality are snow-dependent in a mountain ungulate, the Alpine chamois

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Abstract

Female density and distribution are dependent on resource phenology and female availability strongly influences male mating behaviour and success. When a male adopts a 'resource defence' tactic, his reproductive success depends on the location and attractiveness of his territory. Environmental factors associated with territory quality are expected to influence mating success, for example, through territory features or male–male competition. In a protected population of a mountain-dwelling polygynous herbivore, the Alpine chamois *Rupicapra r. rupicapra*, we investigated the relationships among mating opportunities, some environmental variables (snow depth, topographic features and size of territories) and male intra-sexual competition for mating. We recorded the mating behaviour and territory size of 15 GPS-GSM radio-tagged territorial males, during five rutting seasons (early November to early December: $N = 8$ individuals in 2011, $N = 9$ in 2012, $N = 8$ in 2015, $N = 11$ in 2016, $N = 7$ in 2017; 80% of them were observed for more than one mating season) and related them to snow depth and topography of territories. In ruts with deep snow cover, territorial males had smaller territories and higher number of mating opportunities than in ruts with lower snow cover. Smaller territories showed the highest values of terrain roughness, in turn with little or no snow cover in the mating season, and were visited by a greater number of females, than larger territories. Number of wins was positively influenced by snow depth and negatively related to the frequency of aggressions. The frequency of male–male aggressive interactions was greater during ruts with deep snow cover and for males with territories at higher elevations; additionally, it was negatively related to interactions won. Thus, snow depth, which influences resource distribution and female movements, is confirmed as a strong determinant of male mating opportunities and mating behaviour.

Introduction

A territory is an exclusive area defended by one individual who rarely moves beyond its limits. The territory owner reacts aggressively to intruding conspecifics of the same sex and behaves submissively outside (Burt, 1943: for mammals; Owen-Smith, 1977: for ungulates). Males can compete directly or indirectly for mates, for example, for resources that attract females (Emlen & Oring, 1977). The evolution of one of these mating tactics depends on female availability, which is directly related to female density, distribution, group size and stability, and indirectly related to the distribution of resources (Clutton-Brock, 1989; Gosling, 1986). When the spatial distribution of receptive females is predictable in time and space

(e.g. when they occupy small stable ranges around clumped resources) or in areas where resources are abundant and temporally stable, such as in forests (Geist, 1987; Owen-Smith, 1977), 'resource defence polygyny' will be favoured (Emlen & Oring, 1977). In this system, males gain access to females by exploiting how resources will influence female distribution and by competing for resource-rich sites. Thus, the reproductive success of a male depends on the location and attractiveness of his territory (Carranza et al., 1990; Carranza, 1995, for red deer *Cervus elaphus*). Conversely, a harsh climate and strongly seasonal food resources generate group instability and oestrus synchrony, thus militating against the development of male territoriality (Gosling, 1986; for Caprinae: Corlatti & Lovari 2023).

Territoriality is common in ungulates (Geist & Walther, 1974) with exceptions (Owen-Smith, 1977): it is quite rare in the Caprinae, probably because of the environmental features where most species of this subfamily have evolved, that is, rugged areas with a harsh climate and highly seasonal food resources (Geist, 1985; Schaller, 1977). Thus, understanding the way environmental variables influence the reproductive success of territorial males would be important to shed light on factors shaping the development of territoriality.

Information is controversial on the relationship between size of a territory and the owner's mating success. Johansson (1996) reported that roe deer *Capreolus capreolus* male mating success was related to the availability of nutritious food resources in territories and not to territory size. By contrast, Vanpé et al. (2009) suggested that territory size – not habitat quality – influenced the number of female roe deer in a male territory. Information is missing on the influence of environmental variables and topographic features of a territory (e.g. elevation, slope and aspect) on female attractiveness. Several studies on territorial ungulates have shown a relationship between access to potential mates and territory features such as forage quality/abundance (American pronghorn *Antilocapra americana*: Kitchen, 1974; puku *Kobus vardoni* and topi antelopes *Damaliscus lunatus*: Balmford et al., 1992; red deer: Carranza, 1995) and safety from predators (e.g. percentage of vegetation cover, cliff height and steepness: mountain reedbuck *Redunca fulvorufula chanleri*: Dunbar & Roberts, 1992; puku and topi antelopes, Balmford et al., 1992).

Information on polygynous ungulates indicates that individual dominance can also influence reproductive success (Pelletier & Festa-Bianchet, 2006; Willisch et al., 2012; Wolff, 1998). Females could gain genetic benefits by choosing a 'good' dominant male, for example, with a good territory (Balmford et al., 1992; Byers et al., 1994; Hogg, 1987; Trivers, 1972), with exceptions (Lovari et al., 2009). In fact, territory quality could be indirectly related to the owner's dominance (Balmford et al., 1992), which is costly in terms of energy invested in the defence of an area (Parker, 1974), stress level (Corlatti et al., 2012; Creel, 2001; Mooring et al., 2006) and susceptibility to parasites (Corlatti et al., 2012, 2019; Pelletier et al., 2005).

We investigated the relationships among topographic features and size of territory, male dominance, snow depth and mating opportunities, in a weakly polygynous, mountain-dwelling large mammal, the Alpine chamois *Rupicapra r. rupicapra* (Bovidae: Caprinae). Two alternative reproductive tactics (ARTs) have been described in male chamois (Corlatti et al., 2012; Krämer, 1969): during the rut (November), at the lower elevations, some individuals (territorials, T) defend an exclusive area from intruders and try to keep females there; other males (non-territorials, NT) court females by following them and intruding other males' territories. Territories in chamois have been described as hotspots attractive to females during the rut because of reduced snow cover (von Hardenberg et al., 2000). Moreover, Lovari et al. (2006) suggested that snow cover could have an important effect on determining the success of ARTs in chamois. In autumns with abundant snowfalls, females would move to lower elevations where they can meet territorial males (von Hardenberg

et al., 2000), favouring their mating success. In years with negligible or delayed snow cover, female chamois would rut at higher elevations, where non-territorial males may have an advantage (Lovari et al., 2006). This suggestion has been recently confirmed (Corlatti et al., 2020). Male chamois change mating tactic neither as the rut progresses nor across years (Cotza et al., 2023). They start to show territorial behaviour in late spring (von Hardenberg et al., 2000). However, no information exists on the relationships among mating opportunities, territory features (e.g. size, elevation, slope and terrain roughness), snow depth, intra-sexual competition and dominance (in terms of frequency of male–male aggressive interactions and number of wins) of a territory owner. We used intensive GPS-GSM radio-tracking and individual-level direct behavioural observations to assess these relationships. We assumed that snow cover is a major ultimate determinant of the number of females available to territorial male chamois (Corlatti et al., 2020; Lovari et al., 2006), which has been shown as a reliable predictor of male reproductive success (Corlatti, Bassano, et al., 2015). We investigated environmental and behavioural factors potentially influencing mating opportunities, territory size and indices of dominance and aggression for territorial male chamois. We predicted that (i) mating opportunities will be positively associated with snow cover (Corlatti et al., 2020; Lovari et al., 2006), territory size (Vanpé et al., 2009) and topographic indices of territory roughness because of the relevant potential effect on territory attractiveness to females (Balmford et al., 1992). Additionally, we would expect a strong male–male competition to occupy the best territories in terms of access to the highest number of females (Carranza & Valencia, 1999; Gibson & Guinness, 1980; Vanpé et al., 2009). Accordingly, the best territories should be occupied by the 'dominant' competitors in intra-sexual contests; thus, we expected mating opportunities to be positively associated with the frequency of male–male aggressive interactions and with the number of wins. We predicted that (ii) territory size would be negatively associated with snow cover, which has been repeatedly shown to limit ungulate movements (Rivrud et al., 2010; van Beest et al., 2011), and it would be positively related to the frequency of aggressive interactions and the number of wins because the costs of defence should increase as territory size increases (Hixon, 1980; Schoener, 1983, 1987). In ruts with deeper snow, non-territorial males and females have been shown to move to lower elevations, where territorial males stay (Corlatti et al., 2020; von Hardenberg et al., 2000), which would likely increase the probability of male–male interactions. Thus, we predicted that both (iii) the number of interactions won and (iv) the frequency of male–male aggressive interactions would be positively associated with snow cover and with the number of mating opportunities because a greater number of females in territories would be expected to attract competing males.

Materials and methods

Study area and population

Our study was conducted in the upper part of the Orco Valley (45°27′21″ N, 7°10′27″ E), within the Gran Paradiso National Park (GPNP), Western Italian (Graian) Alps. The area extends

between 1600 and 2300 m a.s.l. Snow cover lasts from November to May. During the study years, mean temperature at rut time (early November to early December) has been −0.6°C (maximum of 12°C in November 2015 and minimum of −10.5°C in December 2012). The chamois population in the Park has been protected since 1922 and its size is estimated at *c*. 6800 individuals presently, over 710.44 km^2 (2018 GPNP count). The density of the population in the study area is estimated at 10 ind/km^2 (Corlatti, Fattorini, & Nelli, 2015). Predation by the golden eagle *Aquila chrysaetos* and by the red fox *Vulpes vulpes* may occur on kids, although occasionally (Bertolino, 2003). Large terrestrial predators were absent (2011–2012) to rare (2015–2017, grey wolf *Canis lupus*; see also Palmegiani et al., 2013). For further details on the study area, see Lovari et al. (2006), Corlatti et al. (2012), and Corlatti, Bassano, et al. (2013).

Data collection and analysis

Capture, marking and behavioural observations

Between February 2010 and January 2013 and between November 2015 and January 2016, 31 adult (4–13 years old) male chamois were darted for sedation and fitted with individually recognizable Global Positioning System (GPS; 1 fix/7 h) collars, with very high-frequency (VHF) beacon devices (Vectronic Aerospace GmbH, Berlin, Germany) and coloured ear tags. In accordance with Italian law, chamois were sedated with a combination of xylazine (40 mg/animal) and ketamine (20 mg/animal) to reduce levels of stress due to handling (Bassano et al., 2004) and reversed by an injection of atipamezole (5 mg/animal; Dematteis et al., 2009), following a standardized procedure already used in previous studies on the species in the same area (Corlatti et al., 2012; von Hardenberg et al., 2000). The study reported in this paper is relevant to territorial males only (*N* = 15) and was conducted during five rutting seasons (6th of November to 5th of December; 2011: *N* = 8 individuals, 2012: *N* = 9, 2015: *N* = 8, 2016: *N* = 11, 2017: *N* = 7). The distinction between territorial (T) and non-territorial (NT) males was based according to Corlatti et al. (2012): during the rutting season, T males show site fidelity, hence a smaller home range size, and win aggressive interactions – within their territories, while losing outside – with intruding males, in respect to NT individuals. The number and the outcome of aggressive interactions (cf. Krämer, 1969; Lovari, 1985; Lovari & Locati, 1991) with other males were recorded for a total of *c*. 7 h of observations/individual/year, by focal animal sampling (Altmann, 1974), during the rutting period (cf. Corlatti et al., 2012; Cotza et al., 2023). Observations were evenly distributed over the entire rut and across all males (cf. Corlatti et al., 2012) and were conducted through binoculars and spotting scope from distant locations to avoid disturbance. For further details of the male classification, see Corlatti et al. (2012).

We collected a total of 281 h of observations on territorial males (median value = 7 h/male; IQR = 4.5–8 h/male).

Mating behaviour indices

For each rutting period and for each male, we calculated: (i) individual home range size (90% fixed kernel, Börger et al., 2006) and (ii) the index of wins in aggressive interactions with other males (IW index: number of interactions won/total number of interactions; cf. Corlatti et al., 2012).

Besides the index of wins in aggressive interactions with other males (IW index), we calculated the hourly frequency of intra-sexual aggressive interactions for each male (number of interactions/number of observation hours). The number of females within 50 m of the focal male was also recorded, every 20 min, during the focal animal sampling bouts (cf. above): we then calculated the mean number of females per hour per each male, as an index of mating opportunities (Corlatti et al., 2012; Corlatti, Caroli, et al., 2013; von Hardenberg et al., 2000).

Topographic features of territory and snow depth data

We considered kernel 90% estimates of home range size to evaluate relationships among territory size, topography, snow depth, dominance and mating opportunities for territorial males. After failure of GPS-GSM radio-tag batteries, efforts were made to replace the collar before the following mating season. Meanwhile, coordinates of visual locations/individual/day were recorded on a map. We found no significant differences between GPS-based and visually based home range estimates (Mann–Whitney test: *U* = 24, *P*-value = 0.44) in a subsample of territorial males (*N* = 8). Through QGIS software (QGIS Development Team, 2016), we visually inspected 90% kernel estimates of home ranges and overlaid them to a digital elevation model (DEM, reference system: WGS84-32N) of the study area, with a spatial resolution of 10 × 10 m (Tarquini et al., 2012; Tarquini, Isola, Favalli, & Battistini, 2007; Tarquini, Isola, Favalli, Mazzarini, et al., 2007), transformed to a resolution of 25 × 25 m, to fit the resolution of the home range shapefiles. From the DEM, we obtained the following parameters/indices (raster maps) for our study area:

- elevation (in m),
- slope, terrain roughness, terrain ruggedness index (TRI) and topographic position index (TPI), as indices of terrain asperity.

In our same study area, Nesti et al. (2010) showed that throughout the year nearly all males used south and south-east facing slopes. Our observations and preliminary analyses have confirmed this pattern (see Fig. S1). Therefore, we did not consider the aspect as a variable in our study.

We used 'terrain' function, from 'raster' library (Hijmans, 2019) in R, to obtain the above maps. Eventually, we extracted the values of the environmental parameters corresponding to each cell defining the territories, using the function 'extract', 'raster' library (Hijmans, 2019) in R, and we calculated their median values.

Table 1 Model selection for the mating opportunity index (mean number of females/h), territory size (HR, 90% KDE), index of wins in male–male aggressive interactions (IW, interactions won/total interactions) and frequency of male–male aggressive interactions (number of interactions/h) of territorial male Alpine chamois in 2011–2012 and 2015–2017

Response	Predictor	df	AICc	ΔAICc	Weight	Evidence ratio
Mating opportunities	**Altitude + (log)HR + (log)Snow + Roughness + TPI**	**8**	**58.5**	**0.00**	**0.947**	
	Altitude + Frequency of Interactions + IW + (log)HR + (log)Snow + Roughness + TPI	10	64.2	5.78	0.053	18
	—	3	80.3	21.88	0.000	56 387.3
	Frequency of Interactions + IW	5	81.4	22.95	0.000	96 278.5
Territory size	**Altitude + (log)Snow + Roughness + TPI**	**6**	**64.1**	**0.00**	**0.932**	
	Altitude + Frequency of Interactions + IW + (log)Snow + Roughness + TPI	8	69.4	5.25	0.068	13.8
	—	2	100.2	36.11	0.000	69 372 424
	Frequency of Interactions + IW	4	103.5	39.42	0.000	363 031 440
Index of wins	**Altitude + Frequency of Interactions + (log)HR + (log)Snow + Mating Opportunities + Roughness + TPI**	**9**	**7.9**	**0.00**	**0.734**	
	Frequency of Interactions + Mating Opportunities	**4**	**10.2**	**2.29**	**0.233**	**3.1**
	Altitude + (log)HR + (log)Snow + Roughness + TPI	7	15.4	7.53	0.017	43.2
	—	2	15.5	7.61	0.016	44.9
Frequency of interactions	**Altitude + IW + (log)HR + (log)Snow + Mating Opportunities + Roughness + TPI**	**9**	**−11.0**	**0.00**	**0.628**	
	IW + Mating Opportunities	**4**	**−8.8**	**2.28**	**0.200**	**3.1**
	—	2	−7.8	3.29	0.122	5.2
	Altitude + (log)HR + (log)Snow + Roughness + TPI	7	−6.0	5.08	0.050	12.7

The table includes: response variables, explanatory variables included in the predictors, degrees of freedom, Akaike information criterion corrected for small sample size (AICc), ΔAICc values, model weight and evidence ratio for the best model (i.e. the relative likelihood of the top-ranked model vs. each model in the list). Selected models are in bold.
TPI, topographic position index.

During the ruts of 2011–2012 and 2015–2017, daily values of snow depth (in cm) were collected from a weather station in our study site (Lake Serrù, 2275 m a.s.l.- A.E.M. Turin). We calculated the median value of snow depth for each rutting season (Table S1).

Statistical analyses

The considered dependent variables were either positive continuous (mating opportunities: median value = 0.75, IQR = 0.33–2.36; territory size: median value = 10.75 ha, IQR = 5.72–16.00 ha; frequency of male–male aggressive interactions: median value = 0.89, IQR = 0.68–1.09) or bounded between 0 and 1 (index of wins in male–male aggressive interactions − IW index: median value = 0.90, IQR = 0.79–1.00), for which it was plausible to assume gamma- and beta-conditional distributions respectively (Bolker et al., 2009; Crawley, 2007). However, a preliminary data exploration suggested that these conditional distributions were not a good fit to our data and that the realized values could be best described by using simple linear models.

The IW index was arcsine square root transformed before model fitting, as customary for percentage data (Crawley, 2007). For the other dependent variables, we first checked if a transformation of it could lead to a better model fit through a Box–Cox transformation for linear models (function 'boxcox', 'MASS' library; Venables & Ripley, 2002). The Box–Cox transformations suggested a square root transformation for mating opportunity index and the frequency of aggressive

interactions, and a logarithms transformation for territory size. Additionally, a log-transformation of median snow and territory size was used, in the predictors, to make their distribution more homogeneous.

We tested for collinearity among the available explanatory variables (snow depth, territory size, elevation, slope, terrain roughness, terrain ruggedness index – TRI, topographic position index – TPI, frequency of aggressive interactions and IW index) by calculating the variance-inflation factors, using the function 'vif', 'car' library (Fox & Weisberg, 2019), in R. Slope and TRI showed very high VIF values (>105).

For each dependent variable, we fitted a global additive model (i.e. a model with all the biologically meaningful variables at hand that could plausibly explain the variation in the dependent variable), first with, then without, individual identity of males (ID) as a random intercept to account for repeated sampling of the same individual. The two models were compared through a F-test (function 'anova', 'stats' library; R Core Team, 2022): if they were not statistically different, we retained the model without the random term. We also visually inspected the residual distribution of the selected global model to check for the fulfilment of the underlying assumptions in terms of linearity, normality and heteroscedasticity. We used functions 'check_model' and 'check_heteroscedasticity' ('performance' library; Lüdecke et al., 2021).

Then, we fitted four *a priori* models for each dependent variable, following prior predictions: a global model (see above), an intercept-only model, a model including only the behavioural predictors (frequency of aggressive interactions, mating

Table 2 Parameter estimates from the models selected to investigate variation in the mating opportunity index (mean number of females/h), territory size (HR, 90% KDE), index of wins in male–male aggressive interactions (IW, interactions won/total interactions) and frequency of male–male aggressive interactions (number of interactions/h) of territorial male Alpine chamois in 2011–2012 and 2015–2017

Response	Predictor	β	SE	95% CI
Mating opportunities	Intercept	1.000	0.078	**0.85; 1.15**
	(log)HR	−0.181	0.097	−0.37; 0.01
	Altitude	0.123	0.064	0.00; 0.25
	Roughness	0.074	0.077	−0.08; 0.22
	TPI	0.070	0.082	−0.09; 0.23
	(log)Snow	0.186	0.069	**0.05; 0.32**
Territory size	Intercept	2.243	0.070	**2.10; 2.38**
	Altitude	−0.009	0.075	−0.16; 0.14
	Roughness	−0.297	0.079	**−0.46; −0.14**
	TPI	−0.336	0.074	**−0.49; −0.19**
	(log)Snow	−0.230	0.075	**−0.38; −0.08**
Index of wins	Intercept	1.285	0.035	**1.21; 1.36**
	Mating opportunities	0.051	0.050	−0.05; 0.15
	Frequency of interactions	−0.136	0.043	**−0.22; −0.05**
	(log)HR	0.033	0.062	−0.09; 0.16
	Altitude	0.007	0.040	−0.07; 0.09
	Roughness	−0.084	0.046	−0.18; 0.01
	TPI	0.013	0.046	−0.08; 0.11
	(log)Snow	0.157	0.046	**0.06; 0.25**
Frequency of interactions	Intercept	0.923	0.029	**0.86; 0.98**
	Mating opportunities	0.029	0.039	−0.05; 0.11
	IW	−0.101	0.036	**−0.17; −0.03**
	(log)HR	0.052	0.049	−0.05; 0.15
	Altitude	0.067	0.030	**0.01; 0.13**
	Roughness	−0.057	0.037	−0.13; 0.02
	TPI	−0.009	0.037	−0.08; 0.07
	(log)Snow	0.104	0.039	**0.02; 0.18**

Confidence intervals that do not include 0 are shown in bold.
CI, Confidence interval; TPI, topographic position index.
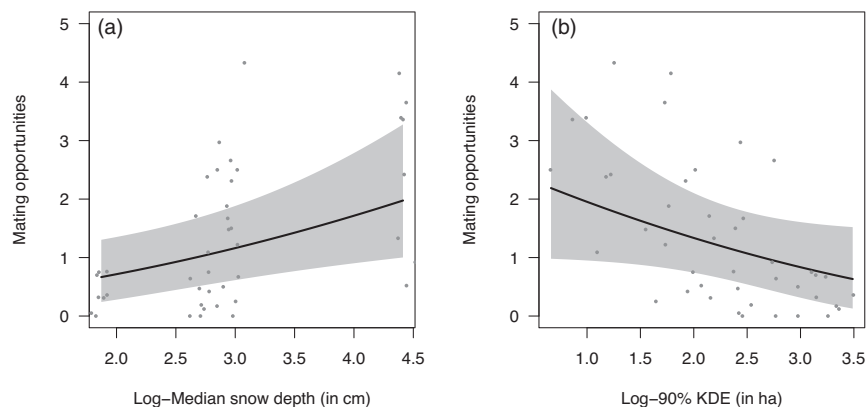
opportunities and index of wins) and a model including only the environmental variables (territory size, elevation, terrain roughness, TPI and median snow depth during the rut), excluding the variable used as the response.

We finally compared the four models following an approach based on the minimum Akaike's information criterion, corrected for small samples (AICc: Hurvich & Tsai, 1989) and selected unnested models with cumulative AICc weight >0.95 (Arnold, 2010; Burnham & Anderson, 2002). If more models were included in the final candidate set, we averaged their parameters to obtain final estimates (Burnham & Anderson, 2002). Data points in the diagrams have been jittered to improve data visualization.
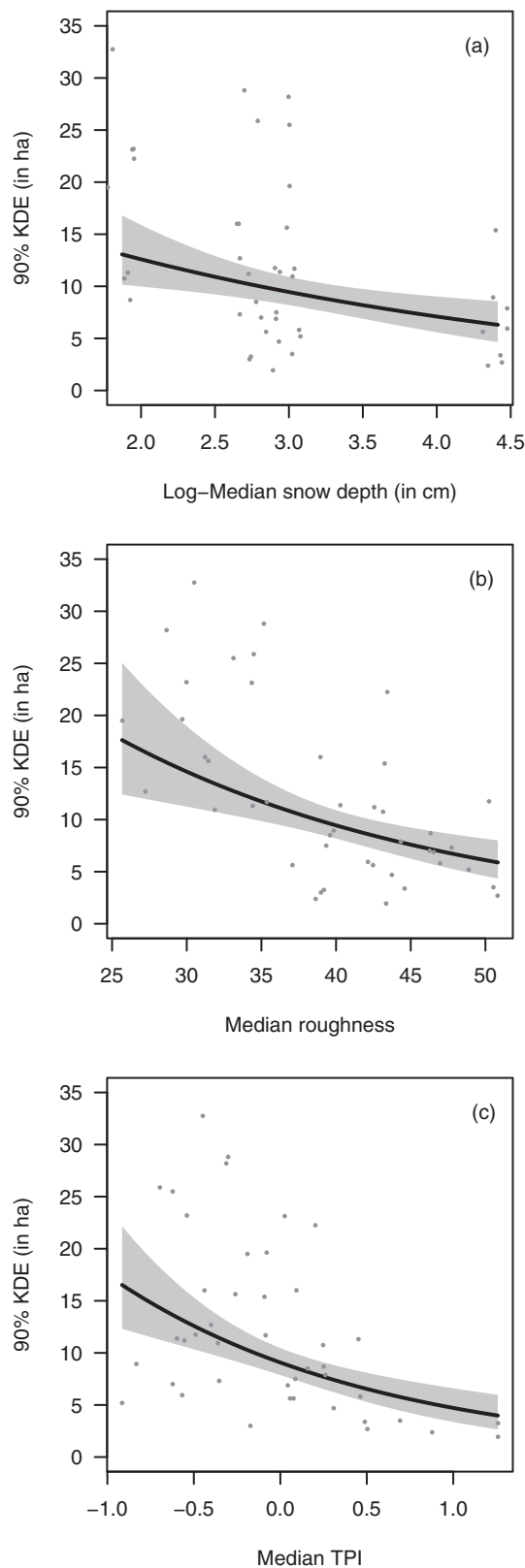
All models were fitted with the '*lm*' function ('*stats*' library), but the models investigating mating opportunities were fitted with the function '*glmmTMB*' ('*glmmTMB*' library; Brooks et al., 2017) in R. All analyses were performed in R 3.6.1 (R Core Team, 2022), in RStudio 2022.07.1 (RStudio Team, 2016).

Results

Selected models supported an effect of snow depth and territory size on the mating opportunity index (Table 1). In particular, we found decreasing mating opportunities with lower snow depth (Table 2; Fig. 1a) and a negative relationship with territory size, with a greater number of females visiting smaller territories, albeit statistically non-significant (Table 2; Fig. 1b).

With respect to territory size, selected models supported an effect of terrain roughness, topographic position index (TPI) and snow depth (Table 1). In particular, we found a negative relationship between snow depth and territory size, with smaller territories in years of deeper snow cover (Table 2; Fig. 2a). Smaller territories showed the highest values of terrain roughness and TPI (Table 2; Fig. 2b, c).

Selected models supported an effect of snow depth and frequency of male–male aggressive interactions on the index of wins (IW index; Table 1). We found a positive relationship

Figure 1 Effects of: (a) snow depth (in cm) and (b) territory size (Kernel 90%, ha), on the mating opportunity index (N females/h), for territorial male Alpine chamois in 2011–2012 and 2015–2017. The predicted values are shown with 95% confidence interval; dots represent raw data.
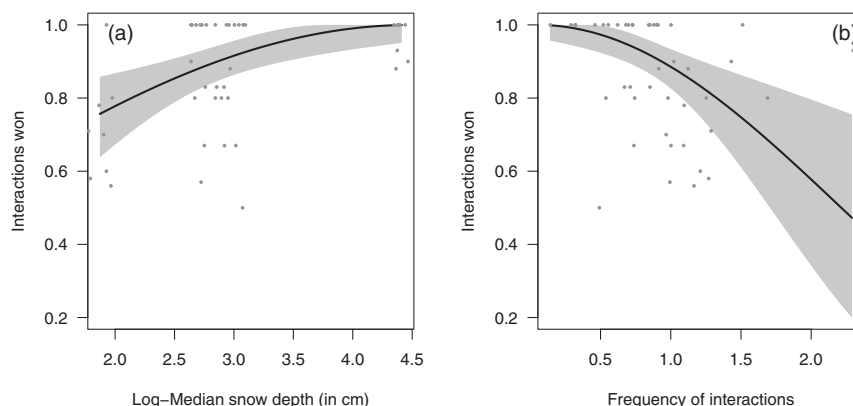
Figure 2 Effects of: (a) snow depth (in cm), (b) terrain roughness index and (c) topographic position index (TPI), on territory size (Kernel 90%, ha), for territorial male Alpine chamois in 2011–2012 and 2015–2017. The predicted values are shown with 95% confidence interval; dots represent raw data.

between snow depth and the IW index, with greater IW index in years with deeper snow cover (Table 2; Fig. 3a) and decreasing IW index with increasing frequency of aggressions (Table 2; Fig. 3b).

Finally, with respect to the frequency of male–male aggressive interactions, selected models supported an effect of snow depth, index of wins (IW index) and elevation (Table 1). We found a positive relationship between snow depth and the frequency of interactions, with higher frequency of aggressions in years with deeper snow cover (Table 2; Fig. 4a). We also found decreasing frequency of aggressions with increasing IW index (Table 2; Fig. 4b) and increasing frequency of interactions for males with the territory at higher elevations (Table 2; Fig. 4c).

Discussion

Throughout our study, during the rut, male territory size was smaller in years with abundant snowfalls than in years with lower snow depth (prediction ii). Several studies have suggested that snow depth strongly influences ungulate movements (Rivrud et al., 2010; van Beest et al., 2011) because of increased costs due to locomotion, food searching and thermoregulation (Dailey & Hobbs, 1989; Parker et al., 1984; Richard et al., 2014). In ungulates, abundant snow cover has been shown to trigger a reduction in home range size (Cederlund, 1983; Georgii & Schröder, 1983; Grignolio et al., 2004), displacement to other areas (Bocci et al., 2012; Mysterud, 1999; Mysterud et al., 2001) and changes in diet (e.g. switch from grazing to browsing; Goodson et al., 1991; Kozena, 1986; Obrtel et al., 1984). Quality and dispersion of food resources influence female distribution (Emlen & Oring, 1977). In mountainous environments, availability of nutritious vegetation is highly seasonal and it is usually reduced in winter (Shackleton & Bunnell, 1987). If so, during the cold period, one would expect females to use clumped resources in snow-free areas. In our study area, in late autumn–winter, the summer range of female chamois (i.e. upper meadows at >2400 m a.s.l.) is often covered with snow. The attraction to snow-free clumped food resources makes female ranging movements broadly predictable, favouring males present in snow-free sites located at lower elevations (Corlatti et al., 2020; Lovari et al., 2006; von Hardenberg et al., 2000). Accordingly (prediction i), during ruts with deeper snow cover (cf. Corlatti et al., 2020; Lovari et al., 2006), our results have shown greater mating opportunities for territorial males – who usually stay at lower

Figure 3 Effects of: (a) snow depth (in cm) and (b) frequency of male–male aggressive interactions (N interactions/h), on the index of wins in male–male aggressive interactions, for territorial male Alpine chamois in 2011–2012 and 2015–2017. The predicted values are shown with 95% confidence interval; dots represent raw data.

elevations than non-territorial ones (Corlatti, Bassano, et al., 2013; our data).

Home range size is negatively related to habitat quality and resource availability (Cimino & Lovari, 2003; Harestad & Bunnel, 1979; Saïd et al., 2009): smaller territories may provide a greater quantity and quality of resources, thus attracting more females (Carranza, 1995; Kitchen, 1974). In contrast with our prediction (i), our results suggest that a greater number of females appeared to be attracted to smaller territories, thus providing greater mating opportunities for the territory owners. These territories were characterized by greater indices of roughness than larger ones: in fact, a steep and precipitous terrain should prevent snow accumulation, thus allowing chamois an easier access to food resources and to refuge areas (Berducou, 1982; Schröder, 1971a, 1971b; von Elsner-Schack, 1985). Our results have suggested that 'quality', in terms of terrain roughness, appears to be more important than territory size, possibly because it allows females the access to snow-free terrain, thus food resources, in that season. Presumably, male Alpine chamois would have greater mating opportunities if holding a territory in a rugged area, free from snow at rut time, in November. This relationship is expected to be stronger in years with abundant snowfalls early in the rut (see also Corlatti et al., 2020; Lovari et al., 2006). Lovari et al. (2006) suggested and Corlatti et al. (2020) showed that, in years with snowfalls early in the rut, territorial males have a greater reproductive success, as females are forced to move to lower elevations to access forage (cf. Introduction). Conversely, non-territorial males could gain reproductive advantage in years with low or delayed snowfalls because females rut at higher elevations (Lovari et al., 2006). The greater number of females observed in male territories during snowy ruts provides support to this prediction.

Female ungulates often select habitats providing safety to them and to their offspring from predators (Ciuti et al., 2005; Hamel & Côté, 2007; Pérez-Barbería & Nores, 1994). Information is less abundant on female selection of habitat features in male territories during the mating period. Dunbar and Roberts (1992) suggested that mountain reedbuck females were mainly attracted to male territories located at a lower distance from escape terrain (see also Howard, 1986, for habitat selection in female mountain reedbuck). In our study area, large terrestrial predators were absent (2011–2012) to rare (2015–2017, grey wolf). It is unlikely that the direct effect of terrain steepness on the number of females in territories was related primarily to searching for safety from terrestrial predators. The only winged predator, the golden eagle, may attack on both, steep or less steep locations. Our results suggest that topographic features play an important role in attracting female chamois to territories with minor snow depth.

Non-territorial males tend to stay at higher elevations than territorial ones (Lovari et al., 2006; Corlatti, Bassano, et al., 2013; our data), follow oestrus females and try to intrude territories of other males (Corlatti et al., 2012; Krämer, 1969; von Hardenberg et al., 2000), thereby possibly influencing the positive relationship between elevation and male–male aggressive interactions.

In ruts with deep snow, non-territorial males, as well as females, tend to move to lower elevations where territorial males are (Corlatti et al., 2020; Corlatti, Bassano, et al., 2013). The increased possibility of male–male interactions could explain the positive relations between snow depth and both the frequency of aggressive interactions and the index of wins in interactions (predictions iii and iv). In fact, territorial males are usually dominant over non-territorial ones (Corlatti et al., 2012).

Aggression and social rank (Corlatti et al., 2012; Patton et al., 2001; Pelletier et al., 2003) and courtship behaviour (Hirschenhauser & Oliveira, 2006; Knapp, 2003) depend on levels of androgen hormones. A previous study showed that territorial males had higher levels of androgen metabolites than non-territorial ones, during the rut (Corlatti et al., 2012). In contrast to our predictions (iii and iv), we found no relationship between frequency of male–male aggressive interactions, as well as win numbers, and mating opportunities of territorial males (i.e. the number of females in their territory). A male
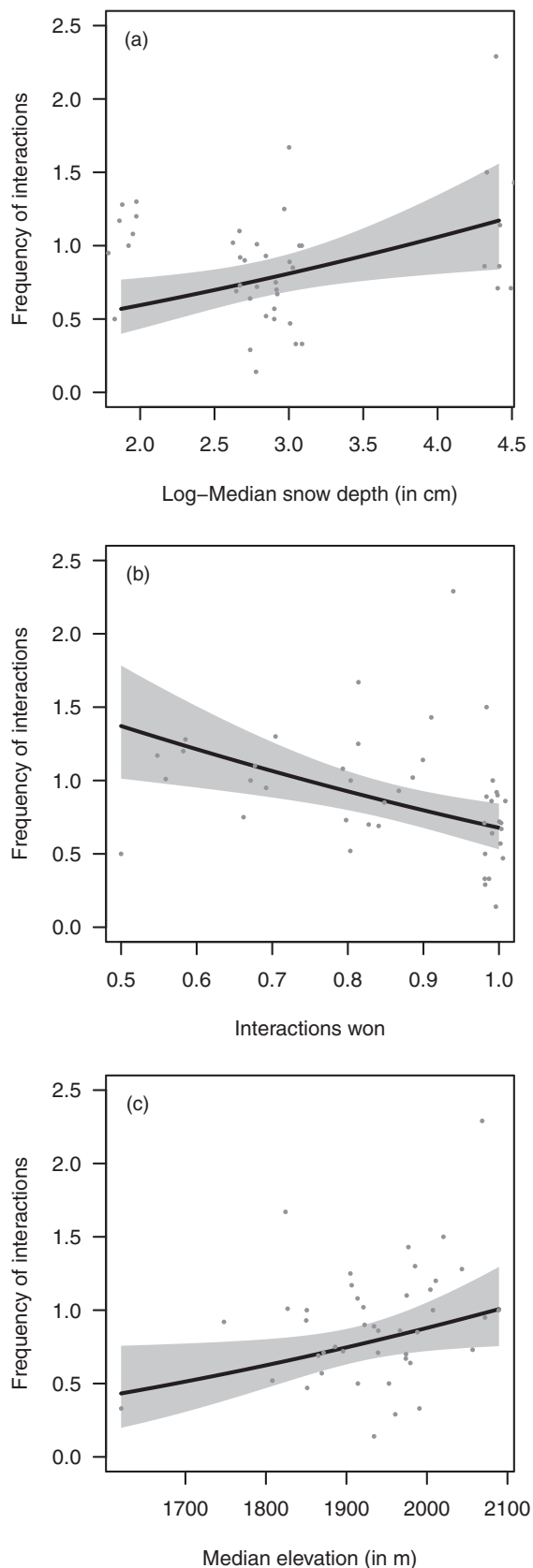
Figure 4 Effects of: (a) snow depth (in cm), (b) index of wins in male–male aggressive interactions and (c) elevation (m), on the frequency of male–male aggressive interactions (N interactions/h), for territorial male Alpine chamois in 2011–2012 and 2015–2017. The predicted values are shown with 95% confidence interval; dots represent raw data.

will defend his territory from intruding males irrespective of the number of females present there and a male capable to defend a territory more attractive to females would gain priority access to mates ('*prior residence advantage*', Braddock, 1949; Maynard-Smith, 1982).

In contrast with our prediction (ii), our analyses supported a relationship neither between territory size and frequency of male–male aggressive interactions, nor with number of wins. Furthermore, in contrast with prediction (i), no relation was found between mating opportunities and dominance of the male (in terms of wins and frequency of interactions).

We found that the frequency of interactions was negatively related to the index of wins in interactions, and vice versa. We may assume that dominant individuals are less frequently challenged in comparison with sub-dominant ones. Displays should be related to actual fighting ability or dominance rank (Geist, 1971) and permit individuals to assess their opponents, allowing them to avoid fights when they are unlikely to win (Zahavi, 1975, 1977). Male chamois manly assess rank in intra-sexual contests through aggressive behaviours patterns (Lovari, 1985), rather than on size-related traits (Corlatti et al., 2012; Corlatti, Caroli, et al., 2013). Quite often rutting males utter a relatively low-pitched grunt, the 'rut call', a vocal dominance display (Lovari, 1985), that it could be a 'honest' advertisement for the opponents (e.g. roaring for red deer: Clutton-Brock & Albon, 1979). In addition, olfactory cues may be important too (Coblentz, 1976; Moore & Marchinton, 1974): during the rut, male chamois often mark the vegetation, sliding up and down their supraoccipital glands and advertising their presence thus (Lovari, 1985); additionally, they often shake their body and urinate at the same time, thus impregnating their flank pelage with scent (Lovari, 1985). Although these observations require experimental confirmation, such displays may advertise dominance to potential opponents.

In conclusion, our study has shown that mating opportunities of territorial males increased during the rutting seasons with deeper snow cover and in territories located on steep, broken terrain, that is, those areas from which snow slides away first, thus making forage easily available. If so, territoriality in chamois could have developed from a combination of female movements to snow-free clumped resources during the rut with some males defending attractive territories, thereby getting greater mating opportunities.

Territoriality is a rare mating tactic among Caprinae, especially in species occurring in open areas (Corlatti & Lovari, 2023). After assessing that territorial and non-territorial behaviour of male chamois seem to be a life-time reproductive tactic, Cotza et al. (2023) have suggested it as an adaptation to

environmental stochasticity or a DNA-fixed behaviour. On the other hand, if we assume that earlier chamois were non-territorial as all other Caprinae – but for the serows *Capricornis* spp., which are forest resource defenders (Akasaka & Maruyama, 1977; Geist, 1987; Kishimoto & Kawamichi, 1996) – environmental stochasticity (i.e. accumulation of snow cover in the rutting season) could have favoured the development of territoriality in male chamois at lower elevations which, on time, could have become a fixed trait. A larger sample size and a longer-term study, combined with *ad hoc* DNA analyses, would allow a better evaluation of the relationships between inter-annual variation of snow cover and mating parameters.

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Conflict of interest

None.

Data availability statement

Methods and data are available from the corresponding author upon reasonable request.

Author contributions

A.C. collected data in the field, performed the statistical analyses and wrote all drafts of this paper; O.T. participated in behavioural observations, as well as data analyses, and revised the draft of the manuscript; L.C. collected data in the field, participated in planning this work and in writing up this manuscript, and planned the statistical analyses of the revised version of the manuscript; F.F. participated in all stages of this work; M.D. participated in behavioural observations and revised the draft of the manuscript; B.B. planned and participated in darting operations and helped with logistics; S.L. planned and supervised all stages of this work, and participated in the writing up of this manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Frequency histogram for the aspect of territories in ruts 2011–2012 and 2015–2017. The aspect was considered as distance from the South (0° = S, 90° = E and O, 180° = N).

Table S1. Median value and interquartile range (IQR) of snow depth, during the rut period (6th of November to 5th of December), of each study year.