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**DOTTORATO DI RICERCA IN SCIENZE DELLA VITA**

CICLO XXXII

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*"Females are not males: evolutionary strategies of the two sexes in chamois"*

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*Ai miei genitori*



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## ABSTRACT

Sex-related constraints could determine different individual responses to environmental stressors (e.g. climate, seasonality of resources). On mountains, the access to high quality pasture for herbivores is limited to the warm months, thus making summer forage crucial for winter survival, in particular to females, who face the costs of motherhood, and kids. In gregarious species, seasonality of resources may also influence social behaviour: thus, pasture depletion may increase feeding interference and endogenous stress levels, in turn leading to the increase of intraspecific aggressive interactions.

My thesis concerns a mountain-dwelling ungulate, the Alpine chamois *Rupicapra rupicapra rupicapra*. I investigated mating and spatial behaviour of adult males (**Chapter 1**), for which two alternative mating tactics (AMTs) have been described (territoriality and non-territoriality). Understanding differences in age, survivorship, mating success, aggressiveness/dominance and space use between individuals adopting different AMTs would help explain their coexistence in the population. One more aim has been assessing the maintenance of the tactics through life. I collected data on 31 individually marked males during 5 rutting seasons (November-early December; 2011-2012, 2015-2017). Both AMTs were reported amongst males, with approximately the same frequency. No individuals changed AMT. Territorial males (T) are known to face higher costs (higher levels of androgen/cortisol metabolites and parasites; hypophagia) than non-territorial ones (NT). However, I found no difference in survivorship. Data suggest no age effect on AMTs. Moreover, I found no difference in the frequency of intra-sexual aggressive interactions. T males consistently showed greater indices of mating opportunities. Finally, I reported the occurrence of different patterns of spatial behaviour across T males (“resident” and “migrant” individuals), suggesting that territoriality does not necessarily involve being resident. This study would support the existence of fixed AMTs in adult male Alpine chamois, which may adopt a conservative mating strategy, i.e. a less intense and energetically demanding competition amongst males compared to that of highly dimorphic species, and probably different spatial strategies, to maximise survival.

Studying how snow cover, topographic features of territories and male aggressiveness/dominance influence mating opportunities of territorial male chamois (**Chapter 2**) would help understand how territoriality is maintained in the population. I recorded mating behaviour and territory features of 15 territorial males (T), during 5 rutting seasons (November-early December; 2011-2012, 2015-2017). T had smaller territories and greater mating opportunities during ruts with deeper snow cover. Smaller territories were visited by more females and showed the highest values of terrain roughness. The frequency of male-male aggressive interactions was positively related to the number of females in a territory and was greater for males with territories located at higher elevations. This supports a role of intrusion of non-territorial males, who usually stay at higher elevations than T ones, in emphasising intra-sexual competition for mates. These results are consistent with recent findings from concurrent studies and support that snow cover and its effect on female distribution may be strong determinants of mating behaviour and success of male chamois, emphasising the role of weather stochasticity in favouring the maintenance of AMTs.

The adoption of a mating tactic may influence space use. Conversely, female spatial behaviour may be influenced by the presence of offspring. I investigated differences in temporal variation of space use (home range size and elevation use) between females, territorial and non-territorial males (13 females, 11 T males, 13 NT males; 2011-2012-2017), using intensive GPS-GSM radio-telemetry and satellite-derived products (i.e. the Normalized Difference Vegetation Index, NDVI). The effects of temperature, snow depth and rainfall on the spatial behaviour of both sexes have also been evaluated (**Chapter 3**). Females and NT males increased their home range size and moved to higher elevations between late spring-autumn, whereas T males showed consistently smaller home ranges and remained at the lowest elevations. NT males showed significantly larger home ranges than other chamois in November-December. Especially for females and, to a lower extent, for NT males, home range size and elevations used were positively related to temperature and negatively related to snow depth. Conversely, T males showed limited variations of space use in response to temperature and snow depth. I found a negative effect of rainfall on daily elevations occupied by chamois.

Vegetation productivity (NDVI values) of the locations used by chamois was greater between April-October than in late autumn-winter. Apparently, locations used by females showed relatively more stable NDVI values between June-October, compared to those of locations used by males, which decreased sharply in September-October. My results strongly support a major role of weather in influencing movements, with particular reference to females. In conclusion, I found significant differences between sexes/AMTs, in both temporal variation of spatial behaviour and response to climatic stressors. Females appear to be more sensitive to short-term weather variations, thus strongly adapting their ranging movements. Conversely, territoriality was associated with a relatively lower response of individuals to short-term weather changes. These results emphasise that AMTs, besides sex and reproductive status, should be considered when studying spatial behaviour and its driving factors.

Seasonal/age variation of the frequency of intra-sexual aggressive interactions, endocrine correlates, nutritional quality of diet, as well as grouping patterns have been investigated in females (**Chapter 4**) through behavioural observations on 10 recognisable individuals and chemical analyses of fresh faecal samples (June-November 2017-2018). The frequency of intra-sexual aggressive interactions and group size decreased throughout summer-autumn. However, no seasonal/age variation in hormone metabolites levels were supported. Younger females appeared to be involved more frequently in aggressive interactions than older ones, but the age effect was not significant. Older females showed greater levels of crude protein and lower levels of crude fibre in their diet than younger ones. Protein content of diet decreased, while crude fibre levels increased, through summer-autumn. Variation of abundance, quality and dispersion of resources could promote avoidance of feeding interference through the decrease of group size. Local variation in food quality may influence the behavioural ecology of group-living species, potentially resulting in aggressive interactions. My results support the hypothesis that feeding interference is stronger when females share highly nutritious resources, suggesting the importance of the access to adequate summer food, to face the high costs of motherhood.



## RIASSUNTO

Vincoli evolutivi, fisiologici, anatomici potrebbero determinare diverse risposte individuali a fattori di stress ambientali (e.g. fattori climatici, stagionalità delle risorse), da parte di maschi e femmine. In ambienti montani, l'accesso a pascoli di alta qualità per gli erbivori è limitato ai mesi primaverili-estivi, rendendo così l'alimentazione estiva cruciale per la sopravvivenza invernale, in particolare per le femmine, che devono affrontare i costi della maternità, e per i nuovi nati. Nelle specie gregarie, la stagionalità delle risorse può influenzare anche il comportamento sociale: la diminuzione della disponibilità e della qualità di risorse alimentari può aumentare la competizione alimentare e i livelli di stress, portando a sua volta un aumento delle interazioni aggressive intraspecifiche.

La mia tesi riguarda un ungulato di montagna, il camoscio alpino *Rupicapra rupicapra rupicapra*. Ho studiato il comportamento riproduttivo e spaziale di maschi adulti (**Capitolo 1**), per i quali sono state descritte due tattiche riproduttive alternative (AMTs) (territorialità e non territorialità). Comprendere le differenze in età, sopravvivenza, successo di accoppiamento, aggressività/dominanza e uso dello spazio tra individui che adottano AMTs diverse aiuterebbe a spiegare la loro coesistenza nella popolazione. Un altro obiettivo della mia tesi è stato valutare il mantenimento delle tattiche riproduttive da parte di uno stesso individuo, in anni diversi. Ho raccolto dati su 31 maschi riconoscibili durante 5 stagioni riproduttive (Novembre-inizio Dicembre; 2011-2012, 2015-2017). Entrambe le AMTs sono state registrate tra i maschi, con la stessa frequenza. Nessun individuo ha cambiato AMT. È noto che i maschi territoriali (T) devono affrontare costi più elevati (livelli più elevati di metaboliti ormonali e parassiti; ipofagia) rispetto a quelli non-territoriali (NT). Tuttavia non ho riscontrato alcuna differenza nella sopravvivenza. I dati non suggeriscono alcun effetto dell'età sulle AMTs. Inoltre, non ho trovato alcuna differenza nella frequenza delle interazioni aggressive intra-sessuali. I maschi T hanno mostrato maggiori indici di opportunità riproduttive. Infine, ho registrato la presenza di due diversi pattern di comportamento spaziale tra i maschi T (individui "residenti" e "migratori"), suggerendo che la territorialità non

implica necessariamente l'essere residente. Questo studio fornirebbe supporto all'esistenza di tattiche riproduttive fisse nel camoscio alpino, che potrebbe adottare una strategia di accoppiamento conservativa, ovvero una competizione tra i maschi meno intensa ed energeticamente costosa rispetto a quella tra maschi di specie altamente dimorfiche, e probabilmente diverse strategie spaziali, per massimizzare la sopravvivenza.

Studiare come la copertura nevosa, le caratteristiche topografiche dei territori e l'aggressività/dominanza influenzino le opportunità riproduttive dei maschi territoriali (**Capitolo 2**) aiuterebbe a capire come questa tattica venga mantenuta nella popolazione. Ho registrato dati su comportamento riproduttivo e caratteristiche dei territori di 15 maschi, durante 5 stagioni riproduttive (Novembre-inizio Dicembre; 2011-2012, 2015-2017). I territori sono risultati più piccoli e visitati da un numero maggiore di femmine durante anni con una copertura nevosa maggiore. Territori più piccoli erano caratterizzati da maggiore asperità e pendenza del terreno. La frequenza delle interazioni aggressive tra maschi è risultata positivamente correlata al numero di femmine nel territorio ed è risultata maggiore per i maschi con territori situati a quote più elevate. Ciò suggerisce un ruolo delle intrusioni dei maschi non territoriali, che solitamente restano a quote più elevate rispetto a quelli territoriali, nell'enfatizzare l'effetto della frequenza di interazioni aggressive sulle opportunità riproduttive. Questi risultati concordano con recenti studi e avvalorano l'importanza della copertura nevosa e dei suoi effetti sulla distribuzione delle femmine sul comportamento riproduttivo e sul successo di accoppiamento nel camoscio, sottolineando il ruolo della stocasticità meteorologica nel favorire il mantenimento delle AMTs.

L'adozione di una AMT potrebbe influenzare l'uso dello spazio. Al contrario, il comportamento spaziale femminile può essere influenzato dalla presenza delle prole. Ho studiato le differenze nella variazione temporale dell'uso dello spazio (dimensioni *home range* e quote occupate) tra femmine, maschi territoriali e non territoriali (13 femmine, 11 maschi T, 13 maschi NT; 2011-2012-2017), usando radio-telemetria GPS-GSM e l'indice satellitare NDVI (*Normalized Difference Vegetation Index*). Sono stati inoltre valutati gli effetti della temperatura, della copertura nevosa e delle

precipitazioni sul comportamento spaziale di entrambi i sessi (**Capitolo 3**). Le dimensioni degli *home range* e le quote occupate di femmine e maschi NT sono aumentate tra la tarda primavera e l'autunno, mentre i maschi T hanno mostrato *home range* costantemente più piccoli e sono rimasti alle quote più basse. I maschi NT hanno mostrato *home range* più grandi rispetto agli altri individui in Novembre-Dicembre. Le dimensioni degli *home range* e le quote occupate sono risultate aumentare con l'aumento della temperatura e diminuire con la copertura nevosa, soprattutto per le femmine e, in misura minore, per i maschi NT. Al contrario, i maschi T hanno mostrato variazioni limitate dell'uso dello spazio in risposta alla temperatura e alla copertura nevosa. Le precipitazioni hanno avuto un effetto negativo sulle quote occupate dai camosci. La produttività della vegetazione (indice NDVI) delle aree utilizzate dai camosci è risultata maggiore tra Aprile-Ottobre. Apparentemente, le aree utilizzate dalle femmine hanno mostrato valori di NDVI relativamente più stabili tra Giugno-Ottobre, rispetto a quelli delle aree utilizzate dai maschi, che sono diminuiti a Settembre-Ottobre. I miei risultati supportano un ruolo importante dei fattori climatici nell'influenzare i movimenti, con particolare riferimento alle femmine. In conclusione, ho trovato differenze significative tra i sessi/tattiche riproduttive, sia nella variazione temporale del comportamento spaziale che nella risposta agli stress climatici. Le femmine sembrano essere più sensibili alle variazioni meteorologiche a breve termine, adattando i loro spostamenti. Al contrario, la territorialità sembra associata a una risposta minore degli individui alle variazioni meteorologiche. Questi risultati sottolineano che le AMTs, oltre al sesso e allo stato riproduttivo, devono essere considerate quando si studia il comportamento spaziale.

Le variazioni stagionali/di età della frequenza delle interazioni aggressive intra-sessuali, della risposta endogena, della qualità nutrizionale della dieta, nonché la variazione delle dimensioni dei gruppi sono state studiate nelle femmine di camoscio alpino (**Capitolo 4**), attraverso osservazioni comportamentali su 10 individui riconoscibili e analisi chimiche di campioni fecali (Giugno-Novembre 2017-2018). La frequenza delle interazioni aggressive e la dimensione del gruppo sono diminuite tra l'estate-autunno. Tuttavia, non sono state supportate variazioni nei livelli di metaboliti

ormonali. Le femmine più giovani sembrano essere state coinvolte più frequentemente in interazioni aggressive, rispetto a quelle più anziane, ma l'effetto dell'età non è risultato significativo. Le femmine più vecchie hanno mostrato livelli più alti di proteine grezze e livelli più bassi di fibre grezze nella loro dieta rispetto a quelle più giovani. Il contenuto proteico della dieta è risultato diminuire, mentre i livelli di fibra grezza sono aumentati, tra l'estate e l'autunno. La variazione della disponibilità, qualità e dispersione delle risorse trofiche potrebbe portare a una riduzione delle dimensioni del gruppo, per evitare competizione alimentare. Variazioni nella qualità delle risorse possono influenzare l'ecologia comportamentale delle specie che vivono in gruppo, con un possibile aumento delle interazioni aggressive. I miei risultati supportano l'ipotesi che l'interferenza alimentare sia più forte quando le femmine condividono risorse altamente nutrienti, suggerendo l'importanza del pascolo estivo, per affrontare gli alti costi della maternità.

## INTRODUCTION

The two sexes respond to different constraints to increase their respective fitness: the priority of females is to maximise offspring survival, through the access to high quality resources, whereas the priority of males is to increase their mating opportunities (Emlen & Oring 1977; Clutton-Brock 1989). There are anatomical, physiological and evolutionary reasons behind this difference (Krebs & Davies 1981). Female density and distribution, indirectly related to the distribution of resources (Clutton-Brock 1989), determine male mating behaviour and reproductive success. Males can compete directly for mates or indirectly for resources that influence female distribution (Emlen & Oring 1977). In the second system (a “resource defence polygyny”), the reproductive success of a male depends on its territory location and ability to attract mates (Carranza 1995).

In polygamous species, intense intra-sexual competition to increase mating opportunities can lead to the development of *alternative mating tactics* (AMTs) (Taborsky et al. 2008). At the individual level, AMTs may be “fixed” or “flexible” (Brockmann 2001; Taborsky 1998). Fixed AMTs are rare in mammals (Crews 1998; Taborsky et al. 2008). When different AMTs co-occur in a population, different cost-benefit trade-offs should be expected to occur in relation to the adoption of each tactic: e.g. differences in parasite susceptibility (Pelletier et al. 2005; Corlatti et al. 2012), feeding intensity (Pelletier 2004; Corlatti et al. 2013), mating success (Corlatti et al. 2015a).

My thesis concerns a mountain-dwelling ungulate, a weakly polygynous (Bocci et al. 2010; Rughetti & Festa-Bianchet 2011; Corlatti et al. 2012) and near-monomorphic large mammal, the Alpine chamois *Rupicapra rupicapra rupicapra* (Linnaeus 1758; Bovidae: Caprinae). Two alternative mating tactics have been described in adult males (Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012). During the rut (November), at the lower elevations, some males (territorials, T) defend an exclusive area from intruders, trying to keep females there (Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012). Other individuals (non-territorials, NT) court oestrus females by following them (the common tactic amongst Caprinae, Schaller 1977), sometimes intruding other males’ territories (Krämer 1969; von Hardenberg et al. 2000; Corlatti et

al. 2012). During the rut, T males bear higher costs than NT ones (i.e. territory defence, rut-induced hypophagia, higher levels of stress and parasites) (Corlatti et al. 2012, 2013, 2019; Corlatti & Bassano 2014). However the former seem to benefit from greater reproductive success (Corlatti et al. 2015a). Territorial males start to defend their territories in late spring, well before the mating season (von Hardenberg et al. 2000), suggesting benefits from their higher knowledge of their defended area and from a “*prior residence advantage*” (Braddock, 1949; Maynard-Smith 1982). Conversely, non-territorial males could benefit from moving to higher elevations in summer, where grasslands are richer in nutrients (Albon & Langvatn 1992; Bassano 1994). No information is available on difference of survivorship of male chamois adopting different AMTs. Additionally, it is unknown whether individuals adopt a fixed mating tactic through life.

Variation in space use throughout the year to favour reproductive opportunities in the mating period has been rarely reported. Lovari et al. (2006) described two alternative spatial tactics in male chamois: some individuals (residents) occupy overlapping or contiguous summer and winter ranges, whereas others (migrants) move between well separated seasonal ranges. However, it is not clear whether males adopting the same AMT show the same tactic of space use (see Melis et al. 2004, for territorial male roe deer *Capreolus capreolus*) and whether all territorial males are residents / all non-territorial males are migrants.

I investigated mating and spatial behaviour of 31 individually recognisable adult male chamois, during 5 years (2011-2012 and 2015-2017) (**Chapter 1: Alternative mating and spatial tactics in male Alpine chamois**), using intensive GPS-GSM radio-telemetry and behavioural observations, to find out about factors explaining evolution and coexistence of AMTs in Alpine chamois. I investigated differences in (i) age, (ii) survivorship, (iii) mating success, (iv) dominance and (v) frequency of male-male aggressive interactions during the rut between individuals adopting AMTs. Two more aims of my thesis have been assessing the maintenance of the tactics through life and investigate patterns of space use among individuals adopting the same AMT.

Out of over 30 species of Caprinae, territoriality has been shown only in 2 species (*Rupicapra rupicapra* included) and suspected in 2 more. One species shows *lek* behaviour. All others use the “following” tactic. Territories in chamois have been described as hotspots attractive to females during the rut because of reduced snow cover (von Hardenberg et al. 2000). Lovari et al. (2006) hypothesised that snow cover could have an important effect in determining the success of AMTs in chamois. This view has been confirmed recently by Corlatti et al. (2020). During ruts with abundant snowfalls, females move to lower elevations where they meet territorial males, allegedly favouring them as mates (Corlatti et al. 2015a). In years with no or delayed snow cover, females will rut at higher elevations, where non-territorial males will have an advantage.

Females could gain genetic benefits by choosing a “good” dominant male (Trivers 1972; Hogg 1987; Balmford et al. 1992a,b; Byers et al. 1994). However, no information is available on the relationships between presence of snow cover, topographic features of a territory (i.e. size, elevation, roughness, aspect), dominance (i.e. frequency of intra-sexual aggressive interactions and index of wins) and mating opportunities of territory holder. I explored the above relationships in 15 individually recognisable adult territorial males, during 5 rutting seasons (2011-2012 and 2015-2017) (**Chapter 2: Territories and territory-holders in the Alpine chamois**), to understand factors that favour the maintenance of territoriality in the population. I used intensive GPS-GSM radio-telemetry and a Digital Elevation Model (DEM) in a GIS software, coupled with individual-level behavioural observations to study male mating behaviour, in terms of (i) mating opportunities, (ii) frequency of intra-sexual aggressive interactions and (iii) index of wins, and their relationships with territory features, in terms of (i) size, (ii) elevation, (iii) roughness, (iv) aspect, and snow cover.

On mountains of temperate ecosystems, climate and seasonality of food resources (Shackleton & Bunnell 1987; Albon & Langvatn 1992) are important determinants of the behaviour and ecology of ungulates. On alpine grasslands, the access to high-quality pasture is limited to late spring and summer (Dunant 1977; Ferrari et al. 1988; Lendrum et al. 2014; Primi et al. 2016). Access to nutritious summer food is fundamental to herbivores to overwinter successfully. In

particular, it is crucial to females to recover from pregnancy and optimise energy intake to face the high costs of lactation and nursing (Pettorelli et al. 2003, 2006; Therrien et al. 2007; Froy et al. 2016; Scornavacca et al. 2016), and it is important to juveniles to grow and store fat reserves for their winter survival (Festa-Bianchet 1988; Pettorelli et al. 2007; Scornavacca et al. 2016).

Sexual differences in space use may develop in response to environmental stressors (e.g. climate and seasonality of resources) (Bonenfant et al. 2004) and sex-related constraints. Seasonal variations of home range size and altitudinal movements have been broadly investigated in ungulates (e.g. Festa-Bianchet 1988; Sabine et al. 2002; Ramanzin et al. 2007; van Moorter et al. 2013). In particular, snow cover and temperature are known to be important determinants of movements (e.g. Georgii & Schröder 1983; Grignolio et al. 2004; Aublet et al. 2009; van Beest et al. 2011; Richard et al. 2014). Moreover, ungulates can capitalise upon the green-up season of plants by moving upslope through spring and summer (e.g. Mysterud et al. 2001; Hebblewhite et al. 2008; Bischof et al. 2012; Merkle et al. 2016), to benefit of high quality food resources at the upper meadows (Albon & Langvatn 1992).

Females may minimise predation risk for them and their offspring by using sites with fewer predators or greater opportunities to escape (Bleich et al. 1997; Rachlow and Bowyer 1998; Panzacchi et al. 2010). A trade-off may arise between selection of food-rich vs. poorer – but safer – areas (Pérez-Barbería & Nores 1994; Ciuti et al. 2005; Grignolio et al. 2007; Hamel & Côté 2007). Conversely, space use of males is expected to be mainly influenced by the necessity of increasing mating opportunities and by the mating tactic adopted (Mysterud 1999).

In spite of its abundance and wide distribution on the Alps (Corlatti et al. *in press*), knowledge of the determinants of spatial behaviour in the Alpine chamois is limited (e.g. Hamr 1984, 1985; Brambilla et al. 2006; Nesti et al. 2010) and there are no studies investigating male movements throughout the year considering alternative mating tactics. Information is also lacking on the effect of weather (temperature, snowfall, rainfall) and vegetation phenology on spatial behaviour of both sexes/AMTs. I investigated differences in temporal variation of spatial behaviour

(home range size and altitudinal movements) between females (N=13), territorial (N=11) and non-territorial males (N=13). The effects of meteorological variables (temperature, snow depth, rainfall) and productivity of the vegetation on the spatial behaviour of both sexes/AMTs have also been evaluated (**Chapter 3: Spatial behaviour and its environmental drivers**). I used intensive GPS-GSM radio-telemetry on adult individuals of both sexes and, as to males, showing different AMTs, and satellite-derived products (i.e. the Normalized Difference Vegetation Index, NDVI).

In gregarious foragers, seasonality, which influences food availability, may also influence social behaviour (e.g. aggressiveness and grouping pattern) and its physiological correlates (e.g. endocrine levels) (Fattorini et al. 2018b, 2019; Favreau et al. 2018). Gregariousness can maximise security, favouring detection and avoidance of predators (Hamilton 1971; Pulliam 1973; Berger 1978), yet it may increase feeding interference. In mammals, females could accept costs of being gregarious, e.g. parasite transmission as well as increased competition for food, to decrease predation risks for them and their offspring (Thaker et al. 2010). Limited access to resources and feeding interference in groups could elicit intraspecific aggressive interactions and endogenous stress response (Kelley 1980; DeVries et al. 2003). Dominance, aggressiveness and endocrine correlates are also expected to change according to age and/or social status of individuals (Côté 2000; DeVries et al. 2003; Bartoš et al. 2010; Beauchamp 2015).

Female chamois form social groups with other adult and subadult females, yearlings and kids. While female aggressive behaviour has been studied in the Apennine chamois (Locati & Lovari 1990, 1991; Lovari & Locati 1993; Fattorini et al. 2018a, b), no information is available on seasonal variation of aggressive interactions and related endocrine levels in the Alpine chamois. I used individual-level behavioural observations on 10 recognisable adult female Alpine chamois, as well as chemical analyses of faecal samples, from June to November (2017-2018), to explore seasonal and age variation of the frequency of intra-sexual aggressive interactions, endocrine correlates levels (faecal androgen and cortisol metabolites) and nutritional component of diet, as well as seasonal variation of group size and structure (**Chapter 4: Group-living and its costs in a**

**mountain-dwelling ungulate**). Investigating social behaviour during summer-autumn, i.e. when food resources decrease from a high to a low abundance and quality (Albon & Langvatn 1992; Ranghetti et al. 2016) and maternal cares decrease (Ruckstuhl & Ingold 1994), would help identifying crucial phases of the females' life-history.

## STUDY AREA

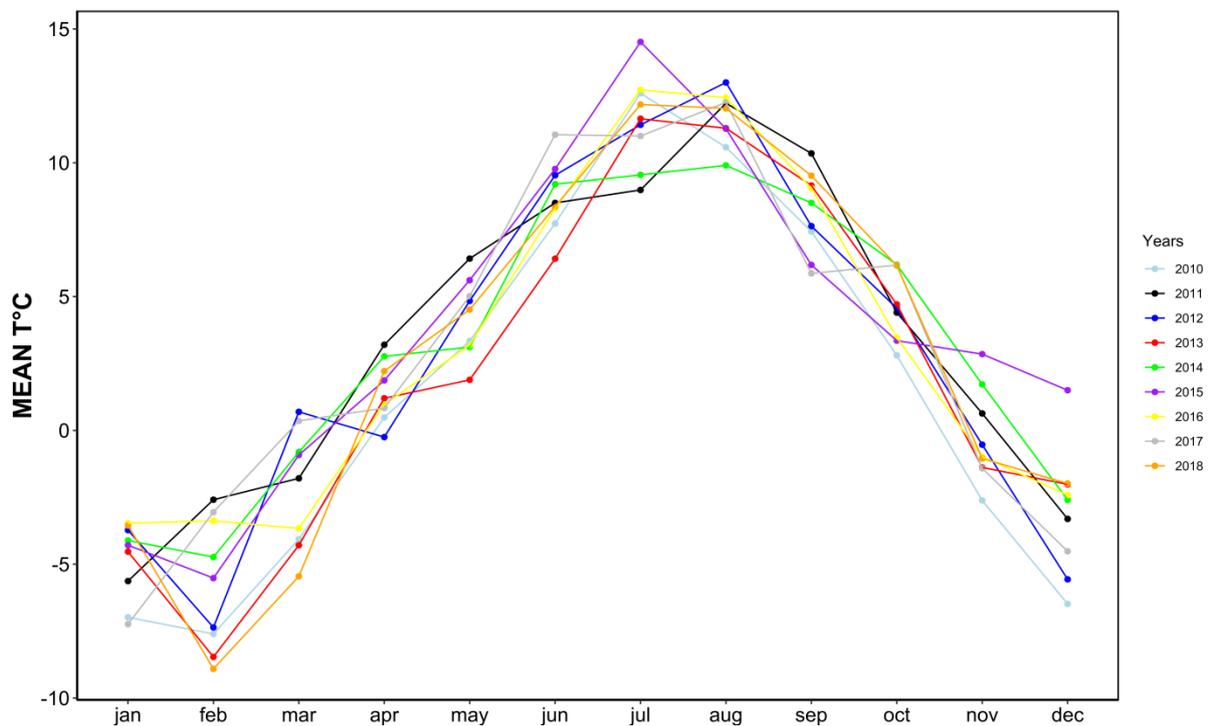
My study was conducted in the upper part of the Orco valley (45°27'21" N, 7°10'27" E, Ceresole Reale – Turin), in the Gran Paradiso National Park (GPNP), Western Italian Alps – Graie Alps. The study area, a typical glacial valley, extends over around 40 km<sup>2</sup> (1600 - 3400 m a.s.l.) and is bordered by the Val Grande southwards, the Vanoise National Park (France) westwards and by the Rhêmes and Valsavarenche valleys northwards. Because of chamois seasonal movements, data collection in summer was also conducted in the upper part of the Valsavarenche valley. The Orco valley is oriented west to east and the north-facing slope is characterised by a mixed wood of larch *Larix decidua* with sparse silver fir *Abies alba* and European spruce *Picea abies*, patches of alder shrubs *Alnus viridis* and shrubs of alpenrose *Rhododendron ferrugineum*, common juniper *Juniperus communis*, Western blueberry *Vaccinium gaultherioides* and European blueberry *Vaccinium myrtillus* (Ferrari 1997). The vegetation on the south-facing slope (c. 90% of the study area) is quite homogeneous and consists of graminoids, forbs and shrubs: most of the area is interested by one ecofacies mainly dominated by coloured fescue *Festuca varia* associated with sedges *Carex* sp., rush *Juncus* sp. and other monocotyledons and dicotyledons (La Morgia & Bassano 2009). Grasslands predominate in the middle part of the area (2200-2700 m, Ranghetti et al. 2016), while in the upper part we also find steeper and rocky areas.

The climate is dry continental and seasonal mean temperatures (2010 to 2018) have been between -4.4 C° in winter and 10.7 C° in summer (min T°C: -6.1 C°, in winter 2013; max T°C: 11.9 C°, in summer 2015), whereas total yearly precipitations have been c. 1,214 mm (min 841 mm, in 2017; max 1,556 mm, in 2018). Snow cover lasts from November to May (yearly mean value, at 2275 m a.s.l.: 104 cm; min 65.5 cm, in 2012; max 160 cm, in 2018). Max snow depth was 295 cm in April 2018 (own data; Fig. 1, 2, 3).

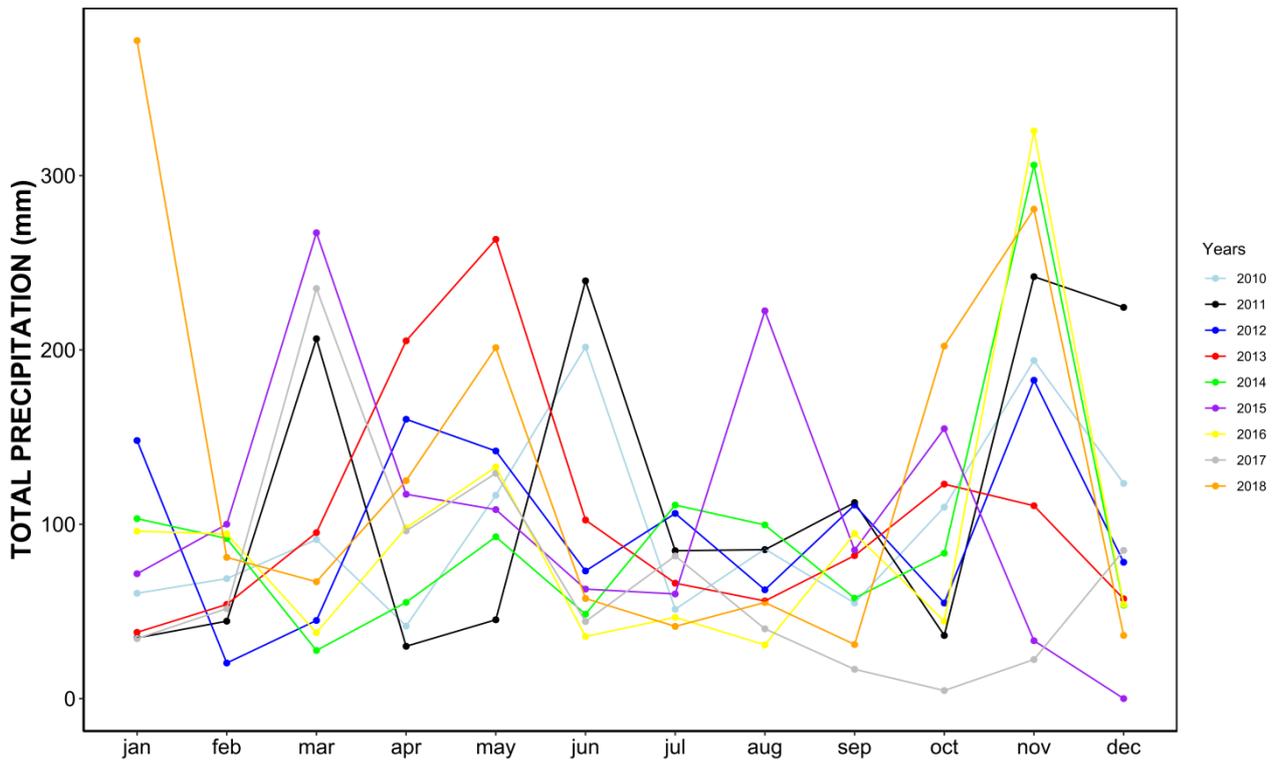
The chamois population in the Park has been protected since 1922 and presently its size is estimated at c. 6,700 individuals, over 710.44 km<sup>2</sup> (2018 GPNP count). The density of the population in the study area is estimated around 10 ind / km<sup>2</sup> (Corlatti et al. 2015b).

In my study site, apart from chamois, only the Alpine ibex *Capra ibex* is present at low densities (< 3 ind / km<sup>2</sup>, 2016 GPNP count), among wild ungulates. Wild boars *Sus scrofa* and roe deer *Capreolus capreolus* do not occupy permanently the area: only sporadically visit the lower parts of the site. During summer (June-September), livestock (< 300 sheep; several tens of cattles at the lowest elevations) occupies up to *c.* 1/3 of the area.

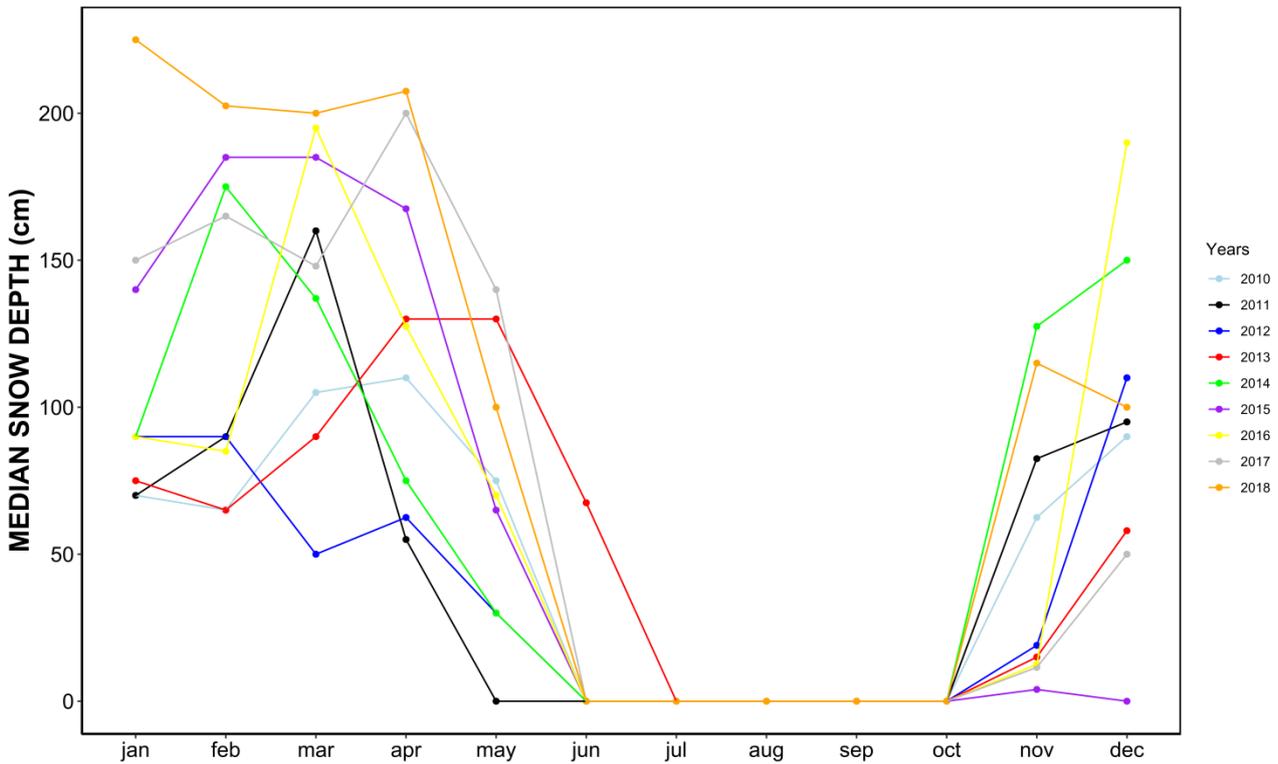
The main limiting factor for the chamois population is winter starvation (Peracino & Bassano 1987; Rughetti et al. 2011), while occasionally predation by golden eagles *Aquila chrysaetos* may occur on kids (Bertolino et al 2003; see also Scornavacca & Brunetti 2016). So far, no large carnivore (i.e. the grey wolf *Canis lupus*) has been present permanently in my study area (absent: in 2011-2012, 2015; occasionally reported: in 2016-present) (see also Palmegiani et al. 2013). The red fox *Vulpes vulpes* is also present in the area, but no predation on chamois kids is reported.



**Fig. 1** Mean monthly temperature (°C) in the study area, during years 2010-2018.

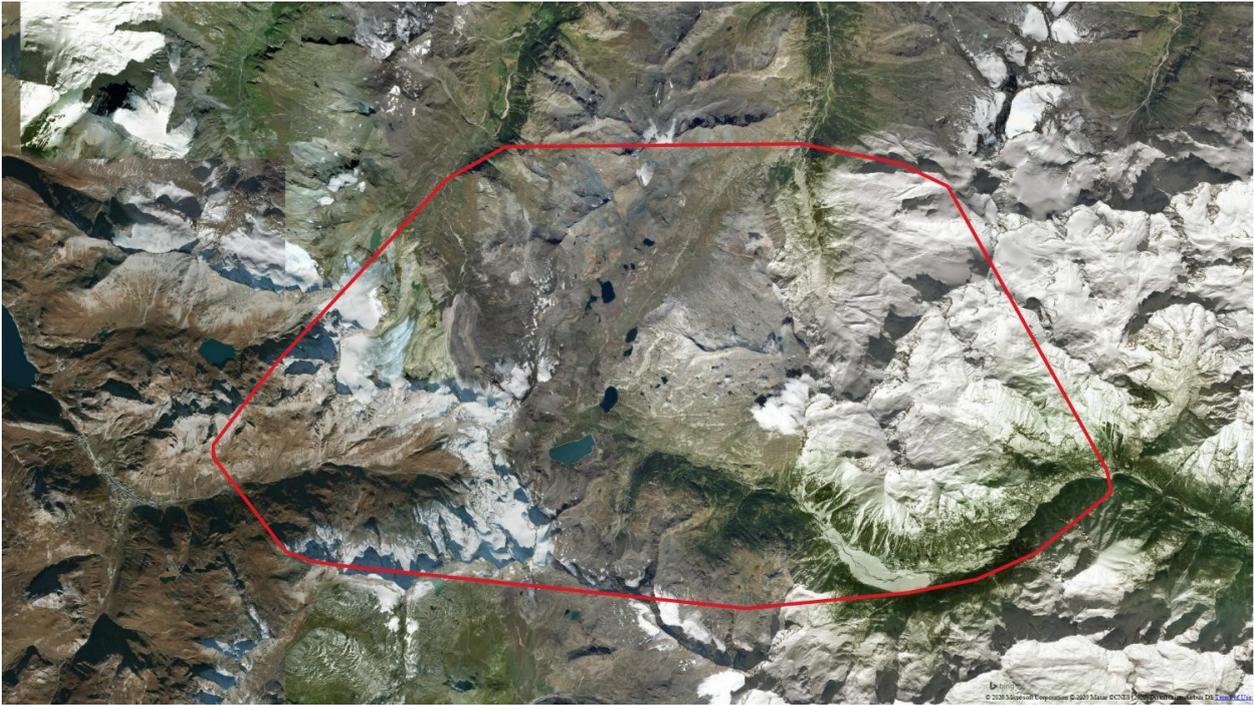


**Fig. 2** Total monthly precipitation (mm) in the study area, during years 2010-2018.

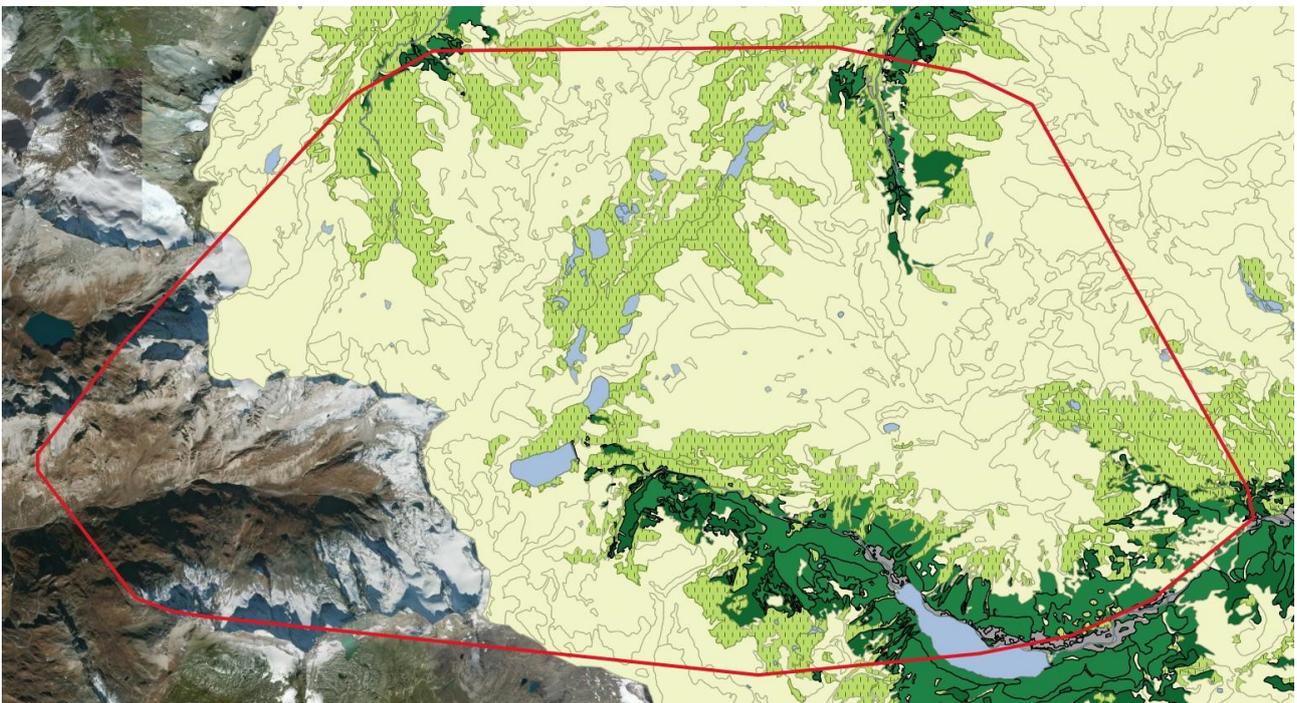


**Fig. 3** Median monthly snow depth (cm) in the study area, during years 2010-2018.

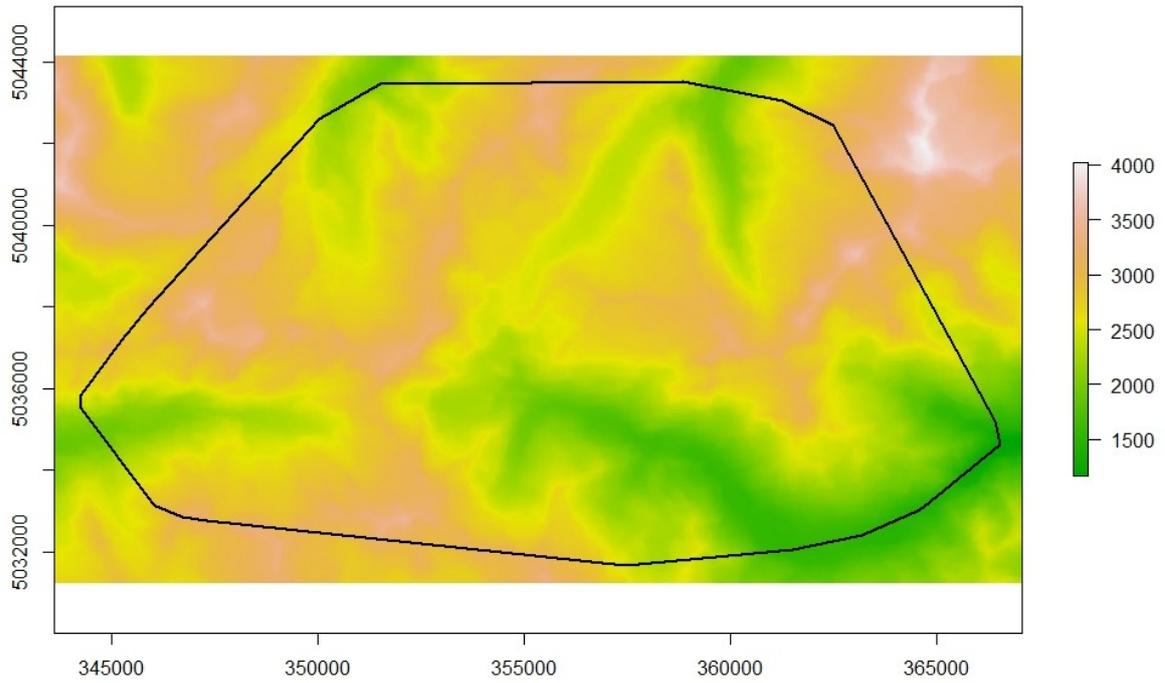




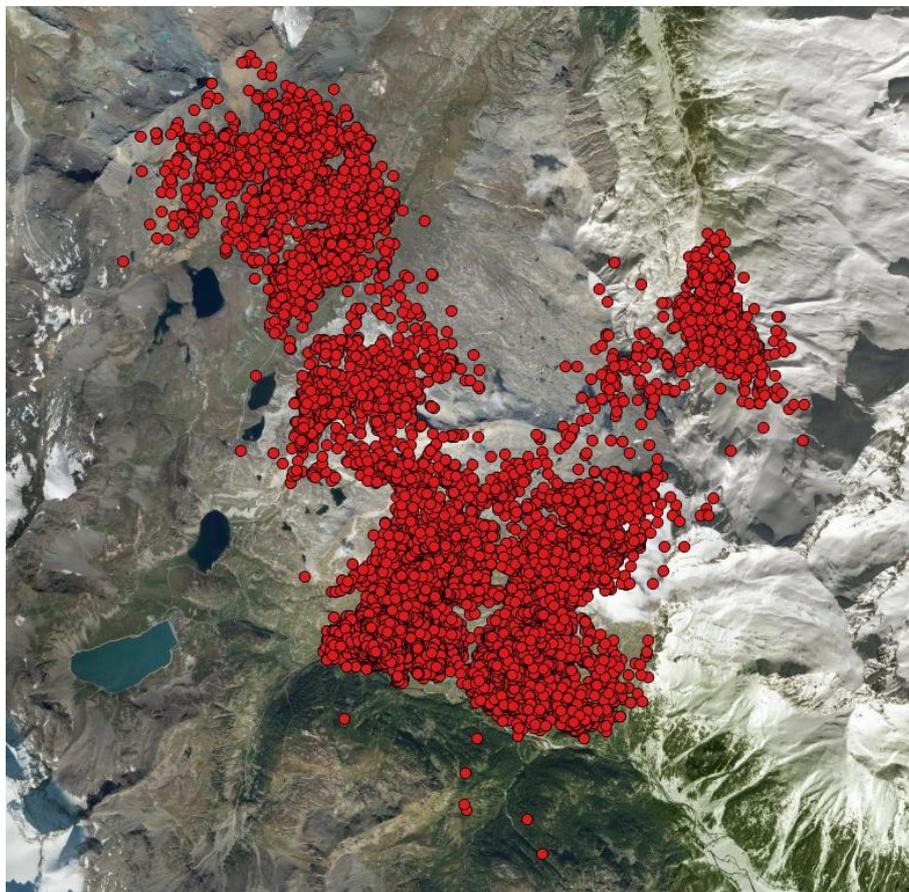
**Fig. 6** Aerial view of the study area. The minimum convex polygon shows the range of all monitored individuals, between 2011 and 2018.



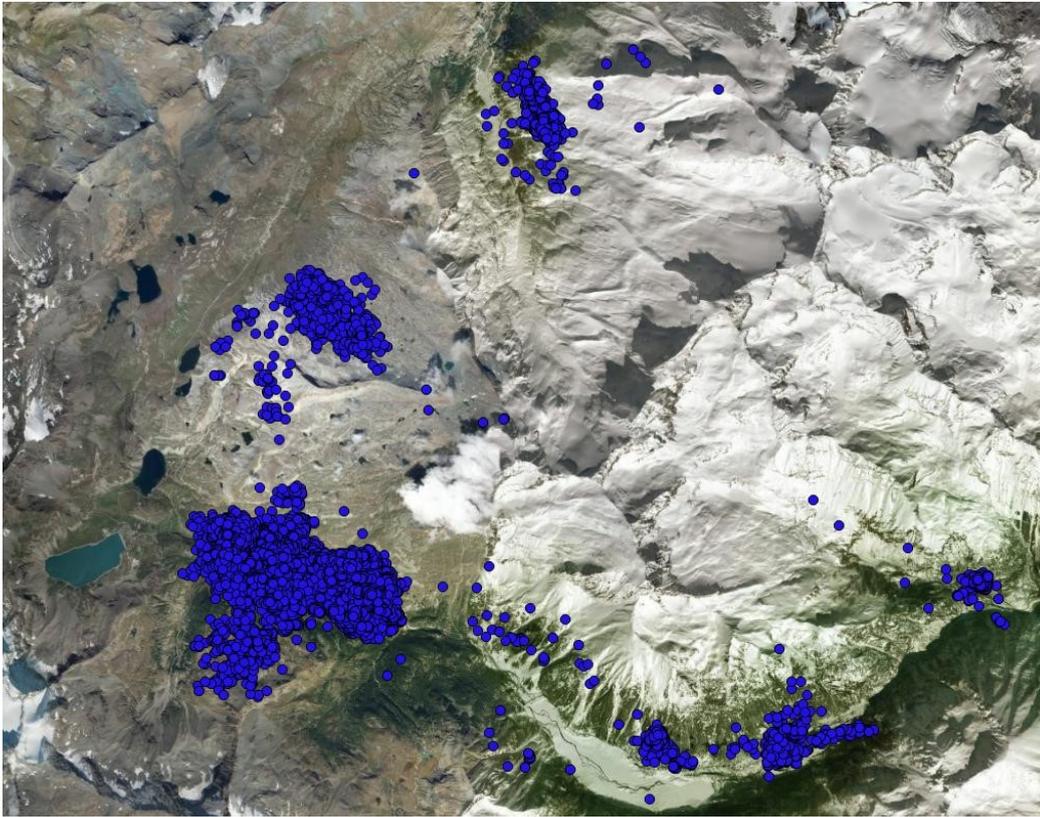
**Fig. 7** Land use classification of the study area: dark green = woods and bushes, light green = grazed grasslands, light blue = water, grey = urbanized areas, beige = not grazed or without vegetation areas. The minimum convex polygon shows the range of all monitored individuals, between 2011 and 2018.



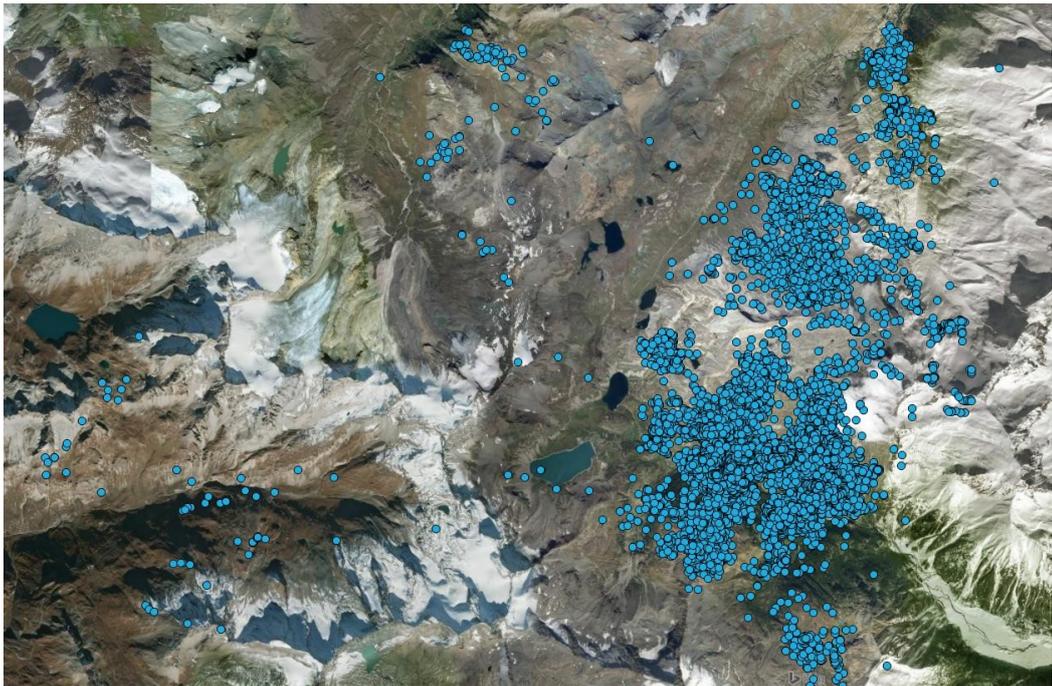
**Fig. 8** Digital Elevation Model (DEM) of the study area. The minimum convex polygon shows the range of all monitored individuals, between 2011 and 2018.



**Fig. 9** GPS locations of female Alpine chamois, during 2011-2012 and 2015-2018.

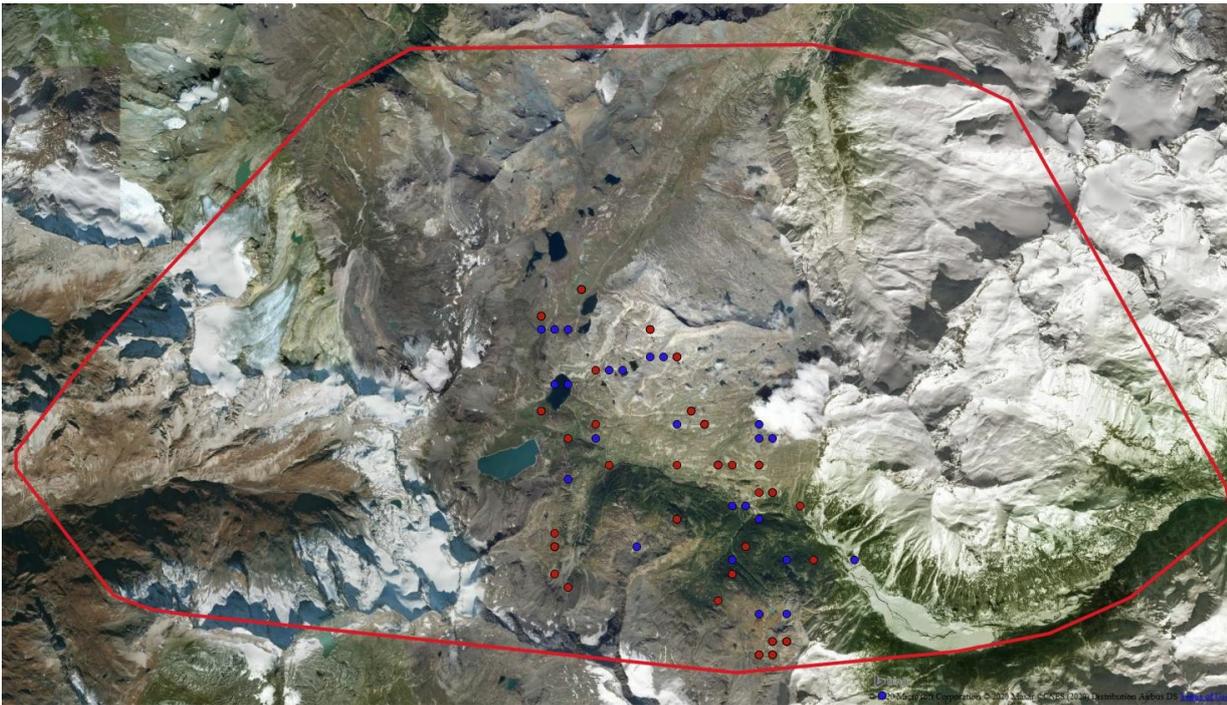


(A)



(B)

**Fig. 10** GPS locations of (A) territorial and (B) non-territorial male Alpine chamois, during 2011-2012 and 2015-2018.



**Fig. 11** Records of livestock presence (mainly sheep and cows) in the study area, between June-September, in 2011 (blue points) and 2012 (red points). The minimum convex polygon shows the range of all monitored individuals, between 2011 and 2018.

## CHAPTER 1

### Alternative mating and spatial tactics in male Alpine chamois



Javier Lazaro



# CHAPTER 1

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## *Alternative mating and spatial tactics in male Alpine chamois*

### **ABSTRACT**

Ungulates show great variability in alternative mating tactics (AMTs) in relation to individual or environmental factors. Different cost-benefit trade-offs could occur in relation to the adoption of each AMT, possibly influencing also spatial behaviour. Understanding differences in key aspects of life-history (e.g. survival and reproductive success) and behaviour (e.g. space use), amongst individuals adopting different AMTs, would help explain their evolution and coexistence in a population.

I collected data on mating behaviour of 31 marked adult male Alpine chamois during 5 rutting seasons (early November-early December, 2011-2012 and 2015-2017) and their spatial behaviour throughout the years. Amongst them 15 have been classified as territorial (T) and 16 as non-territorial (NT). No individuals changed AMT in different years, with the only potential exception of an old male which lost its territory during its last rut. Moreover, I reported a previously undocumented occurrence of different patterns of spatial behaviour across T males. Fifty percent of these individuals had overlapping or continuous winter and summer areas, whereas the others moved between different areas (immediately after the rut, in winter, or in summer-autumn). T males are known to face higher costs (higher androgen and cortisol metabolite levels, higher parasite levels, hypophagia) than NT ones, but I found no difference in survivorship amongst males adopting different mating tactics. Data suggest differences neither in age nor in the frequency of intra-sexual aggressive interactions between males adopting different AMTs. T males, which are known to be dominant over NT ones in aggressive interactions, consistently showed greater indices of mating opportunities than non-territorial ones. Data support that AMTs may be fixed in male

chamois, which may adopt a conservative mating strategy, i.e. a less intense and less energetically demanding competition amongst males compared to that of highly dimorphic species, and probably different spatial strategies, to maximise survival.

## INTRODUCTION

In polygamous species, intense intra-sexual competition to increase mating opportunities can lead to the development of *alternative mating tactics* (hereafter AMTs). AMTs are distinct alternative behavioural and/or morphological traits (e.g. colour or size polymorphism in fish, Gross 1991; plumage variations in birds, Lank et al. 1995; dimorphic morphological structures involved in the defence of resources or mates, such as differences in body weight in mammals, Clutton-Brock et al. 1982), selected to maximise fitness (Taborsky et al. 2008). Most mammalian species (95%) are polygynous (Kleiman 1977; Alcock 2005), thus AMTs are expected to evolve more often in males (Taborsky et al. 2008).

At the individual level, AMTs may be “fixed” (fixed AMTs), when individuals adopt a single tactic over their lifetime, or “flexible”, i.e. when individuals switch back and forth between patterns (simultaneous AMTs) or switch from one pattern to another in a specific phase of their life (sequential AMTs) (Brockmann 2001; Taborsky 1998). If environmental conditions, availability of partners or number of potential competitors either change rarely or unpredictably, fixed AMTs may be selected (Shuster & Wade 2003). If conditions are highly unpredictable, a selection for simultaneous AMTs is expected (Taborsky 1994; Halliday & Tejedó 1995; Westneat 2003). If conditions vary with growth and ageing, sequential AMTs may be selected (Alonzo et al. 2000; Utami et al. 2002). Fixed AMTs are known for insects (Hamilton 1979), fish (Gross 1984) or birds (Widemo 1998), but are rare in mammals (Crews 1998; Taborsky et al. 2008). Fixed tactics are usually characterized by morphological differences between alternative phenotypes, while AMTs diverging only in behavioural traits should be more flexible (Taborsky et al. 2008).

AMTs associated to the occurrence of differential behavioural traits relevant to space use, limited to the mating period, have been reported for different taxa (e.g. insects: Opaev & Panov 2016; fish: Afonso et al. 2008; amphibians: Forester & Thompson 1998; reptiles: Shine et al. 2005; birds: Andersson 1980; mammals: Sandell 1989; among ungulates: Lovari et al. 2008, for female roe deer

*Capreolus capreolus*). Conversely, variation in space use throughout the year to favour reproductive opportunities in the mating period has been rarely reported. Lovari et al. (2006) showed that some male Alpine chamois *Rupicapra rupicapra rupicapra* are resident throughout the year in their home range, whereas others are migrant. These authors suggested that inter-individual differences may be related to different tactics adopted to gain mating opportunities in relation to environmental stochasticity (see also Corlatti et al. 2020). Information is scarce on the occurrence of different tactics of space use across individuals adopting the same AMT (but see Melis et al. 2004, for territorial male roe deer).

Ungulates show a great variability in mating tactics (Isvaran 2005a). Males rarely show irreversible patterns, whereas they often switch between two or more mating tactics during or between mating seasons (Isvaran 2005a), in relation to age (e.g. Clutton-Brock et al. 1982; Mainguy et al. 2008; Willisch & Neuhaus 2009), female density (Carranza et al. 1995; Isvaran 2005b) or weather conditions (Apollonio et al. 2013). If so, one would expect that normally a given AMT would not be used consistently across years by individuals. When different AMTs co-occur in a population, cost-benefit trade-offs should be expected to occur in relation to the adoption of each tactic: e.g. differences in parasite susceptibility (Pelletier et al. 2005; Corlatti et al. 2012a), feeding intensity (Pelletier et al. 2004; Corlatti et al. 2013b), mating success (Corlatti et al. 2015). If so, understanding differences in key aspects of life-history (survival, reproductive success) and behaviour (space use, dominance) between individuals adopting different AMTs would help shed light on factors that favour their coexistence in the population.

I investigated AMTs in a weakly polygynous (Bocci et al. 2010; Rughetti & Festa-Bianchet 2011; Corlatti et al. 2012a) and near-monomorphic mammal, the Alpine chamois (Bovidae: Caprinae), a mountain-dwelling ungulate for which two AMTs have been described in males (Corlatti et al. 2012a). During the rut (November), at the lower elevations some males defend an exclusive area from intruders, trying to keep females there (territorial males, T); others display a following behaviour to females (the common tactic amongst Caprinae, Schaller 1977) and try to access other

males' territories (non-territorial males, NT) (Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012a). Territoriality in chamois has been suggested to be related to a “resident” spatial behavioural tactic, while non-territorial males appear to move to higher elevations, in summer (Lovari et al. 2006). However it is not clear whether all territorial males are residents and whether all non-territorial males are migrants. During the rut, territorial males show an increase in (i) mating effort, while facing rut-induced hypophagia (Corlatti et al. 2013b; Corlatti & Bassano 2014; cf. Willisch & Ingold 2007), (ii) levels of aggressiveness and stress (Corlatti et al. 2012a), (iii) parasite levels, probably caused by an immunosuppressive effect linked to hormones secretion (Folstad & Karter 1992; Corlatti et al. 2012a, 2019). Conversely, non-territorial males have been shown to only present an increase in androgen metabolites, indicators of aggressiveness (e.g. for other ungulates: Mooring et al. 2004; Hoby et al. 2006). Parasite susceptibility, together with high mass loss (Rughetti & Festa-Bianchet 2011), could trigger costs in terms of overwinter survival in territorial males; however these individuals seem to benefit from higher, but not exclusive, reproductive success (Corlatti et al. 2015). Territorial males start to defend their territories in late spring, well before the mating season (von Hardenberg et al. 2000), suggesting benefits from higher knowledge of their defended area and, in particular, from a “*prior residence advantage*” (Braddock, 1949; Maynard-Smith 1982). Conversely, non-territorial males could benefit from moving to higher elevations in summer, where grasslands are richer in nutrients during that season (Albon & Langvatn 1992; Bassano 1994; Bassano et al. 1997; but see Corlatti et al. 2013b). Non-territorial males would gain higher reproductive success in years with absent or delayed snowfalls. Indeed, snowfalls make females move to the lower elevations during the rut (November), where territorial males would monopolise mating events. When snowfalls are late, females would stay longer and rut at the higher elevations, where non-territorial males may have an advantage. This hypothesis could explain the co-occurrence of these two mating tactics (Lovari et al. 2006; Corlatti et al. 2020).

There is no information on (i) whether mating tactics could be switched from one year to another by the same individual, (ii) the occurrence of different patterns of space use in individuals adopting the

same AMT, (iii) differences in survivorship between individuals adopting different AMTs, (iv) differences in mating success between individuals adopting different AMTs, on the long term.

On 2011-2012 and 2015-2017, intensive GPS-GSM radio-telemetry, together with direct behavioural observations of the mating behaviour of 31 adult male Alpine chamois, have been used to evaluate whether (i) individuals repeatedly monitored in different years always adopted the same AMT or not, (ii) differences occurred in patterns of space use among individuals adopting the same AMT, (iii) differences occurred in age, survivorship, intensity of intra-sexual competition during the mating season and mating success, between individuals adopting different AMTs. I predicted that: (i) since chamois assert dominance through aggressiveness, relying on a rich behavioural repertoire (Lovari 1985), rather than on size-related traits (Corlatti et al. 2012a, 2013a), AMTs would be flexible, (ii) territorial males would stay in or close to their territories all year round, to gain advantage from residency (Braddock, 1949; Maynard-Smith 1982), while non-territorial males would migrate in late spring/summer to higher elevations (Lovari et al. 2006), to benefit from richer pasture (Albon & Langvatn 1992; Bassano 1994; Bassano et al. 1997), (iii) no differences would occur in age between males adopting different tactics (Corlatti et al. 2012a), whereas territorial males would show a lower life expectancy because of the higher costs faced (Corlatti et al. 2012a); territorial males would also show a higher frequency of aggressive intra-sexual interactions, to maintain their ownership, and a higher mating success, because of their dominance (Corlatti et al. 2012a, 2013a, 2015).

## MATERIALS AND METHODS

### *Data collection and analysis*

#### *Capture and marking*

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 recognisable GSM-GPS Pro-Light collars, with very high frequency (VHF) beacon devices (Vectronic Aerospace GmbH, Berlin), and coloured ear tags. In accordance with the 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 (e.g. von Hardenberg et al 2000; Corlatti et al. 2012a). At sedation, the age of each male was estimated by counting horn rings (Schröder & von Elsner-Schack 1985).

#### *Mating behaviour: AMTs distinction*

Overall, my study included 5 rutting seasons: 2011 (N = 19 individuals), 2012 (N = 18), 2015 (N = 13), 2016 (N = 17) and 2017 (N = 11). The distinction between territorial (T) and non-territorial (NT) males was based on the following criteria: during the rutting season (early November – early December; Krämer 1969; Willisich & Ingold 2007; Corlatti et al. 2012a) T males would show higher site fidelity, hence smaller home range size, and win more aggressive interactions with other males than NT individuals (von Hardenberg et al. 2000, Corlatti et al. 2012a). I 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: number of interactions won / total number of interactions) during the rut (6<sup>th</sup> of November - 5<sup>th</sup> of December, cf. von Hardenberg et al. 2000, Corlatti et al. 2012a).

For GPS-based home range estimates, I used always high-quality GPS locations (i.e. with at least 4 satellites and Dilution of Precision -DOP- values  $\leq 10$  and 3 satellites and DOP values  $\leq 5$ , Kenward 2000; Lewis et al. 2007).

The number and the outcome of aggressive interactions with other males were recorded through continuous focal animal sampling (Altmann 1974) during 1 h / individual bouts, during the rutting periods. Each mating season was divided in 3 groups of 10 days: 6<sup>th</sup> – 15<sup>th</sup> of November (period I), 16<sup>th</sup> – 25<sup>th</sup> of November (period II), 26<sup>th</sup> of November – 5<sup>th</sup> of December (period III), to homogeneously distribute observations over the entire rut and amongst all males (cf. Corlatti et al 2012a). Observations were evenly distributed throughout daylight hours and conducted with binoculars (e.g. Zeiss 15x60, Avalon 10x42) and spotting scopes (Nikon 20-60x). Behavioural data were recorded on standardized recording sheet. The focal male was considered as involved in intra-sexual interactions if he performed direct or indirect forms of aggressiveness against another male (Lovari 1985, Lovari & Locati 1991). An interaction was recorded *i*) as *won* by the focal male when the opponent was chased away and/or displayed submissive behaviour; *ii*) as *lost* by the focal male when the focal male showed submissive behaviour and/or moved away from the opponent; *iii*) *ended with a “tie”* when neither rival performed submissive behaviour or moved away (Krämer 1969, Lovari 1985).

I then combined the two parameters (rut home range size, index of wins in aggressive interactions with other males) in a matrix and performed multivariate hierarchical clustering each study year (Everitt et al. 2011) using the Mahalanobis distance (Mahalanobis 1936) as metric (*'stats'* library, *'hclust'* function, in R - R Core Team 2019). Individuals monitored during the rut 2015 had been captured and marked between 2010-2013 and the battery of their GPS radio-collars had expired, thus preventing me from estimating their ranging movements: for those individuals only the index of wins in aggressive interactions with other males has been estimated. Also, during the rut 2016 and 2017, for males with inactive radio-collars, I only estimated the index of wins in intra-sexual aggressive interactions. For those individuals, the highest IW value found for NT males in the

previous years was considered as a threshold to tell T males apart from NT ones. All analyses were performed in Microsoft Excel (2010) and R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio.

### *Spatial behaviour*

To investigate alternative tactics of space use (ASTs) in male chamois I used high-quality GPS locations (i.e. with at least 4 satellites and Dilution of Precision -DOP- values  $\leq 10$  and 3 satellites and DOP values  $\leq 5$ , Kenward 2000; Lewis et al. 2007) to calculate (i) the Net Squared Displacement (NSD, Turchin 1998) and (ii) the altitudinal movement, starting from the chamois location on the 1<sup>st</sup> of January of each year, for every male, in every year for which I had annual GPS data and established mating tactic: 2011 (N = 18 individuals), 2012 (N = 14), 2016 (N = 10), 2017 (N = 6). I used the function ‘*spDistsNI*’ to calculate NSD and ‘*move*’ (Kranstauber et al. 2019), ‘*lubridate*’ (Grolemund & Wickham 2011), ‘*adehabitatHR*’ (Calenge 2006) libraries, to handle with spatial data, in R. Then, I calculated the yearly variance for each male for the two distances (“horizontal”, the NSD, and “vertical”, the altitudinal movement). Finally, I combined the variances, two for each male in each year, in a matrix and performed multivariate hierarchical clusterings (Everitt et al. 2011) using the Mahalanobis distance (Mahalanobis 1936) as metric (‘*stats*’ library, ‘*hclust*’ function, in R). I calculated two separated clusters, one for territorial and one for non-territorial males. I also visually inspected the NSD and altitudinal movements for each male, in each year. All analyses were performed in R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio.

### *Statistical analyses - Mating behaviour: differences between AMTs*

I used the Shapiro-Wilk normality test to evaluate the assumption of normality for all the considered response variables. Differences in age among males adopting different mating tactic were investigated: (i) through generalised linear models (GLMs), considering the age at capture as

response variable (Shapiro-Wilk normality test:  $W = 0.89$ ,  $p\text{-value} = <0.01$ ), using the function ‘*glm*’ (‘*stats*’ library) in R, and (ii) through generalised linear mixed models (GLMMs), considering the age a male was in each year of observation as response variable (Shapiro-Wilk normality test:  $W = 0.96$ ,  $p\text{-value} = 0.01$ ), using the function ‘*glmer*’ (‘*lme4*’ library, Bates et al. 2015) in R. I selected a Poisson distribution and a ‘*log*’ link function for both models (Crawley 2007, Bolker et al. 2009). The mating tactic adopted was the predictor in the models. In the second analysis the identity of males was considered as random effect, to account for repeated estimates of the same individual.

I have also investigated whether mating behaviour could have an influence on life expectancy of individuals by analysing differences in age at death (only for males for which the year and the month of death could be clearly established) (Shapiro-Wilk normality test:  $W = 0.89$ ,  $p\text{-value} = 0.05$ ) between territorial and non-territorial males, through the Student’s t-test for independent samples.

Besides the index of wins in aggressive interactions with other males (IW), I calculated the hourly frequency of intra-sexual aggressive interactions for each male (number of interactions / number of observation hours). On the rut, during 1 h / individual bouts (cf. above), the number of females within 50 m from the focal male was also recorded, every 20 minutes: I then calculated the mean number of females per hour per each male, as an index of mating opportunities (von Hardenberg et al. 2000; Corlatti et al. 2012a). I investigated differences in the hourly frequency of aggressive interactions with other males (Shapiro-Wilk normality test:  $W = 0.91$ ,  $p\text{-value} = <0.001$ ) and mating opportunities index (Shapiro-Wilk normality test:  $W = 0.76$ ,  $p\text{-value} = <0.001$ ) between territorial and non-territorial males through GLMMs, selecting a gamma distribution and a ‘*log*’ link function (Crawley 2007, Bolker et al. 2009), using the function ‘*glmer*’ (‘*lme4*’ library, Bates et al. 2015) in R. To investigate differences in the frequency of intra-sexual aggressive interactions, set as response variable, I accounted for the mating tactic adopted, mating opportunities, year and their interactions, as predictors in the global model. To investigate differences in mating opportunities

index, set as response variable, I accounted for the mating tactic adopted, frequency of intra-sexual aggressive interactions, year and their interactions, as predictors in the global model. In each model, the identity of males was considered as random effect, to account for repeated estimates for the same individual.

Model selection was performed considering the minimum Akaike's Information Criterion, corrected for small samples (AICc: Burnham & Anderson 2002), using the '*MuMIn*' library (Barton 2019) in R. For each response variable, a global model was built including all predictors, and all the possible alternative models were built including different combinations of predictors, and were ranked and weighted from the global model. Models with  $\Delta\text{AICc} \leq 2$  in respect to the best model (i.e. with the lowest AICc value), as well as models with an AICc value lower than that of any simpler, nested alternative were selected. All analyses were performed in Microsoft Excel (2010) and R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio. All p-value were considered significant at a level of 0.05.



## RESULTS

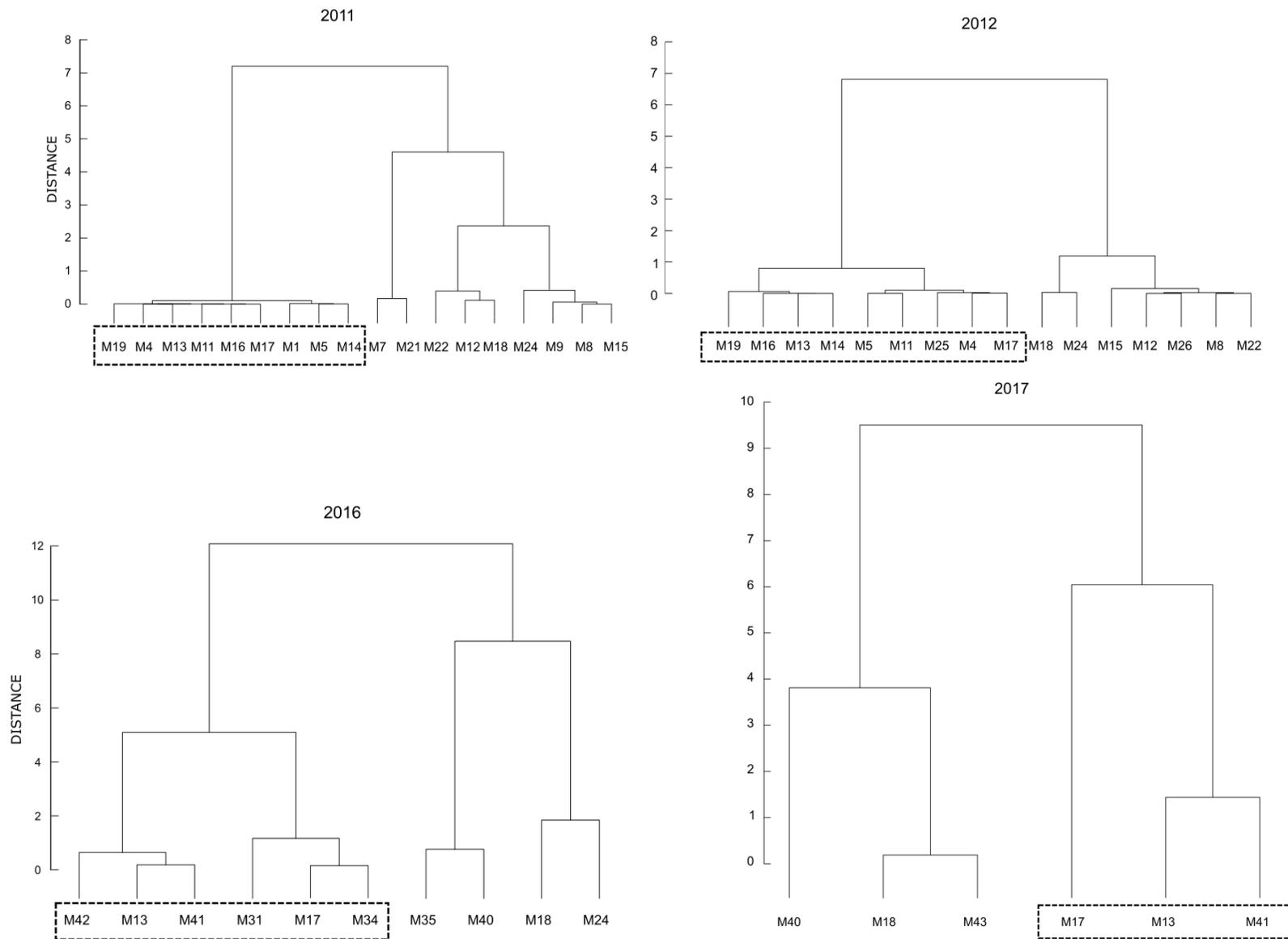
### *Temporal stability of AMTs*

I observed a total of 31 males during 5 rutting seasons (mean of 15 individuals/year) (Table 1), for a total of more than 460 hours of observations (55 – 118 hours/year), i.e. *c.* 6 hours/individual/year (Table 2). Fifteen males (48.4%) have been classified as territorial and 16 (51.6%) as non-territorial (Fig. 1; Table 1).

Out of 21 males (12 territorials, 9 non-territorials) observed for at least two rutting periods, none changed mating tactic classification, but for an old one: M4 (Table 3). This male was classified as "territorial" for 4 rutting seasons, but it was classified as "non-territorial" during its last mating season, in 2017, when it was 14.5 years old and was replaced in its territory by a younger male. On that rut, its index of wins and frequency of intra-sexual aggressive interactions were amongst the highest recorded for males classified as non-territorial (Table 2). Several times we observed it trying to take over again its former territory, chased away probably by the same younger male that forced it out. It died during the following February. Other males have been classified repeatedly as territorial, until the age of 13.5 (M5, M17), before dying.

**Table 1** Numbers and percentage of male Alpine chamois classified as territorial (T) and non-territorial (NT) for each rutting period and for the entire period of study.

<b>Year</b>	<b>T</b>	<b>%</b>	<b>NT</b>	<b>%</b>	<b>Tot</b>
<b>2011</b>	9	47.4	10	52.6	19
<b>2012</b>	9	50.0	9	50.0	18
<b>2015</b>	8	61.5	5	38.5	13
<b>2016</b>	11	64.7	6	35.3	17
<b>2017</b>	7	63.6	4	36.4	11
<b>All years</b>	15	48.4	16	51.6	31



**Fig. 1** Dendrogram of the hierarchical clustering of male Alpine chamois (top-left: 2011, N=18 individuals; top-right: 2012, N=16; bottom-left: 2016, N=10; bottom-right: 2017, N=6), based on the Mahalanobis distance using home range size and index of wins in intra-sexual interactions (IW). The dashed rectangle includes males classified as territorials. M23, during rut 2011, and M21 and M28, during the rut 2012, have not been shown and have been classified as non-territorials because of their exceptionally large home range size and/or their low index IW.

**Table 2** Mating tactic (AMT), index of wins in aggressive interactions with other males (IW), home range (HR K90%, ha), frequency of aggressive interactions with other males (INT.FREQ), observation hours (H/IND), for each male for each studied rutting period (2011, 2012, 2015, 2016, 2017). Med: median; QR: quartiles range; Mn: mean; Sd: standard deviation (*follows*).

2011						2012				
ID	AMT	IW	HR (K90%)	INT.FREQ	H/IND	AMT	IW	HR (K90%)	INT.FREQ	H/IND
M1	T	0.93	4.56	2.29	7.0					
M4	T	1.00	3.13	0.86	7.0	T	0.80	2.83	1.25	4.0
M5	T	0.88	12.00	1.14	7.0	T	0.67	14.75	1.00	3.0
M11	T	1.00	7.81	0.71	7.0	T	0.67	11.56	0.75	4.0
M13	T	1.00	2.25	0.86	7.0	T	1.00	4.38	0.67	3.0
M14	T	0.90	3.00	1.43	7.0	T	1.00	3.10	0.33	3.0
M16	T	1.00	5.75	0.71	7.0	T	1.00	7.13	0.33	3.0
M17	T	1.00	4.63	0.86	7.0	T	0.80	10.00	1.67	3.0
M19	T	1.00	13.00	1.50	2.0	T	1.00	23.69	1.00	1.0
M25						T	0.50	5.56	0.50	4.0
	T	<b>Med= 1.0</b> <b>QR= 0.9-1.0</b>	<b>Med= 4.6</b> <b>QR= 3.1-7.8</b>	<b>Mn= 1.1</b> <b>Sd= ±0.5</b>	<b>Med= 7.0</b> <b>QR= 7.0-7.0</b>	T	<b>Med= 0.8</b> <b>QR= 0.7-1.0</b>	<b>Med= 7.1</b> <b>QR= 4.4-11.6</b>	<b>Med= 0.7</b> <b>QR= 0.5-1.0</b>	<b>Med= 3.0</b> <b>QR= 3.0-4.0</b>
M7	NT	0.00	237.38	0.14	7.0					
M8	NT	0.00	16.63	1.71	7.0	NT	0.00	17.10	0.67	3.0
M9	NT	0.08	23.75	2.00	7.0					
M12	NT	0.38	13.06	1.57	7.0	NT	0.00	7.10	0.67	3.0
M15	NT	0.00	16.00	1.29	7.0	NT	0.00	39.70	1.33	3.0
M18	NT	0.50	16.94	1.71	7.0	NT	0.33	25.00	2.00	3.0
M21	NT	0.00	290.31	1.00	2.0	NT	0.00	384.50	0.33	3.0
M22	NT	0.46	75.50	1.57	7.0	NT	0.00	19.20	0.33	3.0
M23	NT	0.00	598.50	1.00	2.0					
M24	NT	0.25	8.75	2.00	2.0	NT	0.40	22.20	3.33	3.0
M26						NT	0.00	6.40	0.67	3.0
M28						NT	0.00	NA	0.33	3.0
	NT	<b>Med= 0.0</b> <b>QR= 0.0-0.3</b>	<b>Med= 20.3</b> <b>QR= 16.2-196.9</b>	<b>Mn= 1.4</b> <b>Sd= ±0.6</b>	<b>Med= 7.0</b> <b>QR= 3.2-7.0</b>	NT	<b>Med= 0.0</b> <b>QR= 0.0-0.0</b>	<b>Med= 20.7</b> <b>QR= 14.6-28.7</b>	<b>Med= 0.7</b> <b>QR= 0.3-1.3</b>	<b>Med= 3.0</b> <b>QR= 3.0-3.0</b>

**Table 2** Mating tactic (AMT), index of wins in aggressive interactions with other males (IW), home range (HR K90%, ha), frequency of aggressive interactions with other males (INT.FREQ), observation hours (H/IND), for each male for each studied rutting period (2011, 2012, 2015, 2016, 2017). Med: median; QR: quartiles range; Mn: mean; Sd: standard deviation.

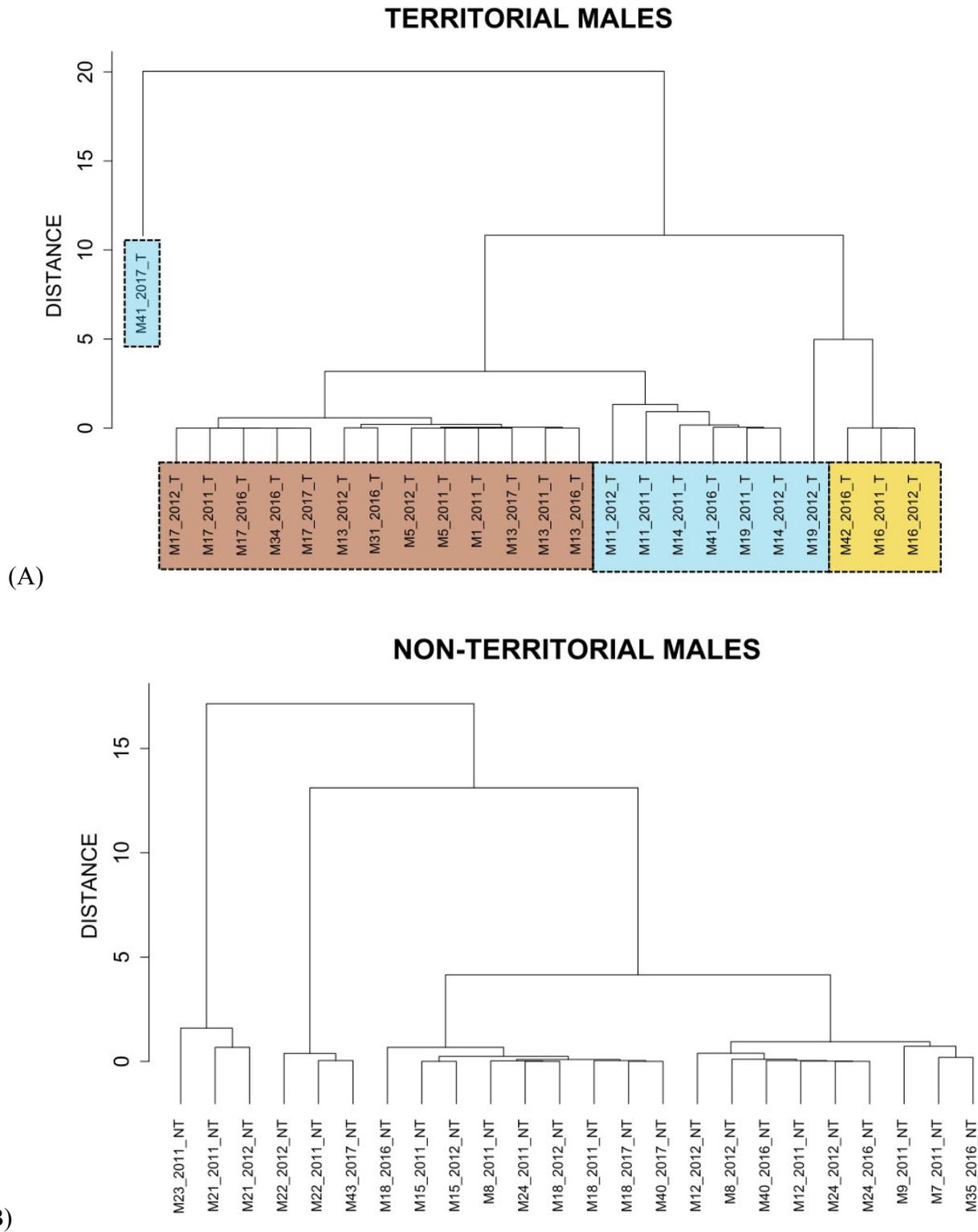
		2015				2016					2017				
ID	AMT	IW	HR (K90%)	INT.FREQ	H/IND	AMT	IW	HR (K90%)	INT.FREQ	H/IND	AMT	IW	HR (K90%)	INT.FREQ	H/IND
<b>M4</b>	T	0.71	37.80	1.30	7.7	T	1.00	11.00	0.29	7.0	NT	0.44	NA	1.00	9.0
<b>M5</b>	T	0.78	19.50	1.08	7.4	T	1.00	12.69	0.90	7.8	T	1.00	28.19	0.89	9.0
<b>M11</b>	T	0.60	11.30	1.20	5.0										
<b>M13</b>	T	0.70	23.10	0.95	5.3	T	1.00	3.25	0.64	4.7	T	0.83	1.94	0.70	8.5
<b>M16</b>	T	0.58	10.80	1.28	6.3	T	0.67	16.00	1.10	8.2	T	0.83	4.69	0.85	7.1
<b>M17</b>	T	0.80	32.80	1.00	7.0	T	0.83	28.81	0.69	8.6	T	1.00	19.63	0.47	10.5
<b>M25</b>	T	1.00	8.30	0.50	8.0	T	1.00	7.00	0.72	8.3	T	0.88	5.63	0.93	8.6
<b>M31</b>	T	0.56	23.20	1.17	8.5	T	0.90	16.00	1.02	9.8					
<b>M34</b>						T	1.00	27.31	0.92	3.3					
<b>M36</b>						T	0.57	22.31	1.01	6.9	T	0.80	11.38	0.52	9.6
<b>M41</b>						T	1.00	8.50	0.14	7.0	T	1.00	10.56	0.57	8.8
<b>M42</b>						T	0.80	3.50	0.73	6.8					
	T	<b>Mn= 0.7</b> <b>Sd= ±0.1</b>	<b>Mn= 20.8</b> <b>Sd= ±10.6</b>	<b>Med= 1.1</b> <b>QR= 1.0-1.2</b>	<b>Med= 7.2</b> <b>QR= 6.0-7.8</b>	T	<b>Med= 1.0</b> <b>QR= 0.8-1.0</b>	<b>Mn= 14.2</b> <b>Sd= ±8.9</b>	<b>Mn= 0.7</b> <b>Sd= ±0.3</b>	<b>Mn= 7.1</b> <b>Sd= ±1.8</b>	T	<b>Med= 0.9</b> <b>QR= 0.8-1.0</b>	<b>Mn= 11.7</b> <b>Sd= ±9.3</b>	<b>Mn= 0.7</b> <b>Sd= ±0.2</b>	<b>Mn= 8.9</b> <b>Sd= ±1.0</b>
<b>M12</b>	NT	0.00	NA	1.00	1.0										
<b>M18</b>	NT	0.20	NA	0.35	5.8	NT	0.20	23.00	0.56	8.9	NT	0.20	20.94	0.58	8.6
<b>M24</b>	NT	0.33	NA	0.57	7.0	NT	0.00	10.50	1.57	7.0					
<b>M28</b>	NT	0.40	NA	1.18	8.5	NT	0.40	NA	0.71	7.0					
<b>M29</b>	NT	NA	NA	0.00	2.0	NT	0.25	NA	0.67	6.0					
<b>M35</b>						NT	0.00	35.69	0.80	5.0					
<b>M40</b>						NT	0.13	43.69	1.30	6.2	NT	0.00	8.31	0.74	9.4
<b>M43</b>											NT	0.00	20.81	0.19	5.4
	NT	<b>Mn= 0.2</b> <b>Sd= ±0.2</b>	NA	<b>Med= 0.6</b> <b>QR= 0.3-1.0</b>	<b>Med= 5.8</b> <b>QR= 2.0-7.0</b>	NT	<b>Med= 0.2</b> <b>QR= 0.0-0.2</b>	<b>Mn= 28.2</b> <b>Sd= ±14.6</b>	<b>Mn= 0.9</b> <b>Sd= ±0.4</b>	<b>Mn= 6.7</b> <b>Sd= ±1.3</b>	NT	<b>Med= 0.1</b> <b>QR= 0.0-0.3</b>	<b>Mn= 16.7</b> <b>Sd= ±7.2</b>	<b>Mn= 0.6</b> <b>Sd= ±0.3</b>	<b>Mn= 8.1</b> <b>Sd= ±1.8</b>

**Table 3** Mating tactic classification (T: territorial, NT: non-territorial) for male Alpine chamois observed for at least two rutting periods (between 2011-2017).

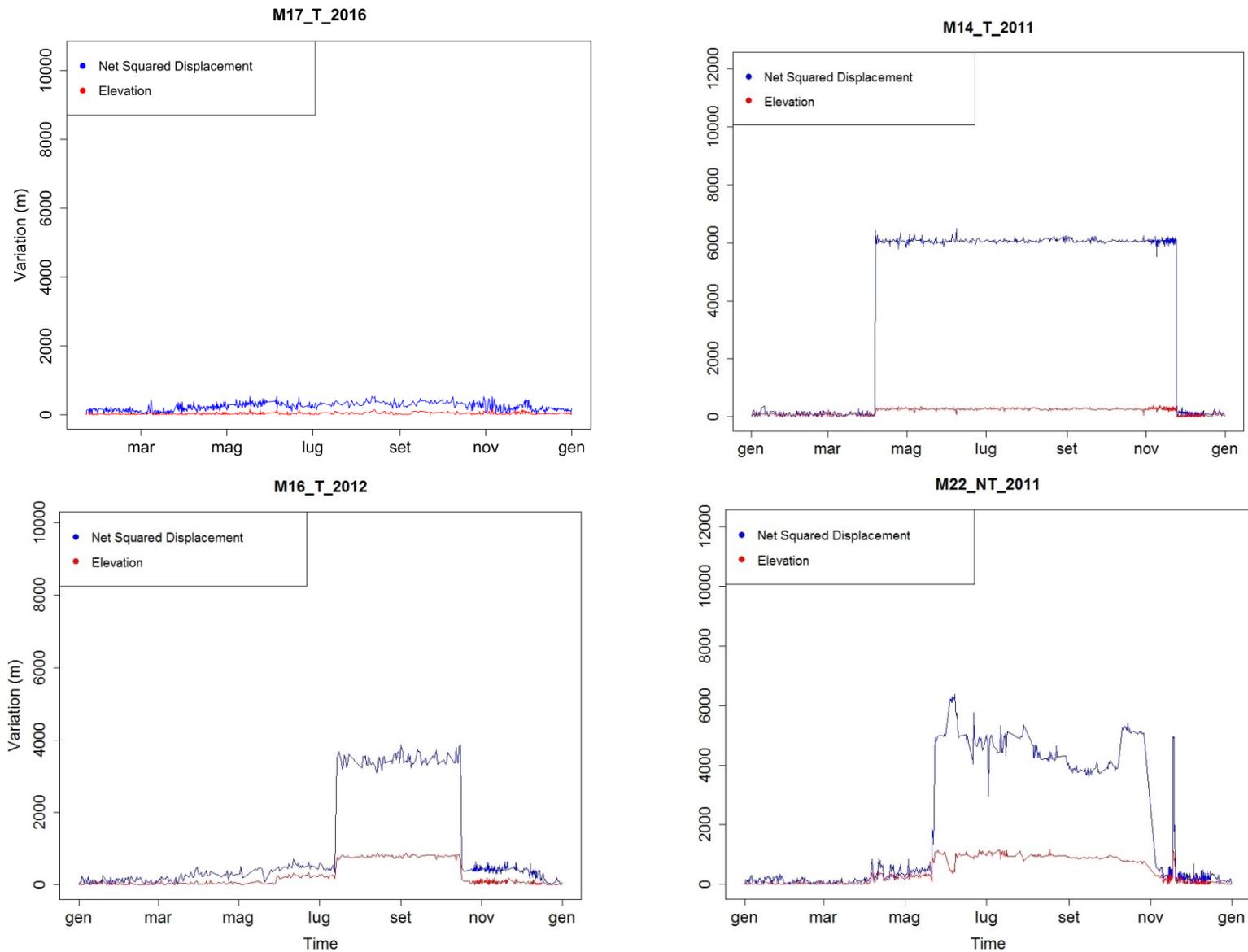
ID	TACTIC				
	2011	2012	2015	2016	2017
<b>M5</b>	T	T	T	T	T
<b>M11</b>	T	T	T		
<b>M13</b>	T	T	T	T	T
<b>M14</b>	T	T			
<b>M16</b>	T	T	T	T	T
<b>M17</b>	T	T	T	T	T
<b>M19</b>	T	T			
<b>M25</b>		T	T	T	T
<b>M31</b>			T	T	
<b>M36</b>				T	T
<b>M41</b>				T	T
<b>M4</b>	T	T	T	T	<b>NT</b>
<b>M8</b>	NT	NT			
<b>M12</b>	NT	NT	NT		
<b>M15</b>	NT	NT			
<b>M18</b>	NT	NT	NT	NT	NT
<b>M21</b>	NT	NT			
<b>M22</b>	NT	NT			
<b>M24</b>	NT	NT	NT	NT	
<b>M28</b>		NT	NT	NT	
<b>M40</b>				NT	NT

### *Alternative Spatial Tactics*

As to the spatial data, I could find no clear difference in the movement patterns amongst non-territorial males (N = 13) (Fig. 2b, 3d): all the individuals moved between summer and winter areas, mainly at different elevations. Conversely, two main patterns of movements were identified amongst territorial males (N = 12). Six individuals stayed the full year in or close to their territory, being residents. Six other males moved away from their territories in some periods, being migrants. Amongst them, 4 individuals moved away from their territories (between *c.* 5 - 10 km away) around late November-December (immediately after the rut), and they came back around late March-early May. In summer, around July-August, 2 other migrant individuals moved to different areas from those where they would stay all year long, rut included (*c.* 4 km away) and came back around October (Fig. 2a, 3a, b, c).



**Fig. 2** Dendrogram of the hierarchical clustering of male Alpine chamois, based on the Mahalanobis distance using variance of Net Squared Displacement (NSD) and variance of altitudinal movements (years 2011, 2012, 2016, 2017). (A) Territorial males (N = 12). The dashed rectangles divide males showing different movement patterns (orange: residents; light blue: moving in winter; yellow: moving in summer). (B) Non-territorial males (N = 13).

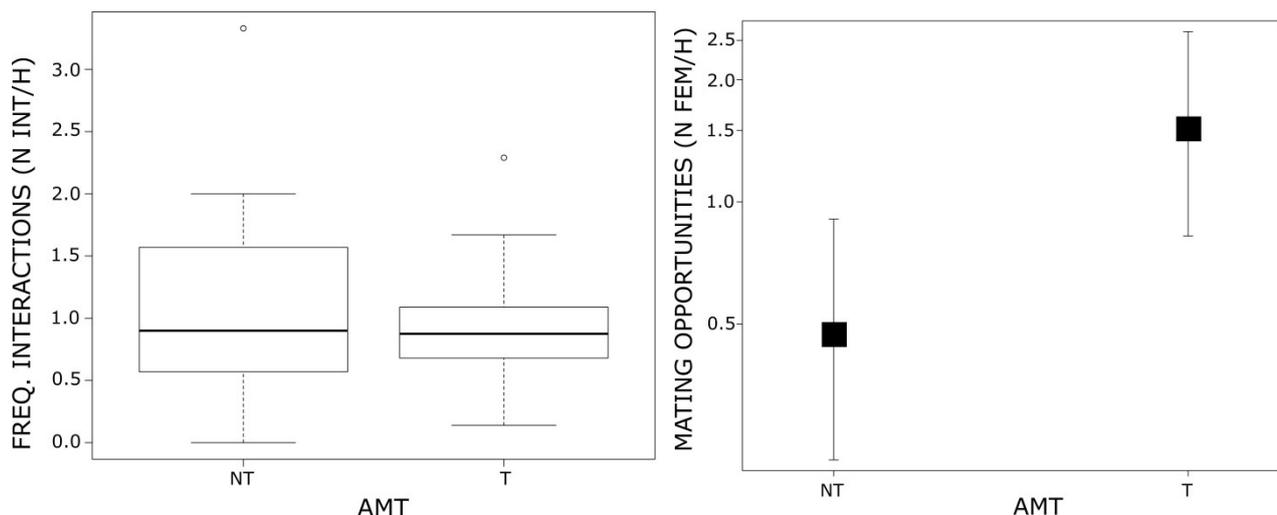


**Fig. 3** Net Squared Displacement and altitudinal movements (Elevation) of three male Alpine chamois classified as territorial (T) (top: M17, M14, bottom-left: M16), as examples respectively of “resident”, “moving in winter”, “moving in summer” behaviour, and a male Alpine chamois classified as non-territorial (NT) (bottom-right: M22).

*Age, survivorship, intra-sexual competition and mating opportunities*

I found no difference in age at capture between territorial and non-territorial males (median age: territorial males: 6.6 years old, QR: 5.1-8.0, N = 15; non-territorial males: 5.9 years old, QR: 4.7-7.6, N = 14. GLMs,  $\beta = -0.05$ , s.e. = 0.04, p-value = 0.22; Table S.1.1). No overall difference in age between territorial and non-territorial males was found (median age: territorial males: 9.5 years old, QR: 7.7-11.2, N = 44; non-territorial males: 8 years old, QR: 6.0-11.5, N = 34. GLMMs,  $\beta = -0.07$ , s.e. = 0.09, p-value = 0.43). Moreover, no difference in life expectancy was found amongst males adopting the two mating tactics (mean age at death: territorial males:  $10.9 \pm 3.7$  years old, N = 8; non-territorial males:  $11.3 \pm 3.1$  years old, N = 9. Welch t-test:  $t = 0.24$ ,  $df = 13.85$ , p-value = 0.81; Table S.1.1).

I found no difference in the hourly frequency of intra-sexual aggressive interactions between males adopting different mating tactics and the null model was selected (Tables 2, 4; Fig. 4a). Models supported only the effect of the mating tactic adopted on mating opportunities index (Table 4). In particular, territorial males had significantly greater mating opportunities than non-territorial ones (Fig. 4b; Table 5; Table S.1.2).



**Fig. 4** (Left) Hourly frequency of intra-sexual aggressive interactions (N interactions/h) (median value and interquartile range are shown); (right) differences in the mating opportunities index (N females/h), for male Alpine chamois adopting alternative mating tactics (AMT: non-territorial males NT; territorial males T), in 2011-2012 and 2015-2017.

**Table 4** (a) Effects of the alternative mating tactic adopted (AMT: territorial male, non-territorial male), mating opportunities index (Mat.opp.: mean number of females/h) and year on frequency of intra-sexual aggressive interactions (Freq.int.: number of intra-sexual interactions/h); (b) effects of the alternative mating tactic adopted, frequency of intra-sexual aggressive interactions and year on mating opportunities index, of male Alpine chamois in 2011-2012 and 2015-2017. Random effect in each model = Id: individual identities. Result of model selection: variables retained, degrees of freedom, logLikelihood, AICc,  $\Delta$ AICc values and model weight are shown.

	Model	Variables retained	df	logLik	AICc	$\Delta$ AICc	Weight
(a)	Freq.int.	(1 Id)	3	-67.39	141.1	0.00	1
(b)	Mat.opp	AMT + (1 Id)	4	14.54	-20.5	0.00	1

**Table 5** Parameters estimated from the best model on the effects of the alternative mating tactic adopted (AMT: territorial male T, non-territorial male NT) on mating opportunities index (Mat.opp: mean number of females/h), of male Alpine chamois in 2011-2012 and 2015-2017 ( $\beta$ : coefficient, SE: standard error, p-value). Reference category for categorical predictor AMT: non-territorial males NT.

Model	Variables	$\beta$	SE	p-value
Mat.opp	Intercept	-0.78	0.34	<0.05*
	AMT.T	1.17	0.45	<0.01**

## DISCUSSION

Alternative mating tactics (AMTs) have been frequently reported in ungulates (Isvaran 2005a). Behavioural mating tactics are frequently flexible in large mammals (Taborsky et al. 2008, e.g. Jarman & Jarman 1973; Clutton-Brock et al. 1982; Saunders et al. 2005), but I did not notice changes in the mating tactic adopted by adult male chamois, in my study sample. All the males observed for at least two different rutting seasons adopted the same mating tactic in different years, with the only potential exception of one old territorial individual (M4), that was classified as non-territorial during its last rutting season and died the following winter. Its several attempts to take over again its former territory and its possible poor health conditions, that led it to death, suggest that it was reasonably forced to switch mating tactic and that this was not a real change of tactic. Previous studies suggested a decline of body mass in old males (Schröder 1971), i.e.  $\geq 8.5$  years old (Bassano et al. 2003). However, my results suggest that males can still be dominant and hold a territory up to 12.5-13.5 years old (cf. Corlatti et al. 2012a), i.e. well beyond their prime (c. 5-9 years old, Stringham & Bubenik 1975), suggesting also a long breeding lifespan (Corlatti et al. 2015; for Apennine chamois *Rupicapra pyrenaica ornata*: Locati & Lovari 1988).

Male Alpine chamois reach their maximum body size when they are 4.5-5.5 years old (Bassano et al. 2003; Garel et al. 2009). In hunted populations, they may start to reproduce at that age, whereas, in protected areas where hunting is forbidden, they probably delay their first reproduction until 6.5 years old (Bassano et al. 2003; Garel et al. 2009; Corlatti et al. 2015; cf. for Apennine chamois: Lovari & Cosentino 1986; Locati & Lovari 1988). Sub-adults and younger individuals are usually subordinates to full-grown older ones (e.g. Rutberg 1983) and they are unlikely to succeed in competition for territories. This study suggests that males can gain and maintain a territory already when they are 5.5 years old (see also Corlatti et al. 2012a).

Non-territorial individuals were found also amongst prime-aged, adult males. According to prediction (iii), no age difference occurred between territorial and non-territorial males, suggesting

that age is not a determinant of the mating tactic in adult chamois (Corlatti et al. 2012a). Thus, AMTs would not change with age in adult chamois, as opposite in respect to what has been recorded for other ungulates (e.g. McElligot et al. 2002; Vanpé et al. 2009). Data over the whole lifespan of marked individuals, including also younger males (<5 years old), would be needed to confirm it.

Snow cover is known to impair herbivore movements (e.g. Dailey & Hobbs 1989; van Beest et al. 2011). Thus, it would probably influence dispersion of females (cf. Boldt & Ingold 2005; see also Corlatti et al. 2020), in turn affecting mating behaviour of males (Emlen & Oring 1977). Changes in mating behaviour related to snow cover have been suggested for another mountain ungulate, the Alpine ibex *Capra ibex* (Apollonio et al. 2013). In my study area, snow cover conditions in the mating season have not been constant throughout the study period (cf. Chapter 2, this thesis), strongly suggesting that the adoption of a mating tactic may not be influenced by snow presence. This 5-year study would support the existence of fixed AMTs (Taborsky et al. 1998) in adult male Alpine chamois. Moreover, both AMTs were reported in the study population with approximately the same frequency. If AMTs were fixed, genetically encoded and maintained by selection, they should be expected to involve comparable costs and benefits, in terms of long-term reproductive success.

While all non-territorial males showed seasonally changing home ranges, moving mainly to higher elevations in summer and to lower ones in autumn-winter, two different patterns of space use were observed across territorial males. Results indicate the occurrence of “resident” and “migrant” individuals, further divided into “moving in winter” and “moving in summer” males, thus suggesting an unprecedented reported variation of space use across individuals adopting the same AMT. Melis et al. (2004) suggested a similar pattern for male roe deer, an obligate territorial ungulate (*sensu* Owen-Smith 1977), in which some males have been “annually site-faithful”, occupying the same home range throughout the year, whereas others, “seasonally site-faithful”, moved to another area in winter, to come back for the following mating season (Melis et al. 2004).

Resident territorial chamois could acquire greater knowledge of the area and benefit from a “*prior residence advantage*” by staying throughout the year in the area where they establish their territory (Braddock, 1949; Maynard-Smith 1982; von Hardenberg et al. 2000). However, territorial males that migrated between winter and spring-summer-autumn ranges came back to the area they defended the previous and the following mating season during spring, which is consistent with males defending their territory well before the rut (von Hardenberg et al. 2000). Moving to winter ranges may allow chamois to reach sites with better environmental conditions during the limiting season and, eventually, to avoid increased potential intraspecific competition, when many individuals clump together at lower elevations, in snow-free areas. Analysis of population density, habitat selection and habitat quality of territories and “wintering” areas would help to clarify this issue and evaluate potential benefits for those males in terms of energies recovery and saving.

During summer, sheep and cows graze in some sectors of my study area. Displacement by livestock has been shown to potentially influence altitudinal movements of chamois (Herrero et al. 1996; La Morgia & Bassano 2009; Chirichella et al. 2013; Mason et al. 2014), thus it might have played a role in triggering migration for territorial males that moved in summer. However, both observed males moved from their territory for a longer period compared to the period of presence of livestock, and moved quite far away, in a completely different area, not providing a strong support to this hypothesis. All territorial males showed fidelity to their previous defended area, across years, coming back to the same territory during the following rut. Hence, AMTs may not necessarily involve the use of the same pattern of spatial behaviour amongst individuals adopting the same mating tactic and territoriality does not necessarily involve being resident all year round. A greater sample size would be needed to assess potential benefits/costs in terms of survivorship, intra-sexual competition and mating success related to territorial males adopting different spatial tactics (Lovari et al. 2006).

Although greater costs in terms of endogenous stress response and parasite load have been reported in territorial than non-territorial males (Corlatti et al. 2012a, 2014, 2019), together with rut-induced

hypophagia (Corlatti & Bassano 2014), I found no difference in life expectancy between males adopting different mating tactics, which would partly explain the maintenance of both tactics in the population. My results support the hypothesis of a conservative male mating strategy (Bocci et al. 2010; Corlatti et al. 2012b, 2015) and, probably, a weak level of polygyny in this species (Bocci et al. 2010; Rughetti & Festa-Bianchet 2011; Corlatti et al. 2012a). Territoriality in Alpine chamois could be probably described as a low-risk territorial strategy (Linnell & Andersen 1998, for roe deer).

Different foraging tactics have been reported for territorial and non-territorial males (Corlatti et al. 2013b). Although non-territorial males have been shown to stay at higher elevations than territorial ones in summer (Corlatti et al. 2013b; Chapter 3, this thesis), i.e. where pastures are seasonally richer in protein contents (Albon & Langvatn 1992; Bassano 1994; Bassano et al. 1997), no significant differences in nutritional quality of diet have been found between them (Corlatti et al. 2013b). Corlatti et al. (2013b) supposed that territorial males may be able to selectively feed on high quality forage, also at lower elevations. Thus, territorial males could find efficient ways to store enough energy to face higher reproductive costs during the rut. Additionally, they probably could find alternative ways to recover in winter, such as migrating to different areas, as found in this work.

Dominance in interactions was by definition greater in territorial males (cf. von Hardenberg et al. 2000; Corlatti et al. 2012a), but both tactics were associated to the same frequency of intra-sexual aggressive interactions – which are expected to be costly for both the sender and the receiver. This would be in agreement with no difference in related costs across mating tactics.

Behavioural observations suggested that territorial males had greater mating opportunities than non-territorial ones (cf. Corlatti et al. 2015). Synchrony in oestrus is an important determinant of temporal payoff variation of male mating tactics (Emlen & Oring 1977). Female distribution over the rut influences male reproductive success strongly. In years with abundant snowfalls early in the rut, female chamois are forced to move to lower elevations, where territorial males may monopolise

mating events (Lovari et al. 2006; Corlatti et al. 2020). When snowfalls are light or late, females would stay longer at higher elevations and would rut there, thus giving non-territorial males an advantage (Lovari et al. 2006; Corlatti et al. 2020). If so, together with environmental stochasticity (Lovari et al. 2006; Corlatti et al. 2020), the same survival probability between tactics may favour the persistence of both AMTs in chamois. A further step is represented by the analysis of the link between snow cover, topographic characteristics of the territories and mating success (see Chapter 2), in turn related to the space use of females during the rut (Corlatti et al. 2020). This analysis would help better investigate relationships between territory/individual features, environmental stochasticity and reproductive success, potentially helping understand aspects shaping the evolution and maintenance of territoriality in chamois. Moreover, belated snowfalls could privilege mating opportunities of non-territorial males through persistence of female chamois at the higher elevations. Thus, further data would help clarify the potential effects of the on-going Climate Change on mating behaviour in relation to snowfall phenology in late autumn.

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## CHAPTER 2

### Territories and territory-holders in the Alpine chamois



Javier Lazaro



## CHAPTER 2

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### *Territories and territory-holders in the Alpine chamois*

#### **ABSTRACT**

Female density and distribution, indirectly related to the distribution of resources, strongly influence male mating behaviour and success. When a male adopts a “resource defence” tactic, its reproductive success depends on the location of its territory and its ability to attract mates. Territoriality is rare amongst Caprinae, but it has been recorded for the Alpine chamois. In a protected population of this mountain-dwelling ungulate, I investigated the relationships between territoriality, mating opportunities and environmental variables, to shed light on factors favouring the maintenance of this mating tactic in the population. I recorded mating behaviour and territory size of 15 territorial males, during 5 rutting seasons (early November-early December, 2011-2012 and 2015-2017) and related them to topographic features of their territories (e.g. elevation, roughness) and snow cover. Throughout my study, during ruts with deeper snow cover, territorial males had smaller territories and higher mating opportunities index. Smaller territories were visited by more females and showed the highest values of terrain roughness. The frequency of male-male aggressive interactions was positively related to the number of females in a territory. The index of wins in male-male aggressive interactions was not influenced by environmental factors. Conversely, the frequency of intra-sexual aggressive interactions was greater for males with territories located at higher elevations. Thus, territorial males had higher mating opportunities index in years with abundant snow cover, particularly if they defended a territory in rugged and steeper areas, likely snow-free in November. These results are consistent with recent findings from concurrent studies and support that, for territorial male chamois, snow cover and its effect on female distribution may

be strong determinants of reproductive success. Predictability of female movements due to snowfalls would explain the evolution and maintenance of territoriality in this species.

## INTRODUCTION

A territory is “a defended and exclusive area” (Burt 1943, for mammals), i.e. “a mutually exclusive area defended by one territorial individual who rarely moves beyond its limits, who challenges intruding conspecifics of the same sex and behaves submissively outside” (Owen-Smith 1977, for ungulates). Males can compete directly for mates or indirectly for resources that influence female distribution (Emlen & Oring 1977). The evolution of one of these tactics depends on the opportunity for defence of females, which is directly related to their density, distribution, group size and stability, and indirectly related to the distribution of resources (Clutton-Brock 1989). When females are spatially and temporally predictable (e.g. when they occupy small stable ranges around clumped resources) or in areas where resources are abundant and temporally stable, such as forests (Owen-Smith 1977; Geist 1987), a “resource defence polygyny” will be favoured (Emlen & Oring 1977). In this system, males gain access to females by anticipating how resources will influence female distribution and competing for resource-rich sites. Thus, the reproductive success of a male depends on the location of its territory (Carranza 1995). Conversely, a harsh climate and strongly seasonal food resources generate group instability and oestrus synchrony, thus usually militating against the development of male territoriality (Gosling 1986).

Territoriality is common amongst ungulates (Geist & Walther 1974), although differences occur among subfamilies (Owen-Smith 1977): it is rare in the Caprinae, probably because of the characteristics of the environment where they have evolved, i.e. rugged areas, with harsh climate and strongly seasonal food resources (Schaller 1977; Geist 1985). Thus, investigating factors which favour territoriality in this group would be important to shed light on its evolutionary determinants.

Information is controversial on the relationship between size of a territory and the owner’s mating success. We also lack information on the influence of environmental variables and topographic features of a territory (e.g. elevation, slope, aspect) on female attractiveness. Johansson (1996) reported that roe deer *Capreolus capreolus* male mating success was related to territory quality (in

terms of presence of *Trifolium* plants) and not to territory size. Several studies on territorial ungulates have shown a relationship between access to potential mates and territory features such as forage quality and abundance, safety from predators (e.g. percentage of vegetation cover, cliffs height, slopiness) (e.g. for American pronghorn *Antilocapra americana*, Kitchen 1974; topi antelope *Damaliscus lunatus*, Balmford et al. 1992a; mountain reedbuck *Redunca fulvorufula chanleri*, Dunbar & Roberts 1982; red deer *Cervus elaphus*, Carranza 1995). By contrast, Vanpé et al. (2009) suggested that territory size - not its habitat quality - influences the number of female roe deer in a male territory. However, usually home range size decreases with increasing habitat quality and resource quantity (Harestad & Bunnell 1979): if so, smaller territories may be characterized by greater quantity and quality of resources, thus attracting more females (e.g. Kitchen 1974; Carranza 1995).

Territory quality could be indirectly related to the owner's dominance (Balmford et al. 1992a), that is known to be costly, in terms of energy invested in the defence of an area, stress, susceptibility to parasites (Parker 1974; Creel 2001; Mooring et al. 2006; Corlatti et al. 2012, 2019). Females could gain genetic benefits by choosing a "good" dominant male, able to maintain a good territory (Trivers 1972; Hogg 1987; Balmford et al. 1992a, b; Byers et al. 1994).

I investigated the relationships among territory topographic features (in terms of size, elevation, roughness and aspect), male dominance (i.e. number of wins in male-male aggressive interactions: IW index, von Hardenberg et al. 2000; Corlatti et al. 2012; frequency of male-male aggressive interactions), snow cover and mating opportunities index (von Hardenberg et al. 2000), in a mountain-dwelling ungulate, the Alpine chamois *Rupicapra rupicapra rupicapra* (Bovidae: Caprinae), a weakly polygynous (Bocci et al. 2010; Rughetti & Festa-Bianchet 2011; Corlatti et al. 2012) large mammal. Two alternative mating tactics (AMTs) have been described in male chamois (Corlatti et al. 2012): 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 intrude other males' territories (Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012).

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) hypothesised that snow cover could have an important effect in determining the success of AMTs in chamois. In fact, they suggested that in autumns with abundant snowfalls, females would move to lower elevations where they can meet territorial males, favouring their mating success. In years with no or delayed snow cover, female chamois would rut at higher elevations, where non-territorial males may have an advantage (Lovari et al. 2006; see also Corlatti et al. 2020). However, there is no information on the relationships between *(i)* territory topographic features (size, elevation, roughness, aspect), *(ii)* snow depth, *(iii)* dominance and *(iv)* mating success of a territory owner.

I used intensive GPS-GSM radio-telemetry and a Digital Elevation Model (DEM) on a GIS software, coupled with direct individual-level behavioural observations of the mating behaviour of 15 marked adult male chamois, identified as territorials, in the ruts 2011-2012 and 2015-2017, to evaluate relationships between male mating opportunities (an index of male mating success, von Hardenberg et al. 2000; Corlatti et al. 2012, 2015), snow depth, behavioural indices of male intra-sexual competition and male dominance (i.e. frequency of intra-sexual aggressive interactions and index of wins) and territory topographic features (i.e. size, elevation, roughness, aspect). I predicted that *(i)* topographic characteristics of a territory should influence mating opportunities, through the influence on the accumulation of snow, thus on female movements (Lovari et al. 2006; Corlatti et al. 2020), but they would not influence territory size, IW index and frequency of male-male aggressive interactions, which are expected to be linked to male dominance; *(ii)* territory size should have a positive effect on mating opportunities (Vanpé et al. 2009) and should positively influence IW index and frequency of male-male aggressive interactions, because costs of defence increase as the territory increases (Hixon 1980; Schoener 1983, 1987); *(iii)* snow depth should influence female movements, thus increasing mating opportunities (Lovari et al. 2006; Corlatti et al.

2020), as well as male movements, thus limiting territory size, but not the IW index and frequency of male-male aggressive interactions. Moreover, one should expect strong male-male competition to occupy the “best” territories (i.e. providing access to the highest number of females). So, the best territories should be occupied by the “best” competitors in intra-sexual contests. Therefore, I expected (iv) a positive relationship between IW index and frequency of male-male aggressive interactions and mating opportunities. Eventually, I predicted that (v) the number of females should trigger an increase of the frequency of male-male aggressive interactions, as more females may attract more rival males. Conversely, it should not influence the IW index, as it is expected to depend on male dominance.

## MATERIALS AND METHODS

### *Data collection and analysis*

#### *Capture and marking*

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 recognisable GSM-GPS Pro-Light collars, with very high frequency (VHF) beacon devices (Vectronic Aerospace GmbH, Berlin), and coloured ear tags. In accordance with the 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 (e.g. von Hardenberg et al 2000; Corlatti et al. 2012). At sedation, the age of each male was estimated by counting horn rings (Schröder & von Elsner-Schack 1985).

#### *Mating behaviour: AMTs distinction*

Overall, my study included 5 rutting seasons: 2011 (N = 19 individuals), 2012 (N = 18), 2015 (N = 13), 2016 (N = 17) and 2017 (N = 11). The distinction between territorial (T) and non-territorial (NT) males was based on the following criteria: during the rutting season (early November – early December; Krämer 1969; Willis & Ingold 2007; Corlatti et al. 2012) T males would show higher site fidelity, hence smaller home range size, and win more aggressive interactions with other males than NT individuals (von Hardenberg et al. 2000, Corlatti et al. 2012). I 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: number of interactions won / total number of interactions) during the rut (6<sup>th</sup> of November - 5<sup>th</sup> of December, cf. von Hardenberg et al. 2000; Corlatti et al. 2012). For

GPS-based home range estimates, I used always high-quality GPS locations (i.e. with at least 4 satellites and Dilution of Precision -DOP- values  $\leq 10$  and 3 satellites and DOP values  $\leq 5$ , Kenward 2000; Lewis et al. 2007).

The number and the outcome of aggressive interactions with other males were recorded through continuous focal animal sampling (Altmann 1974) during 1 h / individual bouts, during the rutting periods. Each mating season was divided in 3 groups of 10 days: 6<sup>th</sup> – 15<sup>th</sup> of November (period I), 16<sup>th</sup> – 25<sup>th</sup> of November (period II), 26<sup>th</sup> of November – 5<sup>th</sup> of December (period III), to homogeneously distribute observations over the entire rut and amongst all males (cf. Corlatti et al. 2012). Observations were evenly distributed throughout daylight hours and conducted with binoculars (e.g. Zeiss 15x60, Avalon 10x42) and spotting scopes (Nikon 20-60x). Behavioural data were recorded on standardized recording sheet. The focal male was considered as involved in intra-sexual interactions if he performed direct or indirect forms of aggressiveness against another male (Lovari 1985; Lovari & Locati 1991). An interaction was recorded *i*) as *won* by the focal male when the opponent was chased away and/or displayed submissive behaviour; *ii*) as *lost* by the focal male when the focal male showed submissive behaviour and/or moved away from the opponent; *iii*) *ended with a “tie”* when neither rival performed submissive behaviour or moved away (Krämer 1969; Lovari 1985).

I then combined the two parameters (rut home range size, index of wins in aggressive interactions with other males) in a matrix and performed multivariate hierarchical clustering each study year (Everitt et al. 2011) using the Mahalanobis distance (Mahalanobis 1936) as metric (*'stats'* library, *'hclust'* function, in R - R Core Team 2019). Individuals monitored during the rut 2015 had been captured and marked between 2010-2013 and the battery of their GPS radio-collars had expired, thus preventing me from estimating their ranging movements: for those individuals only the index of wins in aggressive interactions with other males has been estimated. Also, during the rut 2016 and 2017, for males with inactive radio-collars, I only estimated the index of wins in intra-sexual

aggressive interactions. For those individuals, the highest IW value found for NT males in the previous years was considered as a threshold to tell T males apart from NT ones.

Besides the index of wins in aggressive interactions with other males (IW), I 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 from the focal male was also recorded, every 20 minutes, during 1 h / individual bouts (cf. above): I then calculated the mean number of females per hour per each male, as an index of mating opportunities (von Hardenberg et al. 2000; Corlatti et al. 2012). All analyses were performed in Microsoft Excel (2010), R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio.

#### *Territory topographic characteristics and meteorological data*

To evaluate relationships among topography, home range size, snow cover, dominance and mating opportunities for territorial males (N = 15), during 5 rutting seasons (2011: N = 8 individuals, 2012: N = 9, 2015: N = 8, 2016: N = 11, 2017: N = 7), I considered Kernel 90% estimates of home range size. For individuals with not functioning GPS collars (rut 2015-2017), I used the coordinates of locations visually collected, during individual-level observations on mating behaviour (cf. paragraph “Mating behaviour: AMTs distinction”). For those individuals, 1 location / individual / day was recorded on a map, considering their first position on the landscape when they were sighted and I estimated 90% Kernel home ranges. I tested for differences between the size of territories estimated through GPS data and that estimated using visually collected locations: for a subsample of males for which both kind of data have been collected (N=8) I found no significant differences between GPS-based and visually-based estimates (Wilcoxon signed rank test with continuity correction:  $V = 24$ ,  $p\text{-value} = 0.44$ ). Through QGIS software (QGISDevelopment Team, 2016), I 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  $10 \times 10$  m

(Tarquini et al. 2007, 2012), transformed to a resolution of 25×25 m. From the DEM I obtained the following parameters/indices (raster maps) for my study area:

- Elevation (in m),
- Slope, Roughness, Terrain Ruggedness Index (TRI), Topographic Position Index (TPI), as indices of terrain asperity,
- Aspect (southness), considered as distance from South ( $0^\circ$ =S,  $90^\circ$ = E and O,  $180^\circ$ =N).

I used ‘*terrain*’ function, from ‘*raster*’ library, (Hijmans 2019) in R, to obtain the above maps. Eventually, I extracted the values of the above environmental parameters corresponding with each cell constituting the territories, using the function ‘*extract*’, ‘*raster*’ library (Hijmans 2019) in R, and I calculated the median values. All analyses were performed in QGIS (QGIS Development Team, 2016), in R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio.

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

#### *Statistical analyses - Effect of territory size and topography, male dominance, snow depth*

I used general linear mixed models (GLMM) and generalised linear mixed models (GLMMs) to test the effects of a number of environmental and individual variables on the following response variables: (i) mating opportunities index, (ii) territory size, (iii) frequency of male-male aggressive interactions, (iv) index of wins in male-male aggressive interactions (IW index). I tested for collinearity amongst topographic variables (elevation, slope, roughness, Terrain Ruggedness Index (TRI), Topographic Position Index (TPI), aspect), using Pearson’s correlation coefficient (function ‘*pairs.panels*’, ‘*psych*’ library, in R – Revelle 2018). Slope, roughness and TRI were highly correlated among them (Pearson correlation coefficient: all  $> 0.90$ ) and none of them was correlated with TPI (Pearson correlation coefficient: all  $< 0.30$ ). Thus, I selected elevation, roughness (which had the lowest Pearson’s correlation coefficients with elevation and aspect, compared to slope and

TRI), TPI and aspect, to be inserted in the models. I used the Shapiro-Wilk normality test to evaluate the assumption of normality for each response variable in the models.

To investigate the effect of territory features (size, elevation, roughness, TPI, aspect), snow depth and male “dominance” (i.e. index of wins and frequency of male-male aggressive interactions), inserted as predictors in the global model, on mating opportunities index (Shapiro-Wilk normality test:  $W = 0.88$ ,  $p\text{-value} = <0.001$ ), set as response variable, I used GLMM, using the function ‘*lmer*’, ‘*lme4*’ library (Bates et al. 2015) in R. Residuals showed no obvious deviations from normality/homoscedasticity of residuals or autocorrelations (see Supplementary material 1). I then investigated the effect of elevation, roughness, TPI, aspect and snow depth, predictors in the global model, on territory size (Shapiro-Wilk normality test:  $W = 0.90$ ,  $p\text{-value} = 0.002$ ), set as response variable, through GLMMs, selecting a gamma distribution and a ‘*log*’ link function (Crawley 2007; Bolker et al. 2009), using the function ‘*glmer*’, ‘*lme4*’ library (Bates et al. 2015) in R. To investigate the effect of territory features (size, elevation, roughness, TPI, aspect), snow depth and mating opportunities index, predictors in the global models, on *i*) the frequency of male-male aggressive interactions (Shapiro-Wilk normality test:  $W = 0.94$ ,  $p\text{-value} = 0.03$ ) and *ii*) the index of wins in male-male aggressive interactions (Shapiro-Wilk normality test:  $W = 0.84$ ,  $p\text{-value} = <0.001$ ), set as response variables, I used GLMMs, selecting *i*) a gamma distribution and a ‘*log*’ link function (Crawley 2007; Bolker et al. 2009), using the function ‘*glmer*’, for the first response variable, and *ii*) a beta distribution and a ‘*logit*’ link function (Crawley 2007; Bolker et al. 2009), using the function ‘*glmmadmb*’, ‘*glmmADMB*’ library (Fournier et al. 2012), for the second response variable.

In all models, the identity of males was inserted as random effect, to account for repeated estimates for the same individual.

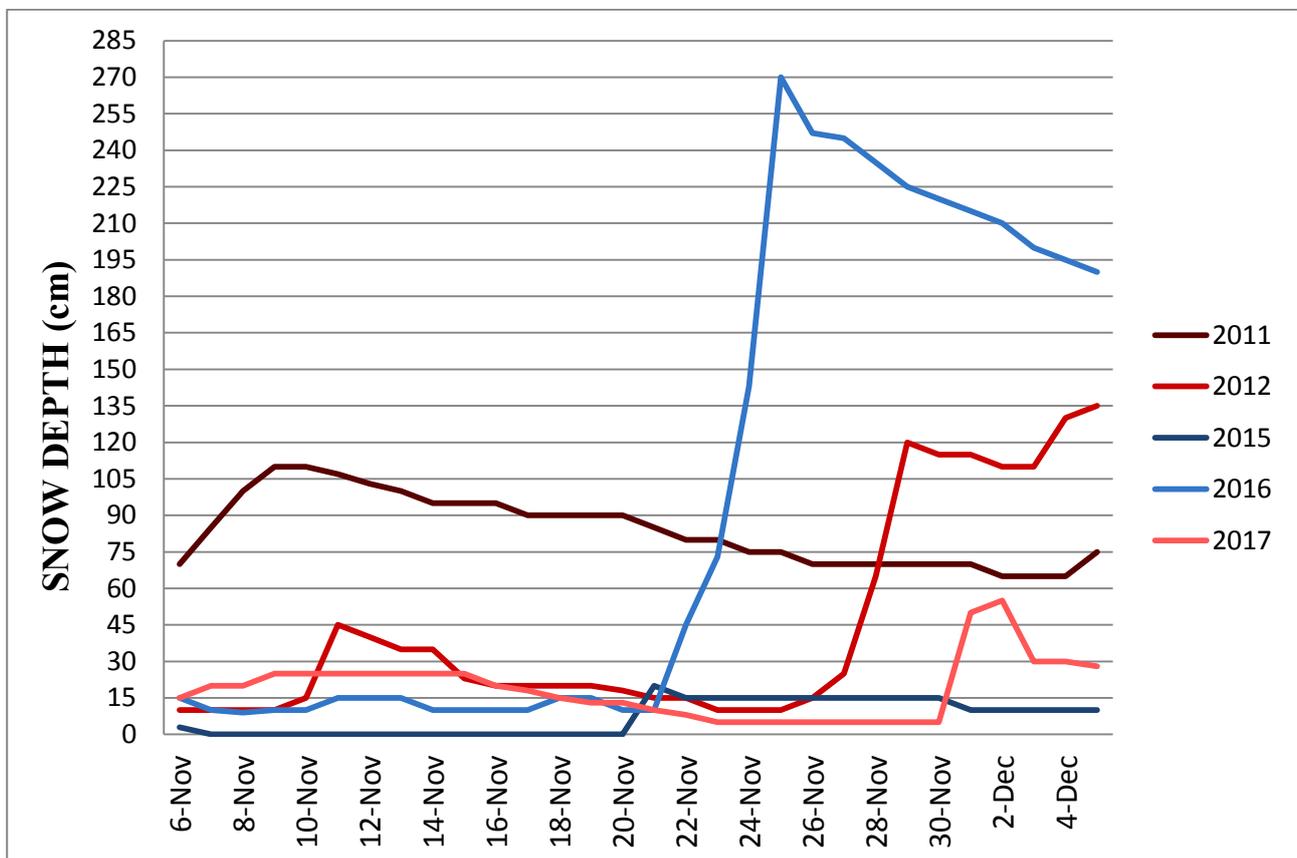
Model selection was performed considering the minimum Akaike’s Information Criterion, corrected for small samples (AICc: Burnham & Anderson 2002), using the ‘*MuMIn*’ library (Barton 2019) in R. For each response variable, a global model was built, including all predictors, and all the possible

alternative models were built, including different combinations of predictors, and were ranked and weighted from the global model. Models with  $\Delta\text{AICc} \leq 2$  in respect to the best model (i.e. with the lowest AICc value), as well as models with an AICc value lower than that of any simpler, nested alternative, were selected. All analyses were performed in R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio. All p-value were considered significant at a level of 0.05.

## RESULTS

### *Snow depth variation*

Snow depth conditions during the mating season varied greatly amongst years (median value: 2011 = 82.5 cm, 2012 = 20 cm, 2015 = 6.5 cm, 2016 = 15 cm, 2017 = 19 cm) and throughout the years (Fig. 1). I classified snow depth in years 2011, 2012 and 2017 as “deep” and in years 2015 and 2016 as “low”, considering the median values and the values during the first half of the rut, i.e. before the oestrus.



**Fig. 1** Daily values of snow depth (cm) during the rutting seasons (6th of November – 5th of December) 2011, 2012, 2015, 2016, 2017, recorded from the weather station in the study area (Lake Serrù, 2275 m a.s.l.-A.E.M. Turin).

### *Mating opportunities index*

Model selection supported an effect of territory size and snow depth on mating opportunities index (Tables 1, 2; Fig. 2a, b). In particular, I found a negative effect of territory size on mating opportunities, as well as decreasing mating opportunities with lower snow depth (Table 2; Fig. 2a, b). Conversely, the frequency of male-male aggressive interactions had a direct effect on mating opportunities index (Table 2; Fig. 2c). The index of wins in intra-sexual aggressive interactions was selected as predictor in the best model, but did not have a significant effect (Table 2).

### *Territory size*

Models supported an effect of roughness, Topographic Position Index (TPI) and snow depth on territory size (Tables 1, 2; Fig. 3). In particular, I found that smaller territories showed the highest values of roughness and TPI (Table 2; Fig. 3a, b) and I found a negative effect of snow depth on territory size, with smaller territories in conditions of deeper snow cover (Table 2; Fig. 3c).

### *Male dominance and intra-sexual competition*

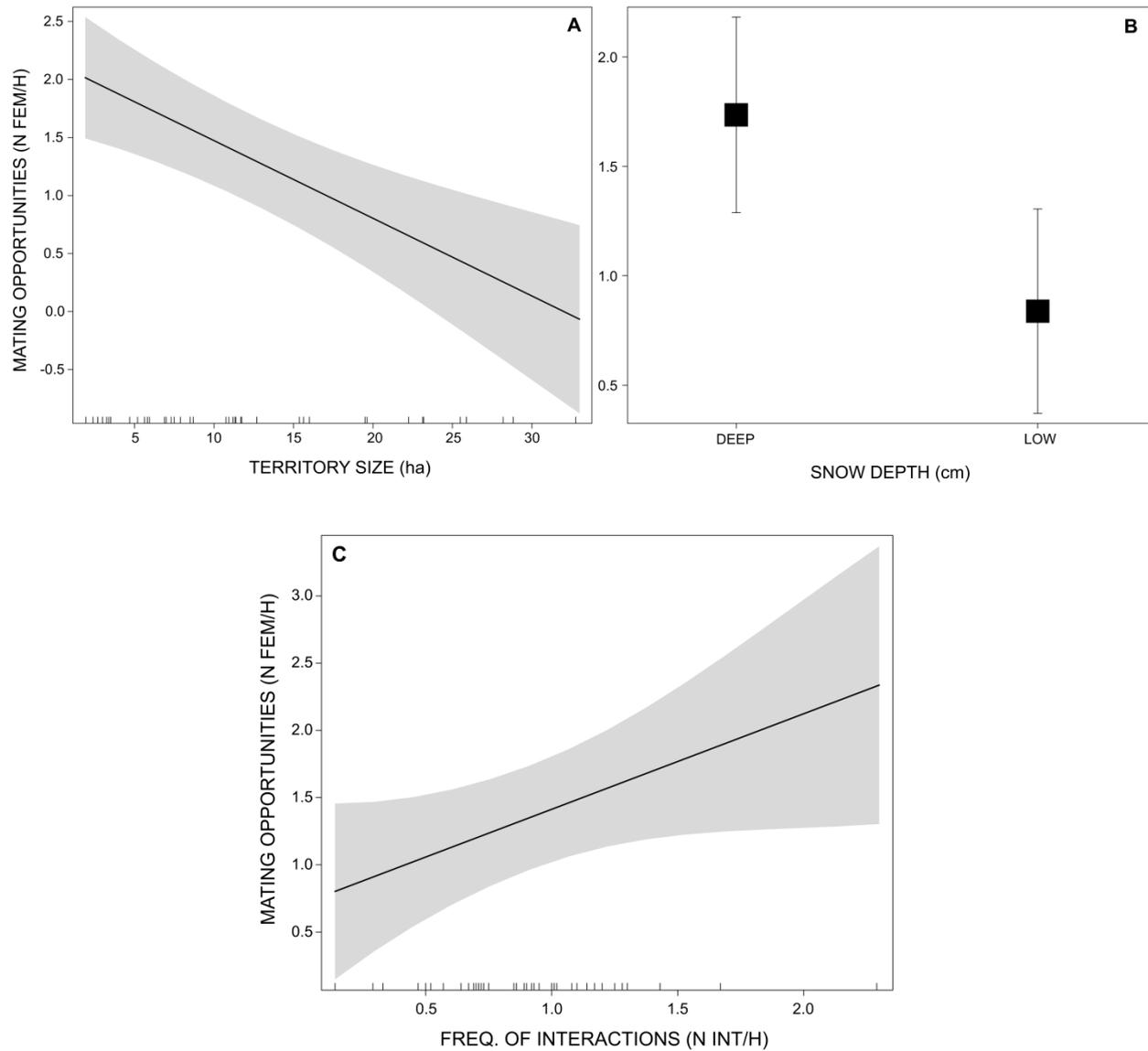
I found a direct relationship between elevation and frequency of male-male aggressive interactions, with increasing frequency of aggression at higher elevations (Tables 1, 2; Fig. 4). However, the null model was also selected (Table 1). Conversely, I found no effects of territory features (size, elevation, roughness, TPI, aspect), snow depth or mating opportunities index on the index of wins in male-male aggressive interactions (IW index), as only the null model was selected (Table 1).

**Table 1** Effects of environmental variables (HR: territory size; snow: snow depth; roughness; TPI: Topographic Position Index; elevation) and aggressiveness/dominance in male-male aggressive interactions (freq.int: frequency of male-male aggressive interactions; IW: index of wins in male-male aggressive interactions) on: (a) mating opportunities index (mat.opp: mean number of females/h), (b) territory size, (c) frequency of male-male aggressive interactions, (d) index of wins in male-male aggressive interactions, of territorial male Alpine chamois in 2011-2012 and 2015-2017. Random effect in each model = Id: individual identities. Results of model selection: variables retained, degrees of freedom, logLikelihood, AICc,  $\Delta$ AICc values and model weight are shown.

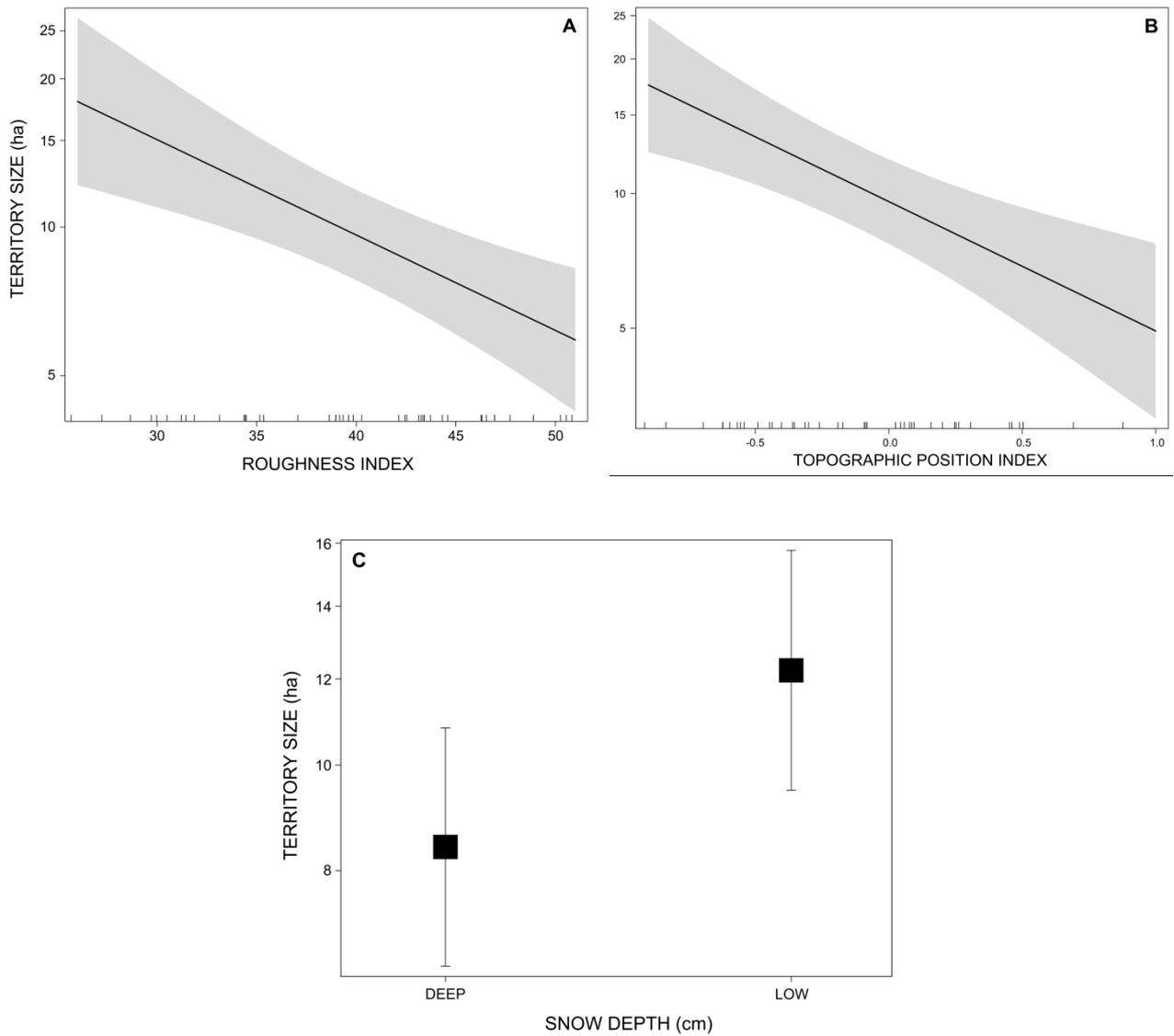
Model	Variables retained	df	logLik	AICc	$\Delta$ AICc	Weight
(a) mat.opp	freq.int + HR + IW + snow + (1 Id)	7	-52.86	123.0	0.00	0.57
	HR + snow + (1 Id)	5	-55.97	123.6	0.58	0.43
(b) HR	snow + roughness + TPI + (1 Id)	6	-124.44	263.2	0.00	1
(c) freq.int	elevation + (1 Id)	4	-16.92	42.9	0.00	0.68
	(1 Id)	3	-18.90	44.4	1.51	0.32
(d) IW	(1 Id)	3	234.72	-462.8	0.00	1

**Table 2** Parameters estimated from the best models of the effects of environmental variables (HR: territory size; snow: snow depth; roughness; TPI: Topographic Position Index; elevation) and aggressiveness/dominance in male-male aggressive interactions (freq.int: frequency of male-male aggressive interactions; IW: index of wins in male-male aggressive interactions) on: (a) mating opportunities index (mat.opp: mean number of females/h), (b) territory size, (c) frequency of male-male aggressive interactions, of territorial male Alpine chamois in 2011-2012 and 2015-2017 ( $\beta$ : coefficient; SE: standard error; p-value). Reference category for the categorical predictor “snow”: deep snow.

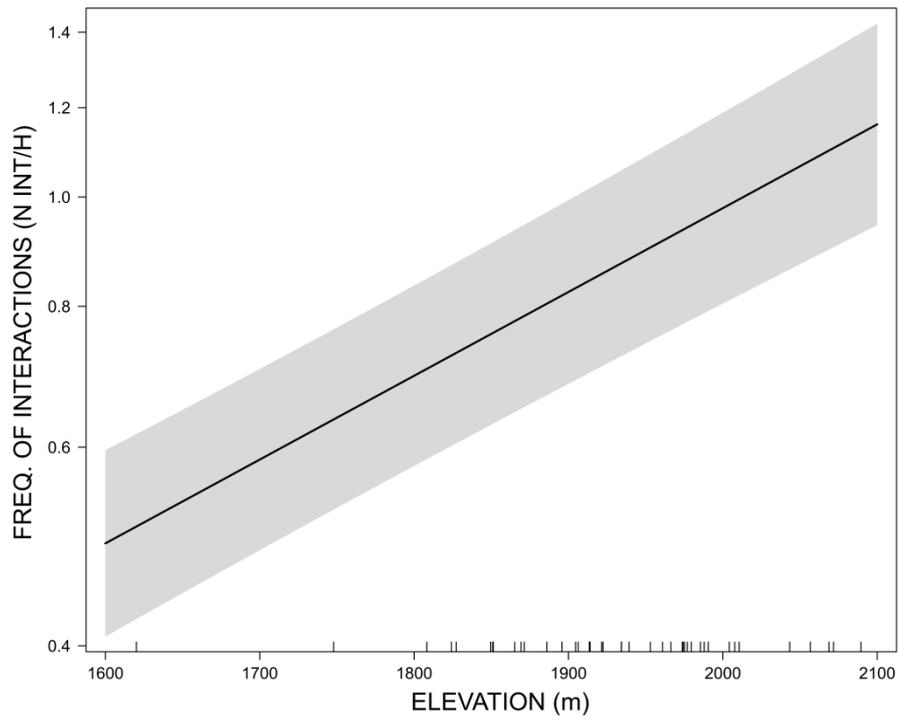
Model	Variables	$\beta$	SE	p-value
(a) Mat.opp	intercept	0.67	0.97	0.49
	freq.int	0.71	0.34	<0.05*
	HR	-0.07	0.02	<0.001***
	IW	1.46	0.84	0.09
	snow.low	-0.90	0.25	<0.01**
(b) HR	intercept	3.85	0.50	<0.001***
	snow.low	0.37	0.14	<0.01**
	roughness	-0.04	0.01	<0.001***
	TPI	-0.67	0.18	<0.001***
(c) Freq.int	intercept	-3.44	0.26	<0.001***
	elevation	<0.01	<0.01	<0.001***



**Fig. 2** Effects of: (A) territory size (K90%, ha), (B) snow depth (cm; deep/low), (C) frequency of male-male aggressive interactions (N interactions/h) on mating opportunities index (N females/h), for territorial male Alpine chamois, in 2011-2012 and 2015-2017.



**Fig. 3** Effects of: (A) roughness index, (B) Topographic Position Index (TPI), (C) snow depth (cm; deep/low) on territory size (K90%, ha), for territorial male Alpine chamois, in 2011-2012 and 2015-2017.



**Fig. 4** Effects of territory elevation (m) on frequency of male-male aggressive interactions (N interactions/h) for territorial male Alpine chamois, in 2011-2012 and 2015-2017.

## DISCUSSION

Throughout my study, male territory size was smaller in years with abundant snowfalls during the rut than in years with lower snow depth. Several studies have suggested that snow depth strongly influences ungulate movements, because of increased costs due to locomotion, food searching and thermoregulation (Parker et al. 1984; Dailey & Hobbs 1989; van Moorter et al. 2013; Richard et al. 2014). In particular, abundant snow cover has been shown to trigger a reduction of home range size (Cederlund 1983; Georgii & Schröder 1983; Cederlund & Sand 1994; Grignolio et al. 2004; Ramanzin et al. 2007), displacement to other areas (Mysterud 1999; Mysterud et al., 2001; Bocci et al. 2012; Chapter 3, this thesis) and/or changes in diet (e.g. switch from browsing to grazing; Obrtel et al. 1984; Kozena 1986; Goodson et al. 1991). Female distribution primarily depends on the dispersion of food resources (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, one would expect females to be attracted to clumped resources in snow-free areas, during the cold period. In my study area, the summer range of female chamois (i.e. upper meadows above 2400 m a.s.l., see Chapter 3, this thesis) is usually covered with snow in late autumn-winter. Thus, in the colder period of the year snowfalls force females to move to lower elevations, where less snow cover allows better access to forage (Nesti et al. 2010; Unterthiner et al. 2012; Corlatti et al. 2020; Chapter 3, this thesis). The attraction to seasonally clumped food resources, free from snow during the rut, makes female ranging movements broadly predictable, favouring males present in snow-free sites located at lower elevations (von Hardenberg et al. 2000; Lovari et al. 2006; Corlatti et al. 2020). Accordingly, my results showed greater mating opportunities index, i.e. a greater number of females available to territorial males - who usually stay at lower elevations than non-territorial males (Corlatti et al. 2013; Chapter 3, this thesis) - during ruts with deeper snow cover (cf. Lovari et al. 2006; Corlatti et al. 2020).

Home range size is negatively related to habitat quality and resource availability (Harestad & Bunnell 1979; Cimino & Lovari 2003; Saïd et al. 2009). My results suggest that a greater number of females was attracted to smaller territories. These territories were characterised by greater indices of terrain roughness than larger ones: a rugged and steep slope should favour snow sliding, thus allowing quicker access to food resources for chamois (Schröder 1971; Berducou 1982; von Elsner-Schak 1985). Vanpé et al. (2009) found greater densities of female roe deer in larger than in smaller male territories, thus supporting a major role of territory size rather than habitat quality in favouring mating success, in that deer species. Conversely, my results showed an opposite pattern in chamois and suggest that “quality”, in terms of terrain roughness, appears to be more important than territory size, possibly because it allows to females the access to snow-free terrain, thus food resources. Data suggest that male Alpine chamois would have greater mating opportunities if holding a territory in a rugged area, thereby free from snow at rut time, in November. The ability to defend a small territory with snow-free pastures may be an important feature to territorial male chamois, as females are expected to concentrate on snow-free areas including food resources. This relationship is expected to be stronger in years with abundant snowfalls early in the rut (see also Lovari et al. 2006; Corlatti et al. 2020). Lovari et al. (2006) suggested that territorial males may have a greater reproductive success in years with abundant snowfalls early in the rut, when females are forced to move to lower elevations to access forage. Conversely, non-territorial males could gain reproductive advantage in years with low or delayed snowfalls, because females would rut at higher elevations (see also Corlatti et al. 2020). The greater number of females observed in male territories during snowy ruts, throughout my study, provides support to this prediction.

Female ungulates often select habitats providing safety from predators to them and to their offspring (e.g. Pérez-Barbería & Nores 1994; Ciuti et al. 2005; Hamel & Côté 2007). Information is less abundant on female selection of habitat features in male territories during the mating period. Dunbar & Roberts (1992) suggested that female mountain reedbuck *Redunca fulvorufula chanleri* 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 my study area, large terrestrial predators (grey wolf *Canis lupus*) were absent (2011-2012, 2015) to occasionally reported (2016-present) (see paragraph Study area). Thus, 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 predators. Conversely, results would support a role of topography in influencing territory attractiveness to females because of its effects on snow accumulation.

Androgen hormones are known to be related to aggression and social rank (Patton et al. 2001; Pelletier et al. 2003; Mooring et al. 2004; Corlatti et al. 2012) and courtship behaviour (Knapp 2003; Hirschenhauser & Oliveira 2006). Moreover, androgens tend to suppress the immune function (Folstad & Karter 1992; Pelletier et al. 2005; Decristophoris et al. 2007). A previous study conducted on my study population showed that territorial males had higher levels of androgen metabolites and parasite load than non-territorial ones, during the rut (Corlatti et al. 2012, 2019). Dominance in male chamois seems to follow the ‘stress of domination’ hypothesis (Mooring et al. 2006). I found a positive relationship between mating opportunities index of territorial males (i.e. the number of females available in their territory) and intra-sexual aggressive interactions, i.e. mating opportunities were relatively more abundant for territorial males showing a greater frequency of interactions with other males. Territorial males able to face the costs of frequent intra-sexual aggressive interactions would invest more energies to maintain a “good” territory, i.e. attractive to females, compared to other territorial males. If so, they may provide “good genes” for reproduction (cf. Byers et al. 1994, for the American pronghorn). Alternatively, the positive relationship between mating opportunities index and male-male aggressive interactions could be indirectly influenced by the action of non-territorial males. These males tend to stay at higher elevations than territorial ones (Lovari et al. 2006; Corlatti et al. 2013; Chapter 3, this thesis) and adopt a “following” mating tactic, i.e. they follow oestrus females and try to intrude male territories (Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012). Accordingly, during my study the frequency of male-male interactions increased with territory elevation, providing support to a role

of intrusion of non-territorial males in emphasising intra-sexual competition for mates. If so, territories with a great number of females could attract non-territorial males attempting to sneak copulations and forcing the owner's territory to a greater number of male-male interactions. However, analyses did not provide support to an effect of mating opportunities on the frequency of male-male interactions. If so, the presence of potential mates, irrespectively from the number of potential mates, could elicit territory owner attempts to chase any intruding male. Contrary to my prediction (*iv*), no relationship was supported between the index of wins in male-male aggressive interactions and mating opportunities index. Accordingly, the index of wins was not influenced by territory features (size, aspect, elevation, roughness). It should be considered that territorial males have by definition high IW indices (von Hardenberg et al. 2000; Corlatti et al. 2012; this thesis) and they are usually dominant inside their territory (Owen-Smith 1977).

In contrast with my prediction (*ii*), analyses did not provide support to a relationship between territory size and frequency of male-male aggressive interactions. The only topographical variable that had an effect on frequency of intra-sexual interactions was the elevation.

As to the exposure, all territories were located on south and south-east facing slopes, where snow cover is less persistent, i.e. aspect was rather homogeneous across all territorial males. Accordingly, in my same study area, studying a sample of 19 "resident" and 4 "migrant" males, Nesti et al. (2010) showed that throughout the year nearly all individuals used south and south-east facing slopes.

In conclusion, my study has shown that mating opportunities of territorial males increased during rutting seasons with deeper snow cover and in territories located on steep, broken terrain, i.e. those from which snow slides away first. In these areas, access to food is expected to be higher, thus making them attractive to females. If so, territoriality in Alpine chamois could be favoured by predictability of female movements towards snow-free clumped resources during the rut, in case of abundant snow cover, emphasising the role of weather factors during the rut in favouring persistence of alternative mating tactics in chamois (Lovari et al. 2006; Corlatti et al. 2020). Male

chamois have shown to adopt the same mating tactic consistently across years (Chapter 1, this thesis) and territoriality starts from late spring (von Hardenberg et al. 2000). If so, investigating spatial movements in relation to environmental factors throughout the year would help elucidating ecological pressures operating on individuals in relation to sex and mating tactic (Chapter 3, this thesis), potentially improving our understanding of their ecological requirements.

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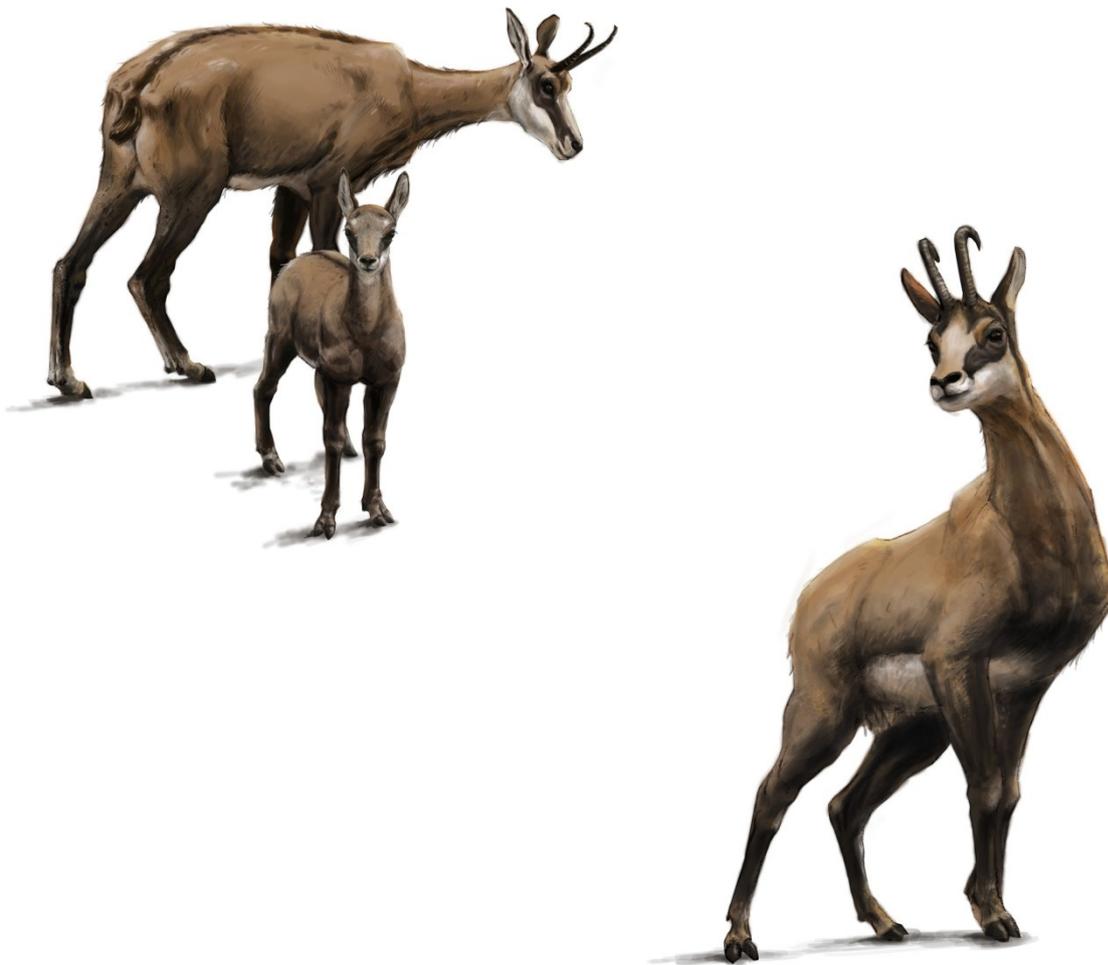
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## CHAPTER 3

### Spatial behaviour and its environmental drivers



Javier Lazaro



## CHAPTER 3

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### *Spatial behaviour and its environmental drivers*

#### **ABSTRACT**

Environmental factors may influence spatial behaviour of large herbivores in different ways, depending on individual features, such as sex and reproductive status. Sex-related constraints could determine different individual responses to environmental stressors. I investigated inter and intra-sexual differences of spatial behaviour and its environmental determinants in a mountain-dwelling ungulate, the Alpine chamois. In particular, I considered adult individuals of both sexes and, as to males, showing different alternative mating tactics (13 females, 11 territorial males, 13 non-territorial males) and used intensive GPS-GSM radio-telemetry and satellite-derived products (i.e. the Normalized Difference Vegetation Index, NDVI). Females and non-territorial males increased their home range size from late spring to early autumn, whereas territorial males showed consistently smaller home ranges. Females and non-territorial males also moved to higher elevations from May to October. During winter, no major significant difference was found in home range size and elevation amongst individuals, although non-territorial males showed significantly larger home ranges than other chamois in November-December. Especially for females and, to a lower extent, for non-territorial males, home range size and elevations used were positively related to temperature and negatively related to snow depth. Conversely, territorial males showed limited variations of space use patterns in response to temperature and snow depth. I found a negative effect of rainfalls on daily elevations occupied by chamois. Vegetation productivity (expressed as NDVI values) of the locations used by chamois were greater between April-October than in late autumn-winter, with a peak in June-July. Moreover, locations used by females appeared to show relatively more stable NDVI values between June and October, compared to those of locations used by males,

which decreased sharply in September and October, although this result requires confirmation. In conclusion, I found significant differences between the two sexes and between territorial and non-territorial males, in both temporal variation of spatial behaviour and response to climatic stressors. Females may be more sensitive to weather changes and, eventually more selective, most likely because of costs induced by nursing/weaning of offspring. Conversely, territorial males are probably forced to actively defend their territories for several months to gain advantages during the mating season, thus showing a less pronounced reaction to short-term weather changes than non-territorial individuals. These results emphasise that alternative mating tactics, besides sex and reproductive status, should be considered when studying spatial behaviour and its driving factors.

## INTRODUCTION

In large mammals, space use is influenced by biotic (e.g. quality, quantity and distribution of food resources: Anderson et al. 2005; van Beest et al. 2011) and abiotic factors (e.g. topography and climate: Kie et al. 2005; Rivrud et al. 2010). These factors could act in different ways on individuals, depending on sex, age, physiology, reproductive status (Dahle & Swenson 2003; Saïd et al. 2009) and social factors (e.g. population density and competition: Kjellander et al. 2004). Females and males respond to different sex-related constraints to increase their fitness, with the former prioritising the search for high quality food resources to maximise offspring survival, and the latter prioritising the increase of their mating opportunities (Emlen & Oring 1977; Clutton-Brock 1989). Sexual differences in space use may develop in time (Bonenfant et al. 2004). In species where newborn offspring follow their mother (“followers”, Lent 1974), females may minimise predation risk by using habitats/sites with fewer predators or greater opportunities to escape (for ungulates: Bleich et al. 1997; Rachlow and Bowyer 1998; Panzacchi et al. 2010). Nevertheless, access to high-quality pasture in spring-summer is fundamental to recover from gestation and to face the high costs of lactation (Gaillard et al. 1996, 1997; Pettorelli et al. 2003, 2006; Parker et al. 2009). Thus, a trade-off may be expected between selection of food-rich vs. poorer – but safer – areas (e.g. for ungulates: Pérez-Barbería & Nores 1994; Ciuti et al. 2005; Grignolio et al. 2007; Hamel & Côté 2007). Conversely, space use of males is expected to be mainly influenced by the necessity of increasing mating opportunities, thus by the mating tactic adopted (Mysterud 1999). Spatial correlates of alternative mating tactics (AMTs) have been mainly studied in the mating season (Carranza 1995; Linnell & Andersen 1998; Corlatti et al. 2012, 2013a). However, the determinants of AMTs may also originate in other parts of the year (e.g. von Hardenberg et al. 2000), in turn influencing space use.

On mountains, climate and resource seasonality (Shackleton & Bunnell 1987) greatly influence herbivore space use. Seasonal variations of home range size and altitudinal movements

have been broadly investigated (e.g. Festa-Bianchet 1988; Sabine et al. 2002; Ramanzin et al. 2007; van Moorter et al. 2013). In particular, snow cover is a determinant of ungulate movements, through increased costs of locomotion, thermoregulation and limited access to food resources (e.g. Parker et al. 1984; Grignolio et al. 2004; Richard et al. 2014). Increasing snow depth has been associated to a reduction of home range size (e.g. Cederlund 1983; Georgii & Schröder 1983; Rivrud et al. 2010; van Beest et al. 2011) and/or a migration to lower (Mysterud 1999) or higher (Bocci et al. 2012) elevations and/or changes in diet (e.g. switch from browsing to grazing; Obrtel et al. 1984; Kozena 1986; Goodson et al. 1991). Moreover, increasing temperature in summer has been associated to upwards altitudinal movements (e.g. for Alpine ibex *Capra ibex*: Grignolio et al. 2004; Aublet et al. 2009) or to a decrease of home range size (e.g. for red deer *Cervus elaphus*: Rivrud et al. 2010). Timing of snowmelt and onset/progress of green-up of the vegetation are other key determinants of herbivore movements. Ungulates can capitalise upon the green-up season of plants by moving upslope as spring and summer progress (e.g. Mysterud et al. 2001; Hebblewhite et al. 2008; Bischof et al. 2012), to benefit of high quality food resources at upper meadows, where forage is richer in nutrient and poorer in fibre contents (Albon & Langvatn 1992). Seasonal differences in the timing of green-up may drive mountain ungulates to areas with delayed plant phenology to prolong their access to high quality forage (Hebblewhite et al. 2008; Bischof et al. 2012; Merkle et al. 2016).

I investigated intra and inter-sexual differences of space use in a weakly polygynous (Bocci et al. 2010; Ruggetti & Festa-Bianchet 2011; Corlatti et al. 2012) near-monomorphic large mammal, the Alpine chamois *Rupicapra rupicapra rupicapra* (Bovidae: Caprinae), a mountain-dwelling ungulate for which two AMTs have been described in adult males (Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012). Some individuals (territorials, T) actively defend an exclusive area from intruders (von Hardenberg et al. 2000; Corlatti et al. 2012) and try to hold female groups there during the rut (November-early December: Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012). Other males (non-territorials, NT) follow oestrus females, sometimes intruding other males' territories (Krämer 1969; von Hardenberg et al. 2000; Corlatti et al. 2012).

Moreover, two alternative spatial tactics have been described for males (Lovari et al. 2006; Chapter 1, this thesis): some individuals (residents) occupy overlapping or contiguous summer and winter ranges, while others (migrants) move between well separated seasonal ranges. The non-territorial mating tactic seems to correspond to the migrant spatial tactic, while territorial males could present at least two different movement patterns (“residents” and “migrants”: Chapter 1, this thesis). Chamois show sexual spatial segregation in summer (Shank 1985; Loison et al. 1999a; for Apennine chamois *Rupicapra pyrenaica ornata*: Lovari & Cosentino 1986), with groups of females, yearlings and kids attending upper meadows (Krämer 1969; Knaus & Schröder 1983), whereas adult males tend to stay solitary (Shank 1985; Unterthiner et al. 2012) or may gather in groups when population density is high (Berducou & Bousses 1985). Females appear to be more selective in food choice, especially between summer and early autumn (e.g. for Apennine chamois, Ferrari et al. 1988; Ferretti et al. 2014), probably because of the high costs of nursing and weaning. Moreover, female chamois, living in groups, likely require areas with greater quantity of food resources than the solitary males (Pérez-Barbería & Nores 1994).

Despite its abundance and wide distribution on the Alps (Corlatti et al. *in press*), knowledge about spatial behaviour of the Alpine chamois is almost limited to VHF telemetry data (e.g. Hamr 1984, 1985; Brambilla et al. 2006; Nesti et al. 2010), that often prevents the collection of extensive information during winter on mountains. Moreover, there are no studies that investigate male movements throughout the year, considering alternative mating tactics. Additionally, information is lacking on the effect of weather factors (e.g. temperature, snowfall, rainfall) and vegetation phenology on spatial behaviour of both sexes and AMTs.

I used intensive GPS-GSM radio-telemetry and remote sensing products (i.e. the satellite-derived Normalized Difference Vegetation Index, NDVI) to investigate inter and intra-sexual differences in: (i) variation of monthly home range size and (ii) altitudinal movements, (iii) the effect of temperature, snow depth and rainfalls on home range size and altitudinal range occupied by individuals, (iv) relationships between locations used by females and males and the productivity

of vegetation in those areas. I predicted that (i) home range size should be greater from late spring to autumn for females and non-territorial males, whereas territorial males should maintain a more constant home range size throughout the year; (ii) females and non-territorial males should show greater variation of altitudinal movements, whereas territorial males should stay at lower elevations all year round; (iii) increasing temperatures in summer should not influence movements of territorial males, whereas they should influence equally those of females and non-territorial males. Moreover, snow depth should lead to a reduction of home range size and it should force individuals to move to lower elevations. Eventually, (iv) females and non-territorial males, moving upslope in spring-summer, should attend areas showing consistent changes in the productivity of vegetation, whereas territorial individuals would be expected to show a different trend.

## MATERIALS AND METHODS

### *Data collection and analysis*

#### *Capture and marking*

Between February 2010 and January 2013 and between November 2015 and November 2017, 31 adult (4 - 13 years old) male and 13 adult (4 - 16 years old) female chamois were darted for sedation and fitted with individually recognisable GSM-GPS Pro-Light collars, with very high frequency (VHF) beacon devices (Vectronic Aerospace GmbH, Berlin), and coloured ear tags. In accordance with the Italian law, chamois were sedated with a combination of xylazine and ketamine to reduce levels of stress due to handling (Bassano et al. 2004) and reversed by an injection of atipamezole (Dematteis et al. 2009), following a standardized procedure already used in previous studies on the species in the same area (e.g. von Hardenberg et al 2000; Corlatti et al. 2012). At sedation, the age of individuals was estimated by counting horn rings (Schröder & von Elsner-Schack 1985).

#### *Spatial and meteorological data*

Analyses of spatial data focused on 37 individuals (13 females F, 11 territorial males T, 13 non-territorial males NT), on three years: 2011 (N = 6 F, 9 T, 10 NT), 2012 (N = 3 F, 9 T, 9 NT) and 2017 (N = 7 F, 3 T, 3 NT), i.e. periods when data from males and females were available at the same time. For GPS-based home range estimates and analyses concerning elevation, I used high-quality GPS locations (i.e. with at least 4 satellites and Dilution of Precision -DOP- values  $\leq 10$  and 3 satellites and DOP values  $\leq 5$ , Kenward 2000; Lewis et al. 2007). I estimated monthly home range size using the Fixed Kernel density estimator (90%, hereafter K90; Silverman 1986; Powell, 2000), using the ‘ks’ (Duong 2019) and ‘GenKern’ (Lucy & Aykroyd 2013) libraries in R. I calculated the mean (daily and monthly) elevation occupied by each individual, for each year. Additionally, I focused on a shorter period of time (May - October), to investigate effects of

temperature and rainfall on daily altitudinal movements in the specific period including births and offspring weaning, before the rutting season.

Daily meteorological data (min and max temperature in °C, snow depth in cm, precipitation in mm) were collected from a local weather station (Lake Serrù, 2275 m a.s.l. – A.E.M. Turin). I calculated the mean temperature (daily and monthly values) and the median snow depth (monthly values) for each study year. I also obtained daily rainfall values, for each study year.

All analyses were performed in Microsoft Excel (2010), in R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio.

#### *Vegetation productivity data*

Satellite-derived vegetation indices offer a way to couple vegetation and herbivores dynamics, providing information on vegetation density, productivity and phenology and assessing changes in plant health (Kerr & Ostrovsky 2003; Schino et al. 2003; Pettorelli et al. 2005; Hamel et al. 2009; Ranghetti et al. 2016). I used the Normalized Difference Vegetation Index (NDVI, Rouse et al. 1974; Tucker et al. 1985; Pettorelli et al. 2005, 2011) to investigate changes in vegetation productivity of locations occupied by chamois. Previous studies suggested that this index correlates with grass biomass (Schino et al. 2003, for a mountainous area in central Italy) or linked the index with faecal crude protein (FCP) or nitrogen faecal content, considered indicators of the quality of vegetation (Hamel et al. 2009; Ryan et al. 2012; Ranghetti et al. 2016). I obtained NDVI data from Landsat Surface Reflectance-Derived Spectral Indices, accessible from the Earth Explorer website of the United States Geological Survey Earth Resources Observation and Science Center (USGS EROS Center; <https://earthexplorer.usgs.gov>) and downloaded through the EROS Science Processing Architecture On Demand Interface (<https://espa.cr.usgs.gov/ordering/new>). I used 96 scenes, relevant to my study area, for years 2011 (31 scenes), 2012 (20 scenes) and 2017 (45 scenes). I used products from Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper Plus (Masek et al. 2006) and Landsat 8 Operational Land Imager/Thermal Infrared Sensor (Vermote

et al. 2016). These products are generated at a 16-days temporal resolution and 30-m spatial resolution. For each scene, I applied the pixel quality mask provided within the downloaded products (as: Pixel Quality Assurance band, in 16-bit format), to identify clear pixels, pixel with water, snow and reject pixel with clouds and not available data. Then, I overlaid the GPS fixes of females and males to the NDVI rasters and extracted the corresponding NDVI values for each available day. I also interpolated NDVI values, when a scene was missing for a certain day: using the first scene available, before and after the “missing day”, I obtained a weighted mean of the NDVI values. Eventually, I calculated a mean monthly NDVI value for each individual, for each year. I used libraries ‘*raster*’ (Hijmans 2019), ‘*rgdal*’ (Bivand et al. 2019), ‘*gdalUtils*’ (Greenberg & Mattiuzzi 2020), ‘*move*’ (Kranstauber et al. 2019), ‘*lubridate*’ (Grolemund & Wickham 2011) to handle with spatial data, in R. All analyses were performed in QGIS (QGISDevelopment Team, 2016), in Microsoft Excel (2010), in R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio.

#### *Mating behaviour: AMTs distinction*

The distinction between territorial (T) and non-territorial (NT) males was based on the following criteria: during the rutting season (early November – early December; Krämer 1969; Willisch & Ingold 2007; Corlatti et al. 2012) T males would show higher site fidelity, hence smaller home range size, and win more aggressive interactions with other males than NT individuals (von Hardenberg et al. 2000, Corlatti et al. 2012). I 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: number of interactions won / total number of interactions) during the rut (6<sup>th</sup> of November - 5<sup>th</sup> of December, cf. von Hardenberg et al. 2000, Corlatti et al. 2012). Aggressive interactions with other males were recorded through continuous focal animal sampling (Altmann 1974) during 1 h / individual bouts, during the rutting periods. Observations were distributed homogeneously over the entire rut and amongst all males (cf. Corlatti et al. 2012). Observations were evenly

distributed throughout daylight hours and conducted with binoculars (e.g. Zeiss 15x60, Avalon 10x42) and spotting scopes (Nikon 20-60x). Behavioural data were recorded on standardized recording sheet. I then combined the two parameters (rut home range size, index of wins in aggressive interactions with other males) in a matrix and performed multivariate hierarchical clustering for each study year (Everitt et al. 2011) using the Mahalanobis distance (Mahalanobis 1936) as metric ('stats' library, 'hclust' function, in R - R Core Team 2019). Individuals monitored during the rut 2015 had been captured and marked between 2010-2013 and the battery of their GPS radio-collars had expired, thus preventing me from estimating their ranging movements. For those individuals, only the index of wins in aggressive interactions with other males was estimated. Similarly, during the rut 2016 and 2017, I only estimated the index of wins in intra-sexual aggressive interactions for males with inactive radio-collars. The highest IW value found for NT males in the previous years was considered as a threshold to tell T males apart from NT ones. For further details see Chapters 1 and 2. All analyses were performed in Microsoft Excel (2010), in R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio.

### *Statistical analyses*

I used generalised linear mixed models (GLMMs) to (i) investigate monthly variation of home range size and elevations occupied by chamois, (ii) test the effects of mean temperature and median snow depth on home range (monthly temporal scale) and elevations (monthly and daily temporal scale), (iii) test the effects of mean temperature and rainfalls on elevations (daily temporal scale) during the period May - October. I used general linear mixed models (GLMM) to (iv) investigate differences in monthly variation of the vegetation productivity (variation of NDVI values) of the locations used by chamois. I tested for collinearity among meteorological variables (temperature, snow depth, rainfalls) using the Pearson's correlation coefficient (function 'pairs.panels', 'psych' library, in R – Revelle 2018): the Pearson's correlation coefficient was  $> 0.60$  between temperature and snow depth. Thus, I performed separated models when temperature and snow depth were the

predictors. I used the Shapiro-Wilk normality test to evaluate the assumption of normality for each response variable in the models.

As to monthly variation of home range size (Shapiro-Wilk normality test:  $W = 0.46$ ,  $p\text{-value} = <0.001$ ) and elevations (Shapiro-Wilk normality test:  $W = 0.89$ ,  $p\text{-value} = <0.001$ ) I used GLMMs selecting a gamma distribution and a 'log' link function, using the function 'glmer', 'lme4' library (Bates et al. 2015) in R. Predictors in the two models were: month, tactic (i.e. female, territorial male, non-territorial male) and their interaction.

Then, I calculated different sets of models to investigate the effect of mean temperature and median snow depth on monthly home range size and elevations, at monthly and daily temporal scale. For this purpose, I used GLMMs selecting a gamma distribution and a 'log' link function, using the function 'glmer', 'lme4' library (Bates et al. 2015) in R. Predictors in the models were: mean monthly/mean daily temperature, tactic and their interaction; median monthly/daily snow depth, tactic and their interaction.

I used GLMMs selecting a gamma distribution and a 'log' link function, using the function 'glmer', 'lme4' library (Bates et al. 2015) in R, to investigate the effects of mean temperature and rainfalls on daily elevations, during the period May-October. Predictors in the models were: mean temperature, rainfalls, tactic and their interactions.

Eventually, I used GLMM, using the function 'lmer', 'lme4' library (Bates et al. 2015) in R, to investigate monthly variation of NDVI values of the locations used by female, territorial and non-territorial male chamois (Shapiro-Wilk normality tests: females,  $W = 0.95$ ,  $p\text{-value} = <0.001$ ; territorial males,  $W = 0.94$ ,  $p\text{-value} = <0.001$ ; non-territorial males,  $W = 0.94$ ,  $p\text{-value} = <0.001$ ).

Predictor in each model was month. I ran separated models for the three groups.

In all models, the identity of individuals and the year were inserted as random effects, to account for repeated estimates for the same individual and year. In the models where the response variable was daily elevation, the month was also inserted as random effect, to account for repeated estimates in the same month.

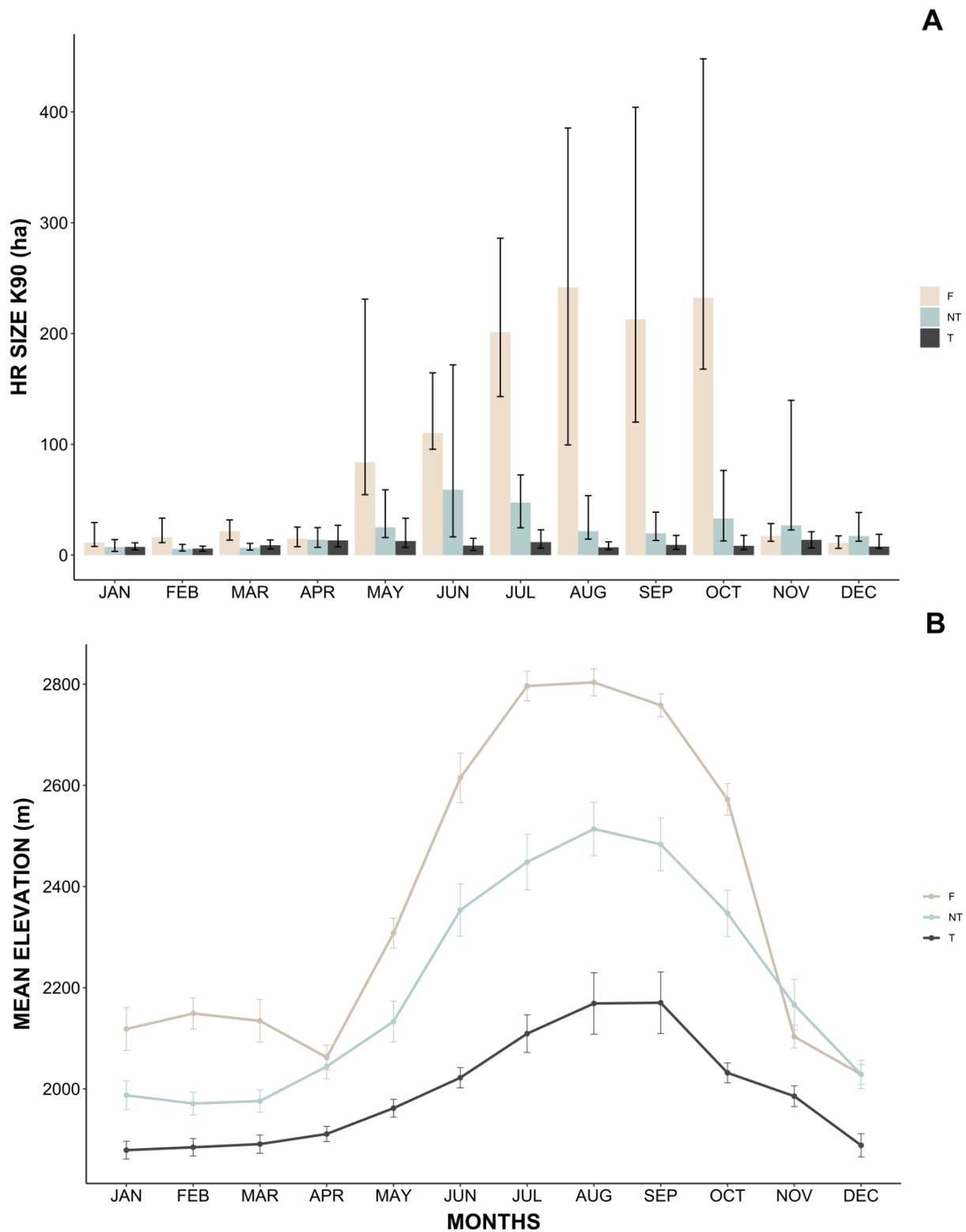
Model selection was performed considering the minimum Akaike's Information Criterion, corrected for small samples (AICc: Burnham & Anderson 2002), using the '*MuMIn*' library (Barton 2019) in R. For each response variable, a global model was built, including all predictors, and all the possible alternative models were built, including different combinations of predictors, and were ranked and weighted from the global model. Models with  $\Delta\text{AICc} \leq 2$  in respect to the best model (i.e. with the lowest AICc value), as well as models with an AICc value lower than that of any simpler, nested alternative, were selected. All analyses were performed in R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio. All p-value were considered significant at a level of 0.05.

## RESULTS

### *Monthly variation of home range size and elevation*

I analysed a total of 632 monthly home ranges (171 for females, 222 for territorial males, 239 for non-territorial males). Month and Sex/Tactic had a significant effect on both monthly home range size and elevation use (Table 1; Fig. 1). Home range size increased between May and October and was greater in females than in males (Fig. 1a; Table S.3.1). Territorial males kept constantly smaller home range size throughout the year, compared to females and non-territorial males (Fig. 1a). Compared to females, non-territorial individuals showed slightly but significantly larger home ranges in April, November and December, but smaller home ranges between August and October (Fig. 1a; Table S.3.1). No other difference between sexes/tactics was found in the winter months (Fig. 1a; Table S.3.1).

I analysed a total of 671 mean monthly elevations of chamois locations (176 for females, 238 territorial males, 257 non-territorial males) and 17,715 daily mean elevations (4,757 for females, 6,232 territorial males, 6,726 non-territorial males). Elevations occupied by chamois were higher between May and October and the lowest in the winter months (Fig. 1b; Table S.3.2). Males generally remained at lower elevations than females, with the exception of November and December (Fig. 1b; Table S.3.2). Females reached the highest elevations in July and August (Fig. 1b). Territorial males remained at the lowest elevations all year round, compared to other individuals (Fig. 1b).



**Fig. 1** (a) Monthly variation of home range size (K90%, ha) for female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in 2011-2012-2017. Median values and 25%-75% quartiles are shown. (b) Monthly variation of elevations occupied by female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in 2011-2012-2017. Mean values and standard errors are shown. See Fig. S.3.1 and S.3.2 for monthly variations of home range size/elevation in each year.

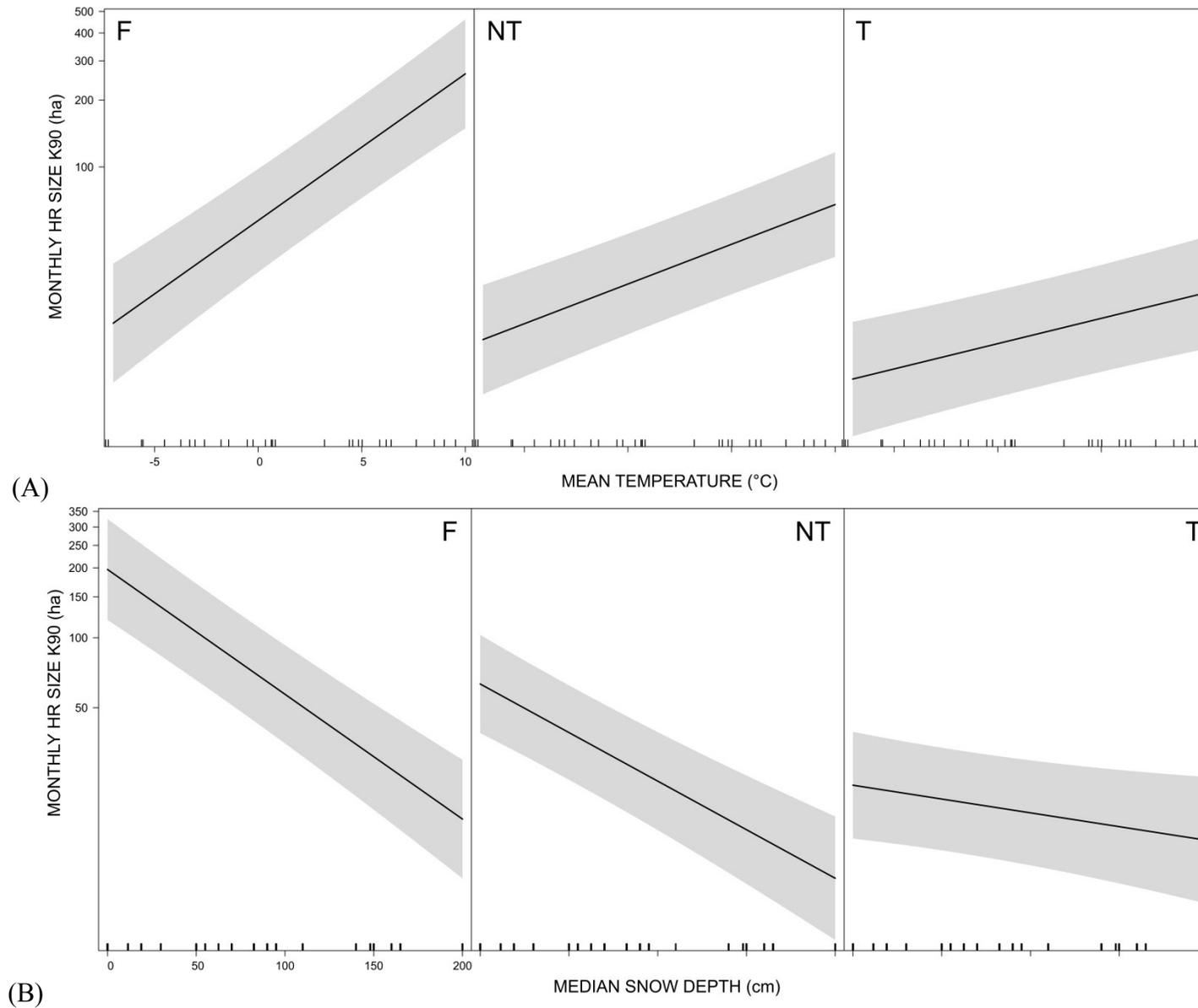
**Table 1** Effects of month, sex/mating tactics, weather and NDVI on space use of adult Alpine chamois: summaries of selected models of effects of (a) Month, Sex/mating tactic (females, territorial males, non-territorial males) on monthly home range size (HR Kernel 90%); (b) Month, Sex/mating tactic on monthly elevations; (c) Monthly mean temperature (T°C) and Sex/mating tactic on monthly home range size; (d) Daily mean temperature (T°C) and Sex/mating tactic on daily mean elevations; (e) Monthly median snow depth (Snow, cm) and Sex/mating tactic on monthly home range size; (f) Daily snow depth and Sex/mating tactic on daily mean elevations; (g) Daily mean temperature (T°C), Rainfall (Rain, mm) and Sex/mating tactic on daily mean elevations, in May-October; (h-i-j) monthly variation of NDVI values on the locations of female, territorial male (T) and non-territorial male (NT) Alpine chamois in 2011-2012-2017. Random effects in each model = Id: individual identities, Year: 2011, 2012, 2017, Month = months (in models d, f and g). Results of model selection: variables retained, degrees of freedom, logLikelihood, AICc,  $\Delta$ AICc values and model weight are shown.

Analysis	Model	Variables retained	df	logLik	AICc	$\Delta$ AICc	Weight
a) HR vs. Month	Best	Month + Tactic + Month×Tactic + (1 Id) + (1 Year)	39	-2903.9	5891.0	0.00	1.00
b) Elevation vs. Month	Best	Month + Tactic + Month×Tactic + (1 Id) + (1 Year)	39	-4145.2	8373.4	0.00	1.00
c) HR vs. Temp.	Best	T°C + Tactic + T°C×Tactic + (1 Id) + (1 Year)	9	-3027.4	6073.1	0.00	1.00
d) Elevation vs. Temp.	Best	T°C + Tactic + T°C×Tactic + (1 Id) + (1 Year) + (1 Month)	10	-113757.4	227534.9	0.00	1.00
e) HR vs. Snow	Best	Snow + Tactic + Snow×Tactic + (1 Id) + (1 Year)	9	-3044.9	6108.2	0.00	1.00
f) Elevation vs. Snow	Best	Snow + Tactic + Snow×Tactic + (1 Id) + (1 Year) + (1 Month)	10	-114051.9	228123.9	0.00	1.00
g) Elevation vs. Temp.Rainfall	Best	T°C + Rain + Tactic + T°C×Tactic + Rain×Tactic + (1 Id) + (1 Year) + (1 Month)	13	-56360.0	112746.0	0.00	0.58
	Second	T°C + Rain + Tactic + T°C×Tactic + (1 Id) + (1 Year) + (1 Month)	11	-56362.3	112746.7	0.68	0.42
h) NDVI – Females	Best	Month + (1 Id) + (1 Year)	15	-888.2	1810.9	0.00	1.00
i) NDVI – T males	Best	Month + (1 Id) + (1 Year)	15	-1109.1	2252.0	0.00	1.00
j) NDVI – NT males	Best	Month + (1 Id) + (1 Year)	15	-1206.5	2446.6	0.00	1.00

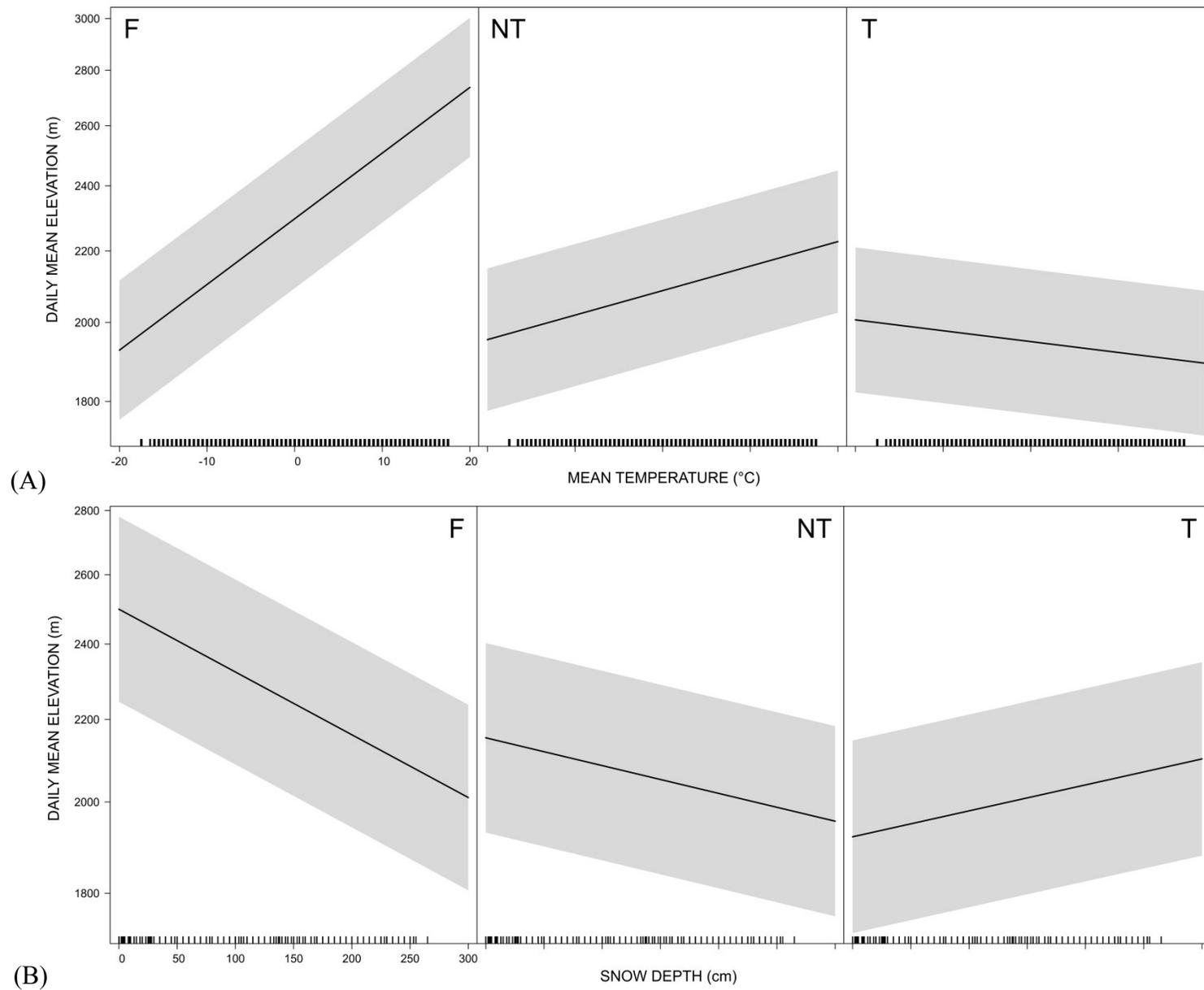
### *Effect of temperature and snow depth on home range size and elevation*

Models supported an interactive effect of mean temperature and sex/mating tactic on home range size and elevations occupied by chamois (Table 1; Table S.3.3; Fig. 2a, 3a; Fig. S.3.3a). With increasing temperatures, females and, to a lower extent, non-territorial males showed larger home ranges and occupied higher elevations; the effect of temperature was much lower on territorial males (Fig. 2a, 3a; Fig. S.3.3a; Table 2; Table S.3.4).

Models supported an interactive effect of snow depth and sex/mating tactic on home range size and elevation use of chamois (Table 1; Table S.3.3; Fig. 2b, 3b; Fig. S.3.3b). Home range size decreased with deeper snow cover, in particular for females and non-territorial males (Fig. 2b; Table 2). Moreover, I found a negative effect of snow depth on the elevations occupied by chamois (both at monthly and daily temporal scale) (Fig. 3b; Fig. S.3.3b; Table 2; Table S.3.4). In particular, females and non-territorial males moved to lower elevations with increasing snow depth, at monthly temporal scale (Table S.3.4; Fig.S.3.3b). Considering a daily temporal scale, the negative effect of snow depth on elevation use was the strongest for females (Table 2; Fig. 3b).



**Fig. 2** (A) Effects of monthly mean temperature (°C) on monthly home range size (K90%, ha) of female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in 2011-2012-2017. (B) Effects of median snow depth (cm) on monthly home range size (K90%, ha) of female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in 2011-2012-2017.



**Fig. 3** (A) Effects of daily mean temperature (°C) on daily elevations (m) occupied by female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in 2011-2012-2017. (B) Effects of daily snow depth (cm) on daily elevations (m) occupied by female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in 2011-2012-2017.

**Table 2** Parameters estimated from the best models on (a) effects of monthly mean temperature (T°C) and sex/mating tactic (female, territorial male T, non-territorial male NT) on monthly home range size (HR Kernel 90%); (b) effects of daily mean temperature (T°C) and sex/mating tactic on daily mean elevations (Elev.day); (c) effects of monthly median snow depth (snow, cm) and sex/mating tactic on monthly home range size (Kernel 90%); (d) effects of snow depth and sex/mating tactic on daily mean elevations, for female and male Alpine chamois in years 2011-2012-2017 ( $\beta$ : coefficient, SE: standard error, p-value). Reference category for categorical predictor Tactic: female.

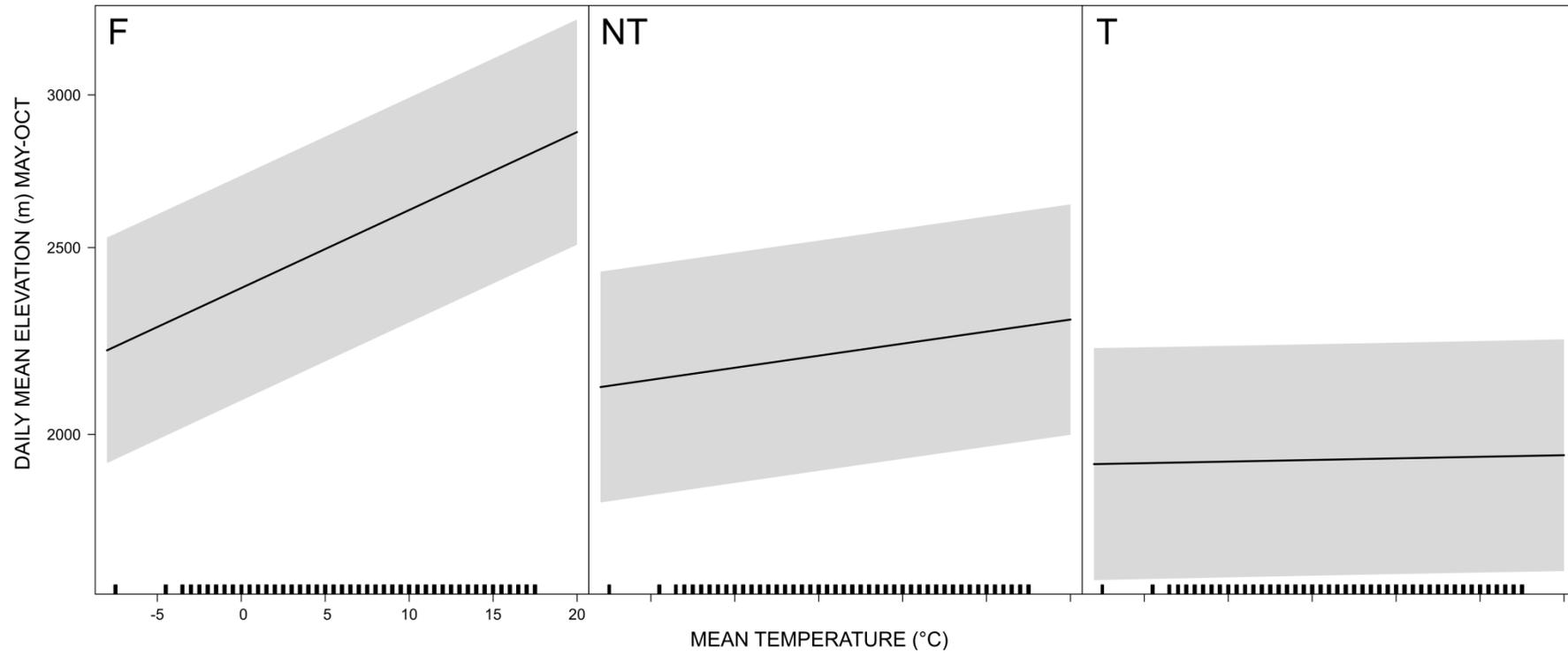
	Model	Variables	$\beta$	SE	p-value
(a)	HR	Intercept	4.05	0.27	<0.001***
		T°C	0.15	0.02	<0.001***
		TacticNT	-0.66	0.33	<0.05*
		TacticT	-1.27	0.35	<0.001***
		T°C×TacticNT	-0.07	0.02	<0.001***
		T°C×TacticT	-0.10	0.02	<0.001***
(b)	Elev.day	Intercept	7.74	0.05	<0.001***
		T°C	0.01	<0.01	<0.001***
		TacticNT	-0.10	0.02	<0.001***
		TacticT	-0.16	0.02	<0.001***
		T°C×TacticNT	< -0.01	< 0.01	<0.001***
		T°C×TacticT	-0.01	<0.01	<0.001***
(c)	HR	Intercept	5.28	0.25	<0.001***
		Snow	-0.01	<0.01	<0.001***
		TacticNT	-1.13	0.35	<0.01**
		TacticT	-2.14	0.37	<0.001***
		Snow×TacticNT	<0.01	<0.01	0.14
		Snow×TacticT	0.01	<0.01	<0.001***
(d)	Elev.day	Intercept	7.82	5.45	<0.001***
		Snow	-7.25	1.88	<0.001***
		TacticNT	-1.48	2.21	<0.001***
		TacticT	-2.63	2.33	<0.001***
		Snow×TacticNT	4.04	2.17	<0.001***
		Snow×TacticT	1.02	2.21	<0.001***

*Effect of temperature and rainfall on elevation (May - October)*

Focusing on the shorter period (May-October, 8,649 daily mean elevations analysed: 2,435 for females, 2,968 for territorial males, 3,246 for non-territorial males), models supported a positive effect of mean temperature and a negative effect of rainfalls on daily elevations occupied by chamois (Table 1; Fig. 4). In particular, females moved to higher elevations with increasing temperatures, more than males (Table 3; Fig. 4). The effect of rainfalls was consistent between individuals of different sex/mating tactic (Table 3).

**Table 3** Parameters estimated from the best models on the effects of daily mean temperature (T°C), rainfall (Rain, mm) and sex/mating tactic (female, territorial male T, non-territorial male NT) on daily mean elevations (Elev.day), in the period May-October, for female and male Alpine chamois in years 2011-2012-2017 ( $\beta$ : coefficient, SE: standard error, p-value). Reference category for categorical predictor Tactic: female.

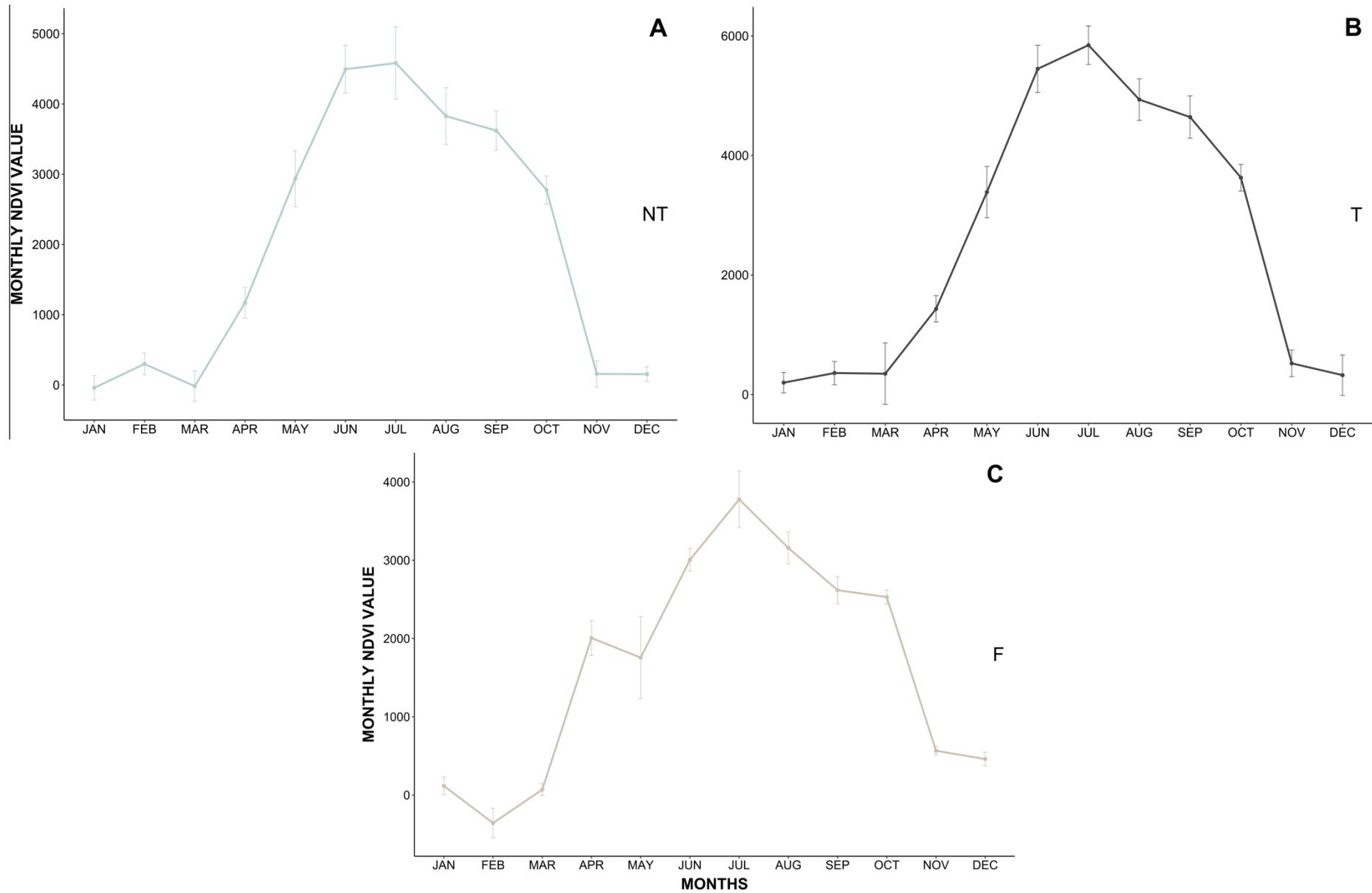
Model	Variables	$\beta$	SE	p-value
Elev.day	Intercept	7.78	0.07	<0.001***
	T°C	0.01	<0.01	<0.001***
	Rain	< -0.01	<0.01	<0.05*
	TacticNT	-0.09	0.03	<0.01**
	TacticT	-0.21	0.03	<0.001***
	T°C×TacticNT	-0.01	<0.01	<0.001***
	T°C×TacticT	-0.01	<0.01	<0.001***
	Rain×TacticNT	< -0.01	<0.01	0.19
	Rain×TacticT	< 0.01	<0.01	0.51



**Fig. 4** Effects of daily mean temperature (°C) on daily elevations (m) occupied by female (F), non-territorial male (NT) and territorial male (T) Alpine chamois, during the period May-October, in 2011-2012-2017.

*Variation of monthly NDVI values of locations used by chamois*

I analysed a total of 418 monthly NDVI values (122 for females, 142 for territorial males, 154 for non-territorial males). In general, for all individuals NDVI values were greater between April-October than in autumn-winter months (Fig. 5). In particular, NDVI values of the locations used by females started to increase in April, did not change significantly between April and May, increased between June and October (with a peak in July) and decreased in November (Fig. 5c; Table 4; Table S.3.5). NDVI values of the locations used by males increased sharply since May; values in July-August were similar to those reported in June; in contrast to the pattern found for females, values in September and October were lower than those in June (Fig. 5a, b; Table 4; Table S.3.5).



**Fig. 5** Monthly variation of NDVI values of the locations used by A) non-territorial male (NT), B) territorial male (T) and C) female (F), Alpine chamois in years 2011-2012-2017. Mean values and standard errors are shown.

**Table 4** Parameters estimated from the best models on the effects of monthly variation on NDVI values of the locations used by female (F), territorial male (T) and non-territorial male (NT) Alpine chamois in 2011-2012-2017 ( $\beta$ : coefficient, SE: standard error, p-value). Reference category for categorical predictor Month: June.

Model	Variables	$\beta$	SE	p-value	Model	Variables	$\beta$	SE	p-value
F	Intercept	2952.6	220.8	<0.001***	T	Intercept	5471.1	308.6	<0.001***
	Jan	-2912.5	295.7	<0.001***		Jan	-5250.6	405.2	<0.001***
	Feb	-3311.9	391.4	<0.001***		Feb	-5085.4	445.4	<0.001***
	Mar	-3030.3	323.2	<0.001***		Mar	-5139.6	498.2	<0.001***
	Apr	-1017.4	279.1	<0.001***		Apr	-4040.3	422.4	<0.001***
	May	-1222.5	307.1	<0.001***		May	-2076.0	433.0	<0.001***
	Jul	748.3	279.3	<0.01**		Jul	365.1	413.2	0.38
	Aug	138.8	272.8	0.61		Aug	-528.1	433.0	0.22
	Sep	-388.8	267.0	0.15		Sep	-807.2	405.2	<0.05*
	Oct	-489.8	272.8	0.07		Oct	-1834.4	433.0	<0.001***
	Nov	-2445.3	279.2	<0.001***		Nov	-4995.5	433.3	<0.001***
	Dec	-2552.1	279.2	<0.001***		Dec	-5125.1	405.2	<0.001***
NT	Intercept	4476.5	313.2	<0.001***					
	Jan	-4444.2	405.2	<0.001***					
	Feb	-4121.5	423.9	<0.001***					
	Mar	-4603.2	513.3	<0.001***					
	Apr	-3289.7	396.7	<0.001***					
	May	-1508.8	405.0	<0.001***					
	Jul	122.2	396.7	0.76					
	Aug	-617.8	404.4	0.13					
	Sep	-833.4	390.5	<0.05*					
	Oct	-1668.6	404.4	<0.001***					
	Nov	-4297.5	390.5	<0.001***					
	Dec	-4287.7	397.3	<0.001***					

## DISCUSSION

Spatial behaviour of mountain ungulates is strongly influenced by seasonal variation of meteorological variables and their effects on food resources (Shackleton & Bunnell 1987; Albon & Langvatn 1992). Sex and reproductive status can also determine significant differences amongst individuals (e.g. Saïd et al. 2009). As predicted (prediction *i*), chamois showed larger home ranges between May and October than in late autumn-winter. This period includes the warmer months (cf. Lovari et al. 2006; Nesti et al. 2010; cf. also Unterthiner et al. 2012 for a different area of the Western Alps). However, the magnitude of monthly differences was not consistent across individuals with different sex/mating tactic, being more pronounced in females and non-territorial males than in territorial males, which maintained smaller and relatively more stable home ranges throughout the year (cf. Nesti et al. 2010). In summer and early autumn, and in particular between August and October, home range size was the greatest in females (cf. Hamr 1984, 1985; Boschi & Nievergelt 2003; Nesti et al. 2010; for females/males comparison). On late spring, when snow starts melting, mountain ungulates may move to higher elevations to follow the vegetation green-up (Bischof et al. 2012; Merkle et al. 2016). Thus, the increase of home range size of females and non-territorial males, in May, could be explained by altitudinal movements from winter ranges to upper meadows and, as to females, to areas where they give birth (Krämer 1969). Conversely, in late spring territorial males start to defend their territories at lower elevations, where they rut in November (von Hardenberg et al. 2000).

Home range size also increases with individual energy requirements (McNab 1963). If so, in spring-summer females would be expected to need larger home ranges than males to recover from the costs of pregnancy and to optimise energy intake for lactation (Loudon 1985; Oftedal 1985; Clutton-Brock 1991). Females can trade high quality areas for safer ones (i.e. closer to rocky and steeper areas, where high quality food resources may be limited or dispersed), especially during the

first months of their newborn life (e.g. Pérez-Barbería & Nores 1994; Ciuti et al. 2005; Grignolio et al. 2007; Hamel & Côté 2007).

During the warm months, females and non-territorial males may benefit from plants richer in nutrients, at the higher meadows (Albon & Langvatn 1992; Bassano 1994; Bassano et al. 1997; but see Corlatti et al. 2013b). In alpine ecosystems, nutritional quality of pasture decreases seasonally from spring to autumn (Dunant 1977; Ferrari et al. 1988; Bassano 1994; La Morgia & Bassano 2009). My results suggest that, in autumn, females and non-territorial males move to lower elevations (after the first snowfalls have covered the higher alpine meadows, usually on late October/early November). Upon that, they reduce their movements, which results in smaller home ranges on late autumn-winter.

During November and December, non-territorial males showed larger home ranges than territorial ones, probably because of their reproductive tactic, i.e. searching for oestrus females and following them (Corlatti et al. 2012). Lovari et al. (2006) described two different tactics of space use in male chamois: resident males, with overlapping or contiguous summer and winter home ranges, and seasonal migrants, with separated summer and winter areas (see also Chapter 1, this thesis). During summer, the former had smaller home ranges, located at lower elevations than the latter (Lovari et al. 2006; Unterthiner et al. 2012). I found both resident and migrant individuals amongst territorial males, whereas non-territorial ones were all migrants (Chapter 1, this thesis). However, although some territorial males migrated between seasonal ranges, my results have confirmed the occurrence of territorial males usually at lower elevations than other males (Lovari et al. 2006; Corlatti et al. 2013b). The lack of significant differences in home range size between females and territorial males in July could be explained by the greater home ranges of two territorial males who moved to separate summer areas (Chapter 1, this thesis; cf. Luccarini et al. 2006 for red deer). At the same time, the significantly greater home range sizes of territorial males in April could be explained by the seasonal migration of other four territorial individuals back to their territories, from winter areas (Chapter 1, this thesis).

As predicted (prediction *iii*), I found an increase of home range size with increasing temperatures and a positive influence of high temperatures on elevation use (Grignolio et al. 2004; Aublet et al. 2009 for Alpine ibex), although the magnitude of this effect was not consistent across individuals. As expected, the effect of temperature has been the lowest on territorial males, being stronger on females than on non-territorial males. Thermal stress in summer may be a major factor influencing physical conditions and survival (Parker 1988). Animals can react to increasing temperatures reducing their activities during the hottest hours or moving to cooler places located at higher elevations (Aublet et al 2009; Mason et al. 2014; Ciach & Peksa 2018). The effect of temperature was reported both at the yearly scale and in the warmer period (May-October), including the growing season of vegetation, nursing/weaning and the pre-rut. Thus, my results strongly support a major role of weather in influencing individual movements during a crucial period for the life cycle of chamois, with particular reference to females.

Moreover, according to prediction (*iii*), snow depth had a negative effect on home range size (Grignolio et al. 2004 for Alpine ibex; Richard et al. 2014 for mountain goat *Oreamnos americanus*) and on elevations used (Mysterud 1999 for roe deer *Capreolus capreolus*), especially for females and non-territorial males. The strongest effect was found for females, considering the daily temporal scale. Snow depth determines an increase of costs of locomotion and thermoregulation, as well as it limits the access to food resources for herbivores (Parker et al. 1984; van Moorter et al. 2013). Several studies reported an increase of winter mortality in years with severe climatic conditions (Clutton-Brock & Albon 1982; Forchhammer et al. 1998; Gonzalez & Crampe 2001; but see Loison et al. 1999b). Thus, energies may be saved by reducing movements and clumping on snow-free areas, with easier accessible food resources, in turn improving winter survival (e.g. Georgii & Schröder 1983).

I found a negative effect of rainfalls on daily elevations used by chamois in the warmer months. During rainy days, temperatures are usually lower than in dry days, limiting the necessity of upslope movements to cooler sites. Moreover, rainfalls may favour hypothermia, especially in

young individuals (Barrett 1981, for pronghorn *Antilocapra americana* calves; Putman et al. 1996 for fallow deer *Dama dama* fawns), and they pose energetic constraints (Parker 1988). Thus, seeking cover to avoid heavy wetting of fur may be a strategy to conserve heat and energy. Other studies suggested a reduction of activity and/or movements during heavy summer rainfall (Miller 1970, for black-tailed deer *Odocoileus hemionus*).

The analysis of NDVI values showed that chamois use sites with greater vegetation productivity from April-May to September-October, although temporal patterns were slightly different between females and males. Apparently, locations used by females showed relatively more constant NDVI values between June and October, while a greater decrease was observed for males in September-October. In my same study area, Corlatti et al. (2013b) showed no significant difference in the variation of faecal crude protein content (FCP, an indicator of forage quality: Gálvez-Cerón et al. 2013) between territorial and non-territorial males. However, these males were reported to show a decrease of FCP in September-October, although not significant (Corlatti et al. 2013b), which would be in agreement with the pattern I found for NDVI values. In summer-autumn months, females occupied sites located at slightly higher elevations than non-territorial males (although differences were not statistically significant). The altitudinal range could probably explain the different pattern of NDVI values. Alternatively, females may actively select more productive vegetation patches throughout weeks, thus maintaining relatively more stable foraging conditions. Analyses of temporal variation of NDVI in areas used by females and males could help clarify relationships between chamois movements and finer-scale changes of vegetation phenology.

Effects of environmental drivers were not consistent across chamois of different sex/mating tactic (i.e. females, territorial males and non-territorial males). Individual tactics are expected to be the result of different individual reactions to environmental pressures, with the ultimate goal of increasing reproductive success and survival. Females adapted strongly their ranging movements to cope with short-term weather variations (temperature, snow depth), which are expected to influence their reproductive success directly, i.e. through effects on survival of their offspring, or indirectly,

i.e. through effects on vegetation (Clutton-Brock et al. 1987; Saether & Gravem 1988; Cederlund et al. 1991; Saether 1997; Gaillard et al. 1998). Thus, pressures related to nursing/weaning of offspring would strongly influence ranging movements of females, which in turn will influence the success of mating strategies adopted by adult males (Chapter 2, this thesis; see also Lovari et al 2006; Corlatti et al. 2020). Moreover, my results have shown that males adopting different mating tactics did not respond consistently to weather variations. In particular, territoriality was associated with a relatively lower response of individual movements to short-term weather changes. The costs of temporarily leaving the territory are probably higher than benefits provided by searching for cooler places at higher elevations. Nevertheless, fine-scale behaviours (e.g. selection for cooler or nutritious patches within their territory; see also Corlatti et al. 2013b) may allow territorial males to partially compensate for costs induced by both thermoregulation and living in relatively less nutritious meadows. Alternative mating tactics, besides sex and reproductive status, should be considered when studying spatial behaviour and its driving factors.

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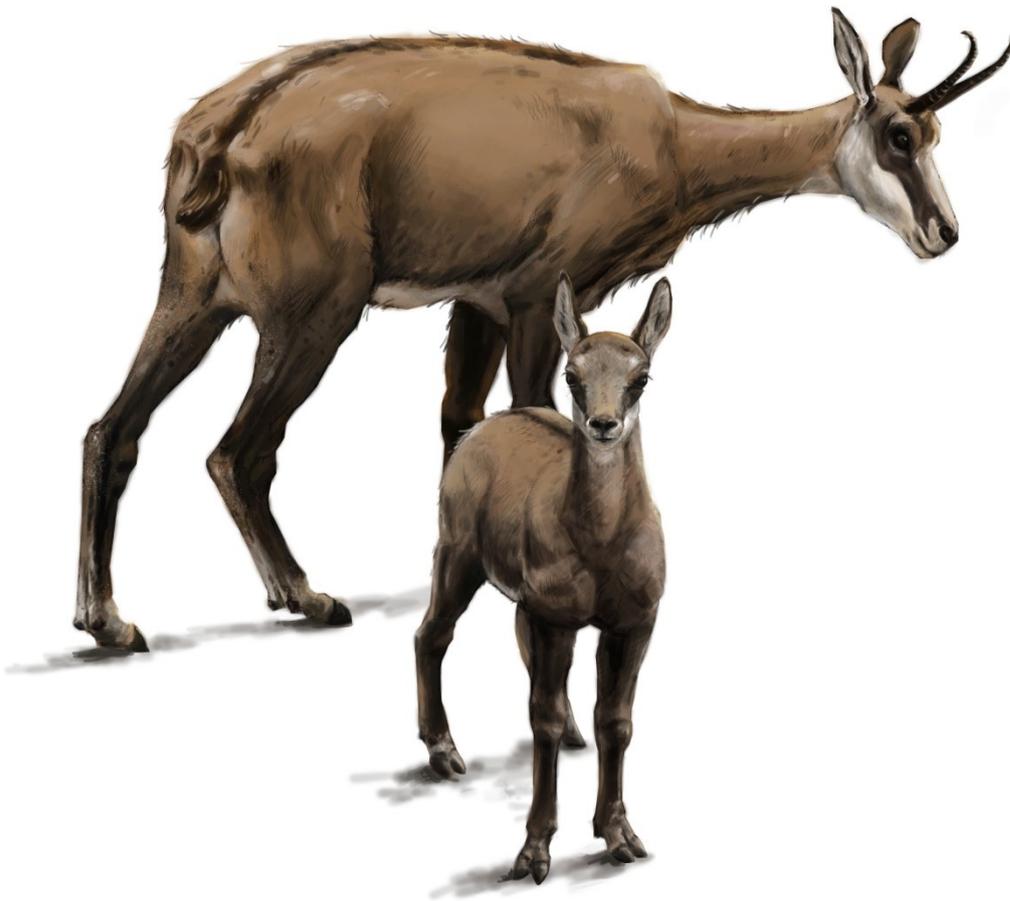
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## CHAPTER 4

### Group-living and its costs in a mountain-dwelling ungulate



Javier Lazaro



## CHAPTER 4

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### *Group-living and its costs in a mountain-dwelling ungulate*

#### **ABSTRACT**

Gregariousness can favour detection and avoidance of predators, yet it may increase intra-specific competition. In turn, feeding interference could elicit aggressive interactions and endogenous stress response. Trade-offs between (i) food intake and self/offspring protection, and (ii) inter-individual aggressiveness as well as the relevant stress response, may arise for group-living ungulates. Seasonality, which influences food availability, and age are two major determinants of social behaviour and its physiological correlates, particularly for mountain ungulates. I investigated female-female aggressive interactions, endocrine correlates, nutritional quality of diet and grouping patterns in a mountain-dwelling herbivore, the Alpine chamois, through behavioural observations on 10 individually recognisable females and chemical analyses of fresh faecal samples (June-November 2017-2018). The frequency of intra-sexual aggressive interactions decreased significantly throughout summer-autumn. However, no seasonal change in faecal androgen metabolite (FAMs) levels, nor in faecal cortisol metabolites (FCMs) levels were supported. Frequency of intra-sexual aggressive interactions and levels of hormone metabolites did not vary significantly with age; however, younger females appeared to be involved more often in aggressive interactions than older ones. Protein content of diet decreased from summer to autumn, while crude fibre levels increased, as expected with decreasing pasture quality. Older females showed higher levels of crude protein and lower levels of crude fibre in their diet than younger ones. Group size decreased from summer to autumn, with herds showing relatively constant proportions of females, yearlings and kids. The proportion of males in groups increased from June to November, because of the approaching rutting season. The proportion of females was greater in smaller groups, whereas

the proportions of the other age classes showed an opposite pattern; as to the proportion of males, the effect of group size was not supported. Access to adequate food resources in summer-autumn is crucial to females, to recover from births and to face the high costs of nursing, as well as to allow their offspring to store enough fat reserves to overwinter. Feeding interference results stronger when females share nutritious pasture, suggesting the importance of summer food resources.

## INTRODUCTION

Ecological and evolutionary theories suggest that gregariousness is an adaptation to maximise security, through group alertness and the “selfish herd” effect (Hamilton 1971). Staying in larger groups allows individuals to benefit from group vigilance and the “dilution” effect, i.e. it increase the possibility to detect a predator and reduces individual probability of being attacked by a predator, without decreasing individual feeding efficiency (Pulliam 1973; Berger 1978). In mammals, females could accept costs of being gregarious, e.g. parasite transmission as well as increased competition for food, to decrease predation risks for them and their offspring (Thaker et al. 2010). It has been suggested that feeding interference may increase in larger groups (Molvar & Bowyer 1994; Riedel et al. 2011), leading to trade-offs between (i) food intake and self/offspring protection, and (ii) inter-individual aggressiveness as well as the relevant stress response (Molvar & Bowyer 1994).

Competitive interactions could vary in response to changes in the availability of resources. Intraspecific competition, including direct aggressions, is reported to be frequent when resources are scarce (Schoener 1973; Taitt & Krebs 1981; Krebs et al. 1986; Sirot 2000). Alternatively, the energy allocated to costly activities by females, e.g. competitive interactions (Mooring et al. 2006), may be the highest when food abundance is high and (i) the contended resource is highly worthy (Geist 1978; Goss-Custard et al. 1984; Shopland 1987) or (ii) when benefits at stake, e.g. successful offspring survival, determine energy investment (Fattorini et al. 2018b).

In temperate ecosystems, seasonality strongly influences availability of resources (Albon & Langvatn 1992), thus being a major determinant of variation in social behaviour and activity of individuals. On alpine grasslands, high quality forage is available to mountain herbivores only between late spring and summer, usually decreasing throughout this period, till autumn (Dunant 1977; Ferrari et al. 1988; Lendrum et al. 2014; Primi et al. 2016). During the warm months, access to nutrient food is necessary to females to recover from pregnancy and build up energies to face the

high costs of lactation and nursing (Therrien et al. 2007; Froy et al. 2016; Scornavacca et al. 2016). Summer forage is important also to juveniles, who have to grow and store fat reserves for their winter survival (Festa-Bianchet 1988; Pettorelli et al. 2007; Scornavacca et al. 2016). Ultimately, the availability of high-quality food resources, in the warm months, influences population dynamics (Gaillard et al. 2000; Côté & Festa-Bianchet 2001; Ferretti et al. 2015; Scornavacca et al. 2016). Therefore, one would expect that a stressor such as the seasonality of resources influences social behaviour (e.g. aggression and grouping pattern) and physiological responses (e.g. endocrine levels) (Fattorini et al. 2018b, 2019; Favreau et al. 2018).

Aggressiveness and its endocrine correlates are also expected to change according to age and/or social status of individuals (DeVries et al. 2003; Bartoš et al. 2010; Beauchamp 2015). Among ungulates, dominant individuals can defend a resource, e.g. food and mate, more efficiently than subordinate ones (Bernstein 1981; Lovari & Rosto 1985; Thouless 1990). Dominance in aggressive interactions between female ungulates could be related to age (Rutberg 1983; Festa-Bianchet 1991; Côté 2000), body size (Clutton-Brock et al. 1982; Hirotani 1990) and/or weapon presence, such as horns or antlers (Geist 1971; Barrette & Vandal 1986), or more than one of them (Locati & Lovari 1991). An increase of social stress may be expected as a result of limited access to resources, in turn eliciting higher rates of aggression (Kelley 1980; DeVries et al. 2003). Aggressive behaviour is linked to testosterone levels (Adkins-Regan 1981; Creel et al. 1992; Pasch et al. 2011; Martin et al. 2013). Additionally, physiological responses to stress include an increase in levels of glucocorticoids or their metabolites (Möstl & Palme 2002; Sheriff et al. 2011). Furthermore, testosterone may elicit immunosuppression, in turn parasite/pathogen attacks (Folstad & Karter 1992; Decristophoris et al. 2007). Long-term production of high levels of glucocorticoids may also reduce survival and reproductive success (Sapolsky 1992; Möstl & Palme 2002).

Seasonality of food abundance and quality is also expected to influence grouping pattern (Fryxell 1991). A lower food availability has been suggested to support smaller groups, as

individuals should avoid feeding competition (Bon et al. 1990; Fryxell 1991; Isvaran 2007; Chirichella et al. 2015).

I evaluated social behaviour and endocrine correlates in a mountain-dwelling gregarious herbivore, i.e. female Alpine chamois *Rupicapra rupicapra rupicapra*, from June to November, i.e. when food resources decrease from high to low abundance and quality (Albon & Langvatn 1992; Ranghetti et al. 2016) and maternal cares decrease (Ruckstuhl & Ingold 1994; see also Scornavacca et al. 2016, 2018, for the Apennine chamois *Rupicapra pyrenaica ornata*), as well as when winter rigours are imminent. Outside the rutting season (i.e. with the exception of November/December) and in particular in summer, the two sexes of Alpine chamois tend to segregate. Females, after giving births between May - June, form social groups with other adult and subadult females, yearlings and kids; whereas young males disperse and adult ones are usually solitary (Krämer 1969; Knaus & Schröder 1983; Hamr 1984, 1985) or may gather in groups when population density is high (Berducou & Bousses 1985). While female aggressive behaviour has been studied in the Apennine chamois (Locati & Lovari 1990, 1991; Lovari & Locati 1993; Fattorini et al. 2018a, b), no information is available on seasonal variation of aggressive interactions and related endocrine levels in the Alpine chamois.

I used individual-level behavioural observations on individually recognisable adult female Alpine chamois, as well as chemical analyses of faecal samples, in 2017-2018 (June-November), to evaluate whether (i) the frequency of female-female aggressive interactions changed throughout months, with decreasing maternal cares (Ruckstuhl & Ingold 1994) and forage quality (Albon & Langvatn 1992; Ranghetti et al. 2016), as well as approaching the winter period; (ii) the frequency of female-female aggressive interactions changed with age; (iii) levels of faecal androgen and cortisol metabolites showed the same season/age pattern of aggressive interactions; (iv) nutritional quality (protein content) of the diet changed from warm months to cold ones; (v) group size and structure (i.e. proportion of adult and subadult females, males, yearlings and kids) changed throughout the months. I predicted that (i) the frequency of female-female aggressive interactions

would increase from early summer to autumn, because of decreasing quality and availability of food resources; alternatively, it would decrease because of decreasing investment and energy expenditure in maternal cares, as weaning progresses (Fattorini et al. 2018b). Furthermore, (ii) I also expected that older individuals should show a lower frequency of aggressive interactions, on the assumption that their rank should already be established, thus granting them priority access to resources, compared to younger/subordinates individuals. Faecal androgen and cortisol metabolites should increase with increasing aggression rate and should be greater for subordinate individuals, thus showing the same pattern of the frequency of aggressive interactions (iii). Protein content in faecal samples should decrease with decreasing forage quality in autumn, whereas fibre content should increase (iv). Finally, (v) group size should decrease between summer and autumn, because of the decrease in pasture availability and quality; conversely, an increase in the proportion of males in the groups, because of the approaching mating season, and no changes in the proportions of the other sex/age classes of individuals should be expected.

## MATERIALS AND METHODS

### *Data collection and analysis*

#### *Behavioural data: aggressive interactions and grouping pattern*

My study was conducted from June to November, in 2017 (N = 8 adult females) and 2018 (N = 6). Individuals (4-16 years old) were darted for sedation and fitted with individually recognisable GSM-GPS Pro-Light collars, with very high frequency (VHF) beacon devices (Vectronic Aerospace GmbH, Berlin), and coloured ear tags, according to procedures described in Bassano et al. (2004) and Dematteis et al. (2009). At sedation, the age of each female was estimated by counting horn rings (Schröder & von Elsner-Schack 1985). Behavioural observations were conducted from dawn to dusk. I tried to distribute observations homogeneously across individuals and across times of day/months. Chamois were observed through binoculars (e.g. Zeiss 15x60, Avalon 10x42) and spotting scopes (Nikon 20-60x). Data were collected using a standardized recording sheet and a dictaphone. I avoided recording data whenever I felt that the animals were reacting to my (or other human) presence. Behaviour and group size/structure were recorded through continuous focal animal sampling on individually recognisable marked females and instantaneous scan sampling, respectively (Altmann 1974). Focal females were observed for 1-hour bouts each, divided into 15-min sampling intervals, separated by 5-min breaks. For each 1-hour bout, group size and structure (number of: adult and subadult females, adult and subadult males, yearlings, kids) were recorded at the beginning of the bout and every 15 min. Sex and age classes were determined according to Corlatti et al. (*in press*). All occurrences of aggressive interactions between the focal female and other individuals were recorded during each 15-min sampling interval. For each aggression event I recorded: time, sex/age class of the target animals (adult and subadult female, adult and subadult male, yearling, kid) and its outcome. Dominance and

submissive behaviour patterns (Lovari 1985) performed by the opponents were also recorded. Schaller (1977) recognised two types of aggression: direct, “that involves overt threats (warnings of imminent attack) or actual physical contact”, and indirect, “during which the animal attempts to assert or achieve dominance not by a test of strength but by intimidating the opponent solely through the use of its rank symbols”, i.e. dominance displays. I followed Lovari (1985) to define dominance (direct and indirect aggressions) and submissive displays. The dominant individual was termed as the one who performed the last dominance pattern and/or did not withdraw (Locati & Lovari 1991). Conversely, the subordinate was the individual who escaped and/or responded with a submissive pattern (Locati & Lovari 1991). An interaction was considered as “resolved” when one of the opponents withdrew during the encounter. I then calculated the hourly frequency of female-female aggressive interactions per female (number of interactions with other females / observation hour) and the mean number of females per hour present in the group of the focal female. I also calculated the mean group size for each observation bout and the proportion of the mean number of adult and subadult females, males, yearlings and kids in the group. All analyses were performed in Microsoft Excel (2010), R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio.

#### *Hormone metabolites and nutritional quality of diet*

Levels of hormone metabolites have been assessed through chemical analyses of faecal samples (Millsbaugh & Washburn 2004; Sheriff et al. 2010, 2011). Data collection occurred from June to November 2017 (N = 35 faecal samples) and 2018 (N = 47), to assess levels of faecal androgen metabolites (FAMs, indicator of aggressiveness) and faecal cortisol metabolites (FCMs, indicator of stress) (Dalmau et al. 2007; Corlatti et al. 2012; Zwijacz-Kozica et al. 2013; Hadinger et al. 2015). Extraction and determination of faecal steroids were conducted as reported by Pecorella et al. (2016) and conducted by E. Macchi (Turin, Italy). Additionally, I collected faecal samples (2017: N = 37; 2018: N = 42) to assess forage quality by chemical methods (Weender analyses), to determine crude protein and fibre (neutral detergent fibre - NDF, acid detergent fibre - ADF and crude fibre)

content levels. All chemical analyses to assess forage quality were conducted in the Chemistry laboratory of the University of Veterinary Medicine, by O. Hekmat (Wien, Austria). I collected fresh faecal samples after observing defecation, either immediately or after max 2 hours. Each sample was placed in a plastic bag and stored in freezer, at -20°C, no later than 10 hours from collection.

### *Statistical analyses*

I discarded from the analyses focal bouts that lasted < 30 min, i.e. bouts interrupted because females moved out of sight. I investigated seasonal/age variation of the frequency of female-female aggressive interactions, hormone levels, protein/fibre contents and seasonal variation of grouping patterns through General linear Mixed Models (GLMM) and Generalised linear mixed models (GLMMs). I used the Shapiro-Wilk normality test to evaluate the assumption of normality for each response variable in the models. I considered the followings response variables: (i) frequency of female-female aggressive interactions (Shapiro-Wilk normality test:  $W = 0.71$ ,  $p\text{-value} = <0.001$ ); (ii) faecal androgen metabolite (FAMs) (Shapiro-Wilk normality test:  $W = 0.98$ ,  $p\text{-value} = 0.12$ ) and faecal cortisol metabolite (FCMs) (Shapiro-Wilk normality test:  $W = 0.98$ ,  $p\text{-value} = 0.22$ ) levels; (iii) crude protein (Shapiro-Wilk normality test:  $W = 0.99$ ,  $p\text{-value} = 0.60$ ), neutral detergent fibre (NDF) (Shapiro-Wilk normality test:  $W = 0.98$ ,  $p\text{-value} = 0.51$ ), acid detergent fibre (ADF) (Shapiro-Wilk normality test:  $W = 0.97$ ,  $p\text{-value} = 0.12$ ), crude fibre (Shapiro-Wilk normality test:  $W = 0.98$ ,  $p\text{-value} = 0.17$ ) contents; (iv) mean group size (Shapiro-Wilk normality test:  $W = 0.84$ ,  $p\text{-value} = <0.001$ ); (v) proportion of adult females (Shapiro-Wilk normality test:  $W = 0.93$ ,  $p\text{-value} = <0.001$ ) and subadult females (Shapiro-Wilk normality test:  $W = 0.65$ ,  $p\text{-value} = <0.001$ ), males (Shapiro-Wilk normality test:  $W = 0.43$ ,  $p\text{-value} = <0.001$ ), yearlings (Shapiro-Wilk normality test:  $W = 0.73$ ,  $p\text{-value} = <0.001$ ), kids (Shapiro-Wilk normality test:  $W = 0.95$ ,  $p\text{-value} = <0.001$ ).

I used a GLMMs, selecting a gamma distribution and a 'log' link function, using the function '*glmmadmb*', '*glmmADMB*' library (Fournier et al. 2012) in R, to investigate patterns of frequency

of female-female aggressive interactions. Predictors in the global model were: age of the focal female, the presence of offspring, the mean number of adult and subadult females present in the group (the Pearson's correlation coefficient between mean group size and mean number of adult and subadult females was 0.97, so I selected the second one to be inserted in the model). Moreover, to evaluate the role of seasonality, I included the linear effect of Julian day (i.e. the number of days from the first of January) as numeric predictor. I also included both linear and quadratic effects of time of the day (hours from midnight) as numeric predictors, to account for bimodal daily variation of behaviour.

I used GLMM, using the function '*lmer*', '*lme4*' library (Bates et al. 2015) in R, to test significance of seasonal and age variation of hormone metabolites (FAMs and FCMs contents) and diet content levels (crude protein, NDF, ADF, crude fibre contents). Predictors in the global models were age of the focal female and Julian day as numeric predictor.

I used GLMMs, selecting a gamma distribution and a '*log*' link function, using the function '*glmmadmb*', '*glmmADMB*' library (Fournier et al. 2012) in R, to evaluate temporal variation in the observed mean group size. Predictor in the global model was Julian day as numeric predictor.

I used GLMMs, selecting a beta distribution and a '*logit*' link function, using the function '*glmmadmb*', '*glmmADMB*' library (Fournier et al. 2012) and the function '*glmmTMB*', library '*glmmTMB*' (Brooks et al. 2017) in R, to investigate variation in the proportion of adult and subadult females, males, yearlings and kids in the group. Predictors in the global model were the Julian day as numeric predictor and the mean group size.

In all models, the identity of females, the month and the year were inserted as random effects, to account for repeated estimates for the same individual, during the same month and year.

Model selection was performed considering the minimum Akaike's Information Criterion, corrected for small samples (AICc: Burnham & Anderson 2002), using the '*MuMIn*' library (Barton 2019) in R. For each response variable, a global model was built, including all predictors, and all the possible alternative models were built, including different combinations of predictors, and were ranked and

weighted from the global model. Models with  $\Delta\text{AICc} \leq 2$  in respect to the best model (i.e. with the lowest AICc value), as well as models with an AICc value lower than that of any simpler, nested alternative were selected. All analyses were performed in R 3.4.4 and R 3.6.1 (R Development Core Team 2019), in RStudio. All p-value were considered significant at a level of 0.05.



## RESULTS

### *Female aggression frequency and endogenous stress response*

I analysed data collected in a mean number of *c.* 43 hours of observations/month (129 hours of observations/year), for a total of 258 observation hours. Models supported an effect of Julian day on the frequency of female-female aggressive interactions (Table 1). In particular, the frequency of interactions decreased from June to November (Table 2; Fig. 1). Model selection also retained age as predictor in the best model: the frequency of aggression tended to decrease with age, but the effect was not significant (Tables 1, 2). I found no support for a temporal variation of faecal androgen metabolite (FAMs) and faecal cortisol metabolite (FCMs) levels (Table 1, 2; Fig. 2). Models did not support an effect of age on FAMs and FCMs (Tables 1, 2).

### *Nutritional quality of female diet*

Crude protein content decreased from June to November, whereas crude fibre content showed the opposite trend (Tables 1, 2; Fig. 3a, d). No temporal variation was found for neutral detergent fibre (NDF) and acid detergent fibre (ADF) levels (Table 1, 2; Fig. 3b, c). Moreover, age had an influence on nutritional contents of female diet (Table 1): crude protein levels were higher, whereas crude fibre levels were lower, in older females than in younger ones (Table 2).

### *Group size and structure*

I analysed 395 group sizes and structures. Models supported an effect of Julian day on mean group size, with decreasing group size from June to November (Tables 1, 2; Fig. 4a). No effect of Julian day was found on the proportion of adult and subadult females, yearlings and kids in the groups, whereas the proportion of males increased from June to November (Tables 1, 2; Tables S.4.1, S.4.2; Fig. 4b, c; Fig. S.4.1). The models supported an effect of group size on the proportion of adult and subadult females, yearlings and kids in the groups and no effect of group size on the proportion of

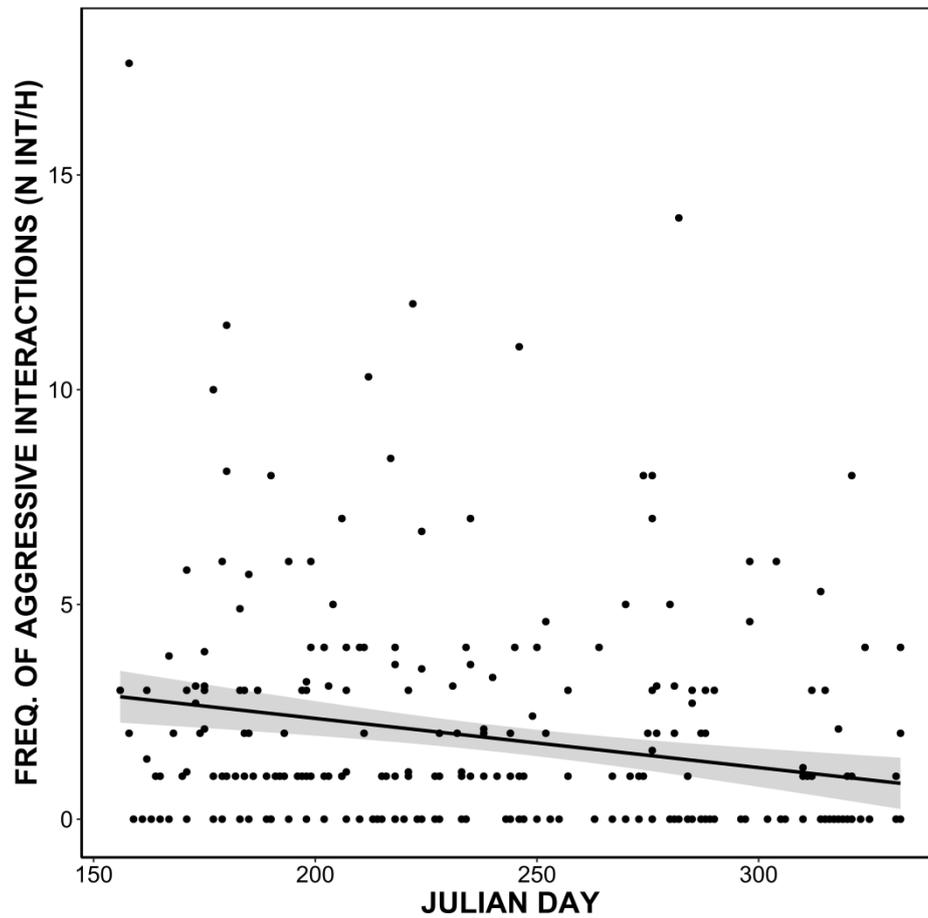
males in the groups (Table 1; Table S.4.1). In particular, the proportion of adult females decreased in larger groups, whereas the proportion of subadult females, yearlings and kids increased in larger groups (Table 2; Table S.4.2). Group size ranged from 2 to 65 individuals (Fig. 4a) (Median value = 8; IQR = 4 - 15).

**Table 1** Effects of seasonality, age and group size on social behaviour, endogenous correlates and grouping pattern in adult female Alpine chamois: summaries of selected models of effects of: (a) age, Julian day, mean number of adult and subadult females in the group (n females), time of the day (time: linear; time<sup>2</sup>: quadratic) on the frequency of female-female aggressive interactions (Interaction Freq.); (b) age and Julian day on faecal androgen metabolites (FAMs) and faecal cortisol metabolites (FCMs); (c) age and Julian day on crude protein, neutral detergent fibre (NDF), acid detergent fibre (ADF), crude fibre contents; (d) Julian day on observed mean group size; (e) Julian day and mean group size on proportion of females and subadult females in the group, of female Alpine chamois, in 2017-2018. Random effects in each model = Id: individual identities, Year: 2017, 2018, Month. Result of model selection: variables retained, degrees of freedom, logLikelihood, AICc,  $\Delta$ AICc values and model weight are shown.

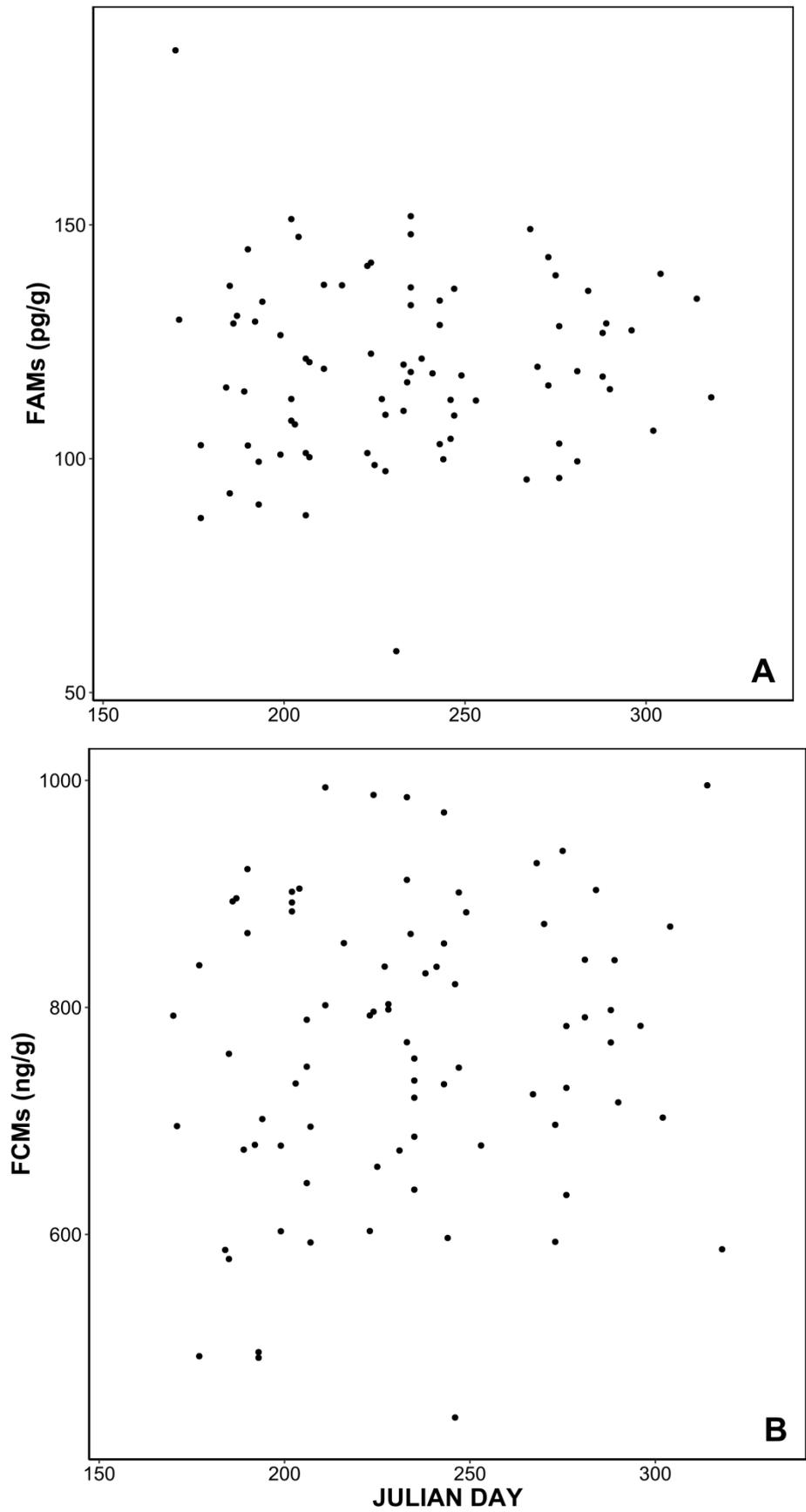
Analysis	Model	Variables retained	df	logLik	AICc	$\Delta$ AICc	Weight
(a) Interaction Freq.	Best	age + julian day + (1 Id) + (1 Year) + (1 Month)	7	1101.7	-2189.0	0.00	0.29
	Second	n females + time + time <sup>2</sup> + (1 Id) + (1 Year) + (1 Month)	8	1102.3	-2188.0	0.96	0.18
	Third	julian day + (1 Id) + (1 Year) + (1 Month)	6	1100.0	-2187.8	1.20	0.16
	Fourth	age + time + time <sup>2</sup> + (1 Id) + (1 Year) + (1 Month)	8	1101.9	-2187.4	1.60	0.13
	Fifth	n females + (1 Id) + (1 Year) + (1 Month)	6	1099.7	-2187.2	1.80	0.12
	Sixth	time + time <sup>2</sup> + (1 Id) + (1 Year) + (1 Month)	7	1100.7	-2187.0	1.92	0.11
(b) FAMs	Best	(1 Id) + (1 Year) + (1 Month)	5	-352.30	715.40	0.00	1.00
	FCMs	Best	age + julian day + (1 Id) + (1 Year) + (1 Month)	7	-493.65	1002.80	0.00
(c) Protein	Second	age + (1 Id) + (1 Year) + (1 Month)	6	-495.20	1003.50	0.72	0.41
	Best	age + julian day + (1 Id) + (1 Year) + (1 Month)	7	-183.31	382.20	0.00	0.70
NDF	Second	julian day + (1 Id) + (1 Year) + (1 Month)	6	-185.35	383.90	1.66	0.30
	Best	age + (1 Id) + (1 Year) + (1 Month)	6	-204.68	422.80	0.00	0.59
ADF	Second	(1 Id) + (1 Year) + (1 Month)	5	-206.25	423.50	0.70	0.41
	Best	(1 Id) + (1 Year) + (1 Month)	5	-236.99	484.80	0.00	1.00
Fibre	Best	age + julian day + (1 Id) + (1 Year) + (1 Month)	7	-191.81	399.20	0.00	0.34
	Second	julian day + (1 Id) + (1 Year) + (1 Month)	6	-193.36	399.90	0.70	0.24
	Third	age + (1 Id) + (1 Year) + (1 Month)	6	-193.43	400.00	0.83	0.22
	Fourth	(1 Id) + (1 Year) + (1 Month)	5	-194.69	400.20	1.01	0.20
(d) Group size	Best	julian day + (1 Id) + (1 Year) + (1 Month)	6	-1261.5	2535.2	0.0	0.63
	Second	(1 Id) + (1 Year) + (1 Month)	5	-1263.1	2536.3	1.1	0.37
(e) Proportion of females	Best	julian day + group + (1 Id) + (1 Year) + (1 Month)	7	379.9	-745.5	0.00	0.55
	Second	group + (1 Id) + (1 Year) + (1 Month)	6	378.7	-745.1	0.43	0.45
Proportion of subadult females	Best	group + (1 Id) + (1 Year) + (1 Month)	6	3297.6	-6582.9	0.00	1.00

**Table 2** Parameters estimated from the best models on the (a) effects of age and Julian day on the frequency of female-female aggressive interactions (Interaction Freq.); (b) effects of age and Julian day on faecal cortisol metabolites (FCMs); (c) effects of age and Julian day on crude protein, neutral detergent fibre (NDF), crude fibre contents; (d) effects Julian day on observed mean group size; (e) effects of Julian day and mean group size on proportion of females and subadult females in the group, of female Alpine chamois, in 2017-2018 ( $\beta$ : coefficient, SE: standard error, p-value).

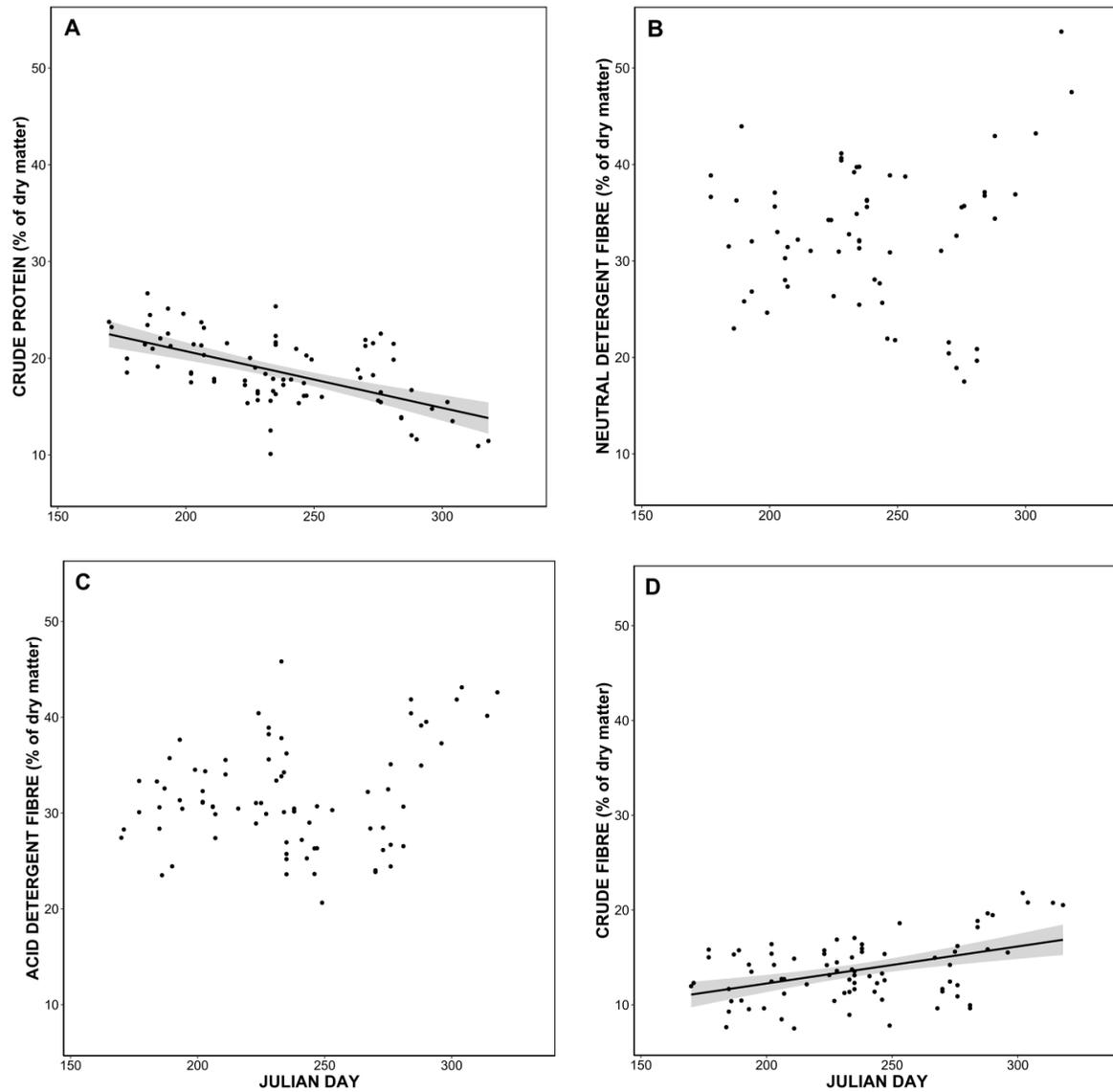
	Model	Variables	$\beta$	SE	p-value
(a)	Interaction Freq.	intercept	3.42	1.12	<0.01**
		age	-0.11	0.06	0.06
		julian day	-0.01	<0.01	<0.05*
(b)	FCMs	intercept	686.88	120.87	<0.001***
		age	-10.58	7.79	0.21
		julian day	0.73	0.35	0.10
(c)	Protein	intercept	30.63	2.71	<0.001***
		age	0.35	0.12	<0.05*
		julian day	-0.07	0.01	<0.001***
	NDF	intercept	42.09	4.59	<0.001***
		age	-0.64	0.32	0.07
	Fibre	intercept	4.91	4.15	0.27
		age	-0.33	0.14	<0.05*
		julian day	0.05	0.01	<0.05*
	(d)	Group size	intercept	3.05	0.35
julian day			<-0.01	<0.01	<0.05*
(e)	Proportion of females	intercept	2.64	0.57	<0.001***
		julian day	<-0.01	<0.01	0.06
		group	-0.08	<0.01	<0.001***
	Proportion of subadult females	intercept	-3.71	0.15	<0.001***
		group	0.03	<0.01	<0.001***



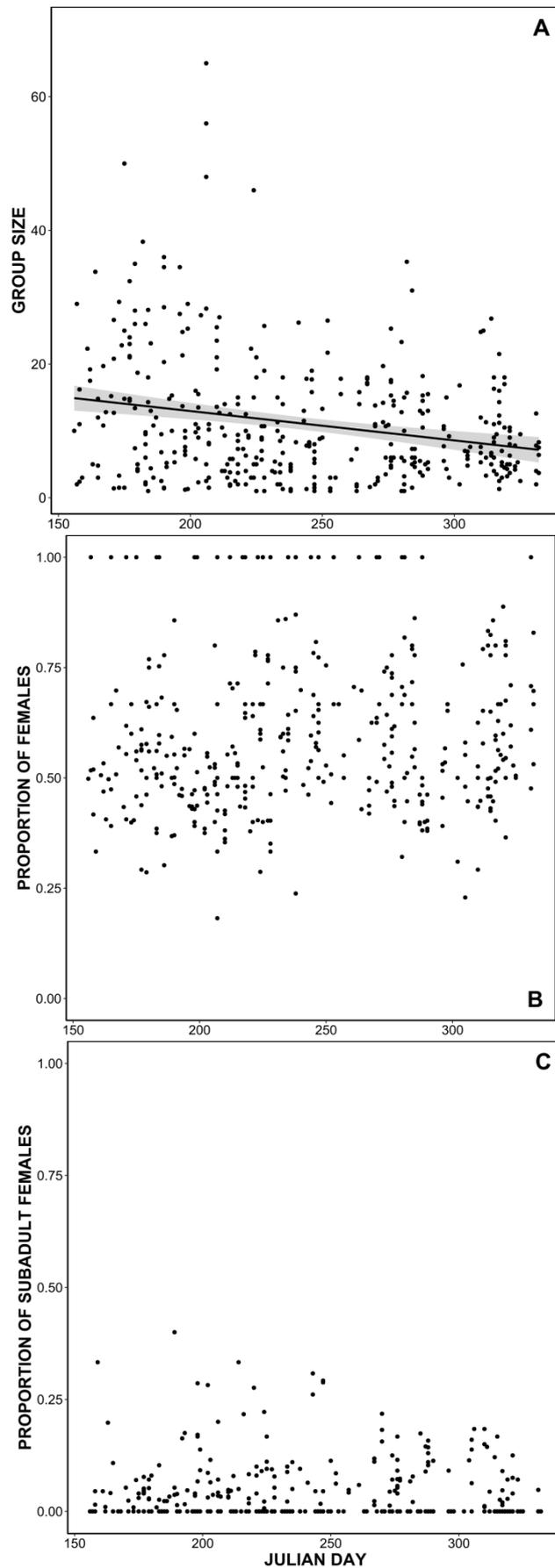
**Fig. 1** Seasonal variation in the frequency of female-female aggressive interactions (N interactions/h) for female Alpine chamois, in 2017-2018. The black line and the shaded grey area indicate the predicted relationship and its standard error, when the variation through Julian day was supported by the model.



**Fig. 2** Seasonal variation in (A) faecal androgen metabolites (FAMs) and (B) faecal cortisol metabolites (FCMs) for female Alpine chamois, in 2017-2018.



**Fig. 3** Seasonal variation in (a) crude protein, (b) neutral detergent fibre (NDF), (c) acid detergent fibre (ADF), (d) crude fibre contents in faecal samples, for female Alpine chamois, in 2017-2018. The black line and the shaded grey area indicate the predicted relationship and its standard error, when the variation through Julian day was supported by the model.



**Fig. 4** Observed group size (a) and proportion of females (b) and subadult females (c) in groups of female Alpine chamois, in 2017-2018, in relation to Julian day. The black line and the shaded grey area indicate the predicted relationship and its standard error, when the variation through Julian day was supported by the model.

## DISCUSSION

The frequency of aggressive interactions and the grouping pattern of female Alpine chamois appeared to be influenced by seasonality. I found a decrease of the frequency of female-female aggressive interactions and a decrease of the mean group size between summer and late autumn. Fattorini et al. (2018b) found a similar result for the Apennine chamois, a related species, which showed a higher aggression rate in summer than in autumn. Heavy energetic demands imposed by lactation and nursing (Clutton-Brock et al. 1982; Clutton-Brock 1991; Gross et al. 1995; Ruckstuhl et al. 2003) may force females to higher rates of aggression, even when food quality and quantity are the highest (Ferrari et al. 1988; Albon & Langvatn 1992). This would support that females may allocate more energies to costly activities, e.g. competitive interactions (Mooring et al. 2006), when food abundance allows the selection of particularly worthy resources (Geist 1978; Goss-Custard et al. 1984; Shopland 1987) or when benefits at stake are evolutionary high, e.g. successful offspring winter survival (Fattorini et al. 2018b).

Fattorini et al. (2018b) suggested another potential explanation for the high rate of aggression when food is abundant. If vegetation patches are close to antipredator escape terrain, e.g. cliffs and rocky areas, aggression rate might show an increase when kids are more vulnerable, to access safer sites. Their study area was visited by potential terrestrial predators, i.e. grey wolf *Canis lupus* and brown bear *Ursus arctos* (Fico et al. 1984; Baruzzi et al. 2017). Females may have evolved specific antipredator strategies (Baruzzi et al. 2017). Wild ungulates in the Gran Paradiso National Park have lived in absence of terrestrial predators for more than one century. The grey wolf has only recently recolonized the Park (Palmegiani et al. 2013) and it visited my study area rarely (see also Study Area). Yet, female antipredator behaviour could be active also with low predation pressure, and help explaining the higher interaction frequency during the first life-stage of offspring also in my study site.

Group size is expected to be greater when food availability and quality are the highest (Fryxell 1991). Other studies have reported a positive influence of nutritional quality of pasture on group size of chamois (for the Apennine chamois: Lovari & Cosentino 1986; Bruno & Lovari 1989; Fattorini et al. 2018a; for the Alpine chamois: Chirichella et al. 2015). Accordingly, I found a decrease of the mean number of individuals in the groups through summer-autumn. The comparatively poorer food resources available to chamois in the autumn may not allow the maintenance of large groups (cf. Lovari & Cosentino 1986), as group size is influenced by the productivity of meadows (Chirichella et al. 2015). Additionally, I found no temporal variation of the proportion of adult females in the groups. By contrast, Fattorini et al. 2019 found that size of mixed groups did not vary between summer-autumn, whereas the proportion of females in the groups increased, possibly because they concentrated on patchily distributed nutritious forbs (Ferrari et al. 1988). They suggested that, in a relatively rich area (see Ferretti et al. 2015), group splitting to avoid competition would not be necessary if the best food is available: indeed, a relatively high proportion of nutritious forbs in diet from summer to autumn has been suggested for their study population (Ferretti et al. 2015). By contrast, a decrease of crude protein content and an increase of crude fibre (raw cellulose) content in the autumn diet of females have been found in my study site. This would support the hypothesis of decreasing quality of forage throughout summer-autumn, with group splitting, to avoid feeding interference. If so, variation of abundance, quality and dispersion of resources could promote avoidance of feeding interference, through the decrease of group size.

A larger group can provide a greater collective protection against predators, especially for offspring (e.g. Pipia et al. 2009; Lingle 2001). Thus, females may accept to cope with greater potential feeding interference to maximise offspring protection, especially during the first months of their newborn life. Conversely, males can maximise their energy intake, thus increasing their potential to compete for mating opportunities during the rut (see Chapter 1, this thesis), remaining alone or in small groups through summer-autumn (Bleich et al. 1997). The increase in the proportion of males

in groups in autumn is in accordance with other studies and, most likely, it is explained by the approaching of the mating season (November) (e.g. Lovari & Cosentino 1986, for the Apennine chamois).

I also found no variation of the proportion of kids in the groups. Mothers and kids tend to remain very close during the first six months of the kid life (for Pyrenean chamois *Rupicapra pyrenaica pyrenaica*: Richard-Hansen & Campan 1992; for Alpine chamois: Ruckstuhl & Ingold 1999; for Apennine chamois: Scornavacca et al. 2018). This might lead to a relatively low summer mortality of kids in the study area, because of cooperative defence (Scornavacca & Brunetti 2016).

Fighting ability may be related to age and experience (Thouless & Guinness 1986), thus younger individuals are usually subordinates in intra-sexual interactions (with one exception: the Himalayan tahr *Hemitragus jemlahicus*; Lovari et al. 2009 and 2015). Amongst ungulates, dominant individuals can access a resource, e.g. food and mate, more efficiently than subordinate ones (Lovari & Rosta 1985; Thouless 1990). My data suggest that younger females may be involved more frequently in aggressive interactions than older ones, but the age effect was not significant. The outcomes of intra-sexual interactions in relation to the age of the opponents would support a role of age to assess dominance in aggressive interactions (Rutberg 1983; Festa-Bianchet 1991; Locati & Lovari 1991; Côté 2000). Krämer (1969) suggested that female Alpine chamois do not establish a fixed, long-term inter-individual hierarchy, despite they could establish short-term hierarchies and rank differences could be determined by age. Conversely, Fattorini et al. (2018b) found that dominance increased with age (cf. also Locati & Lovari 1991, for the Southern chamois; Ingold & Marbacher 1991, for the Northern chamois) and that in particular prime-aged females (4-8 years old) showed higher frequency of aggressive interactions, higher cortisol and testosterone levels compared to other ones. In the Alpine chamois, female breeding success peaks in prime-aged females (5-13 years old; Tettamanti et al. 2015), decreasing around 8 years old (Morin et al. 2016). Thus, energies allocated in motherhood could be the greatest in this period. However, I found no effect of age on levels of hormone metabolites. Females in my study were 5-16 years old (median

age = 10, IQR = 7–13), indicating that further data on < 7 years old individuals are needed to clarify the pattern. Allegedly, I found a positive effect of age on nutritional contents of female diet. Older females showed higher levels of crude protein and lower levels of crude fibre (raw cellulose) in their diet compared to younger ones, whereas no effect was supported on neutral and acid detergent fibre levels. Older females, thereby dominant individuals (Locati & Lovari 1991, Lovari & Rosto 1985), could have priority access to better quality forage compared to younger ones. Alternatively, they could benefit from a greater experience in searching for high quality pasture (e.g. De Roos et al. 2009).

In contrast to my prediction (*iii*), faecal androgen metabolites (FAMs) and cortisol metabolites (FCMs) did not show the same temporal pattern of the frequency of aggressive interactions. For the Apennine chamois, Fattorini et al. (2018b) found a decrease of FCMs throughout summer-autumn, supporting a greater importance of nursing costs than seasonality of food resources to determine stress in females. Lack of adequate food resources is stressful (Kitaysky et al. 1999; Clinchy et al. 2004). Accordingly, pasture depletion can lead to an increase of cortisol metabolites (Saltz & White 1991; Fattorini et al. 2018a). Apparently, my results would suggest that variation of resource availability was not enough to trigger an increase of endogenous stress response in female chamois, in my study area. However, faecal sample size was smaller in autumn than in summer ( $N_{\text{summer}} = 51$ ,  $N_{\text{autumn}} = 31$ ), perhaps inadequate to detect seasonal differences, thus in need of confirmation.

The number of females in the group appeared not to influence the frequency of female-female aggressive interactions in my study population. Conversely, in the Apennine chamois, Fattorini et al. (2018b) showed that the frequency of aggressions increased with the number of potential competitors, suggesting the occurrence of feeding interference over resources. Feeding interference has been suggested to be greater in larger groups compared to smaller ones (Molvar & Bowyer 1994; Riedel et al. 2011). In fact, median group size for the Apennine chamois was greater than that in my study area.

The presence of offspring appears to be an important factor in determining a tendency to aggregate (Pérez-Barbería & Nores 1994). If so, one would expect mothers to stay in groups more often and to interact aggressively comparatively more often. In some species, females reach the highest social rank when they have a kid at heel (Koutnik 1981; Cassinello 1985). By contrast, as in my study, the presence of offspring did not affect aggressive behaviour of females in mountain goats *Oreamnos americanus* (Côté 2000).

I found a slight support for an effect of time of day on the frequency of female-female interactions, i.e. the effect of this variable was retained only in the second selected model. This result is in agreement with Fattorini et al. (2018b), suggesting a higher frequency of interactions in the first and in the last part of the day, i.e. consistently with the bimodal daily variation of activity rhythms reported in their study area.

My results support the hypothesis that the access to highly nutritious summer forage is crucial to female chamois, to face the high costs of motherhood. Food availability allows individuals to aggregate in larger groups, which in turn triggers aggressive interactions. Access to adequate, high-quality pasture in summer is fundamental to increase female reproductive success and offspring survival (e.g. Johnson et al. 2002; Therrien et al. 2007; Scornavacca et al. 2016). Therefore, local variation in food quality may influence the behavioural ecology of group-living species, potentially resulting in aggressive interactions.

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## CONCLUSIONS

Sex-related constraints (access to high quality resources to maximise offspring survival for females vs. the increase of mating opportunities for males) determine different individual responses to environmental stressors (e.g. seasonality).

Results in **Chapter 1** show that both (territoriality and non-territoriality) alternative mating tactics (AMTs) were reported amongst males, with approximately the same frequency. Behavioural mating tactics are frequently flexible in large mammals (Isvaran 2005; Taborsky et al. 2008). However, I report no individual change of AMT in different years, strongly suggesting that the adoption of a mating tactic may be fixed in male Alpine chamois and may not be influenced by environmental factors, such as snow presence. No age effect on AMTs has been reported either. Moreover, I found no difference in the frequency of intra-sexual aggressive interactions, which are expected to be costly for both the sender and the receiver. Territorial males (T), which are known to be dominant over non-territorial (NT) ones in aggressive interactions (Corlatti et al. 2012), consistently showed greater indices of mating opportunities. Although greater costs in terms of endogenous stress response, energies and parasite load have been reported in T than NT males (Corlatti et al. 2012, 2019; Corlatti & Bassano 2014), I found no difference in life expectancy between males adopting different AMTs, partially explaining the persistence of both AMTs in Alpine chamois. Finally, I reported a previously undocumented occurrence of different patterns of spatial behaviour across T males, suggesting that territoriality does not necessarily involve being resident. Fifty percent of T individuals had overlapping or continuous winter and summer areas, whereas the others moved between different seasonal areas (immediately after the rut, in winter, or in summer-autumn).

This 5-year study would support the existence of fixed AMTs (Taborsky et al. 1998) in adult male Alpine chamois, which may adopt a conservative mating strategy (Bocci et al. 2010; Corlatti et al. 2015a), i.e. a less intense and energetically demanding competition amongst males compared to that of highly dimorphic species, and probably different spatial strategies, to maximise survival.

Snow cover and resource distribution would be expected to influence dispersion of females over the rut (Lovari et al. 2006; Corlatti et al. 2020), in turn affecting male mating behaviour and success (Emlen & Oring 1977). Results in **Chapter 2** show that territorial males had smaller territories and greater mating opportunities index during ruts with deeper snow cover (cf. Lovari et al. 2006; Corlatti et al. 2020). Additionally, smaller territories were visited by more females and showed higher values of terrain roughness than larger ones: a rugged and steep area should favour snow sliding, thus allowing easier access to food resources (Schröder 1971; Berducou 1982; von Elsner-Schak 1985), in turn attracting more females. The frequency of male-male aggressive interactions was positively related to the number of females in a territory and was greater for males with territories located at higher elevations. This suggests intrusion of non-territorial males, who usually stay at higher elevations than territorial ones (Lovari et al. 2006; Corlatti et al. 2013; Chapter 3, this thesis), while following oestrus females (Corlatti et al. 2012), in emphasising intra-sexual competition for mates. Territorial males facing the costs of frequent intra-sexual aggressive interactions may provide “good genes” for reproduction (cf. Byers et al. 1994, for the pronghorn *Antilocapra americana*).

My results are consistent with recent findings of Corlatti et al (2020) and support the hypothesis of Lovari et al. (2006). Territoriality in Alpine chamois could be favoured by the predictability of female movements during snowy ruts. The importance of snow cover and its effect on female distribution as strong determinants of mating behaviour and success in male chamois is supported, emphasising the role of weather stochasticity in favouring maintenance of AMTs in the population (Lovari et al. 2006; Corlatti et al. 2020). Climatic changes may favour one or the other tactic alternatively, thus keeping both of them in the genotype of this species.

Results in **Chapter 3** suggest that females and non-territorial males increased their home range size and moved to higher elevations from late spring to early autumn, whereas territorial males showed consistently smaller home ranges and remained at the lowest elevations. During winter, no major significant difference was found, although NT males showed significantly larger home ranges than

those of T males and females in November-December, probably as a consequence of their reproductive tactic, i.e. searching for oestrus females and following them.

Especially for females and, to a lower extent, for NT males, home range size and elevations used were positively related to temperature (cf. Grignolio et al. 2004; Aublet et al. 2009 for Alpine ibex *Capra ibex*) and negatively related to snow depth. Conversely, T males showed limited variations of space use in response to temperature and snow depth. Vegetation productivity (expressed as NDVI values) of the locations used by chamois was greater between April-October than in late autumn-winter. Apparently, locations used by females showed relatively more stable NDVI values between June and October, compared to those of locations used by males, which decreased sharply in September and October. The altitudinal range occupied by females in summer-autumn could probably explain the different pattern of NDVI values. Alternatively, females may actively select more productive vegetation patches, thus maintaining relatively more stable foraging conditions.

My results strongly support a major role of weather in influencing individual movements, with particular reference to females, during the crucial periods of the growing season of vegetation, nursing/weaning and the pre-rut. In conclusion, I found significant differences between the two sexes and between territorial and non-territorial males, in both temporal variation of spatial behaviour and response to climatic stressors. Females need great energies to face costs of nursing and may be more sensitive to short-term weather variations (temperature, snow depth), thus adapting strongly their ranging movements. Weather changes are expected to influence their reproductive success directly, i.e. through effects on survival of their offspring, or indirectly, i.e. through effects on vegetation (Clutton-Brock et al. 1987; Saether & Gravem 1988; Cederlund et al. 1991; Saether 1997; Gaillard et al. 1998). Conversely, territoriality was associated with a relatively lower response of individual movements to short-term weather changes. Territorial males are probably forced to actively defend their territories for several months (von Hardenberg et al. 2000) to gain advantages during the mating season. Leaving the territory would have costs probably higher than benefits provided by searching for cooler places at higher elevations. Nevertheless, fine-

scale behaviours (e.g. selection for cooler patches within their territory) may allow T males to partially compensate for costs induced e.g. by thermoregulation. These results emphasise that AMTs should be considered when studying spatial behaviour and its driving factors, besides sex and reproductive status.

Results in **Chapter 4** show that the frequency of intra-sexual aggressive interactions and the grouping patterns of female Alpine chamois are influenced by seasonality. The frequency of aggressive interactions and group size decreased through summer-autumn, with herds showing relatively constant proportions of adult and subadult females, yearlings and kids. The comparatively poorer food resources available to chamois in the autumn may not allow the maintenance of large groups (cf. Lovari & Cosentino 1986), as group size is influenced by the productivity of meadows (Chirichella et al. 2015). No seasonal/age variation in faecal androgen and cortisol metabolites levels were supported. Pasture depletion can lead to an increase of cortisol metabolites (Saltz & White 1991; Fattorini et al. 2018a). Apparently, my results would suggest that variation of resource availability was not enough to trigger an increase of endogenous stress response in female Alpine chamois. Alternatively, group size decrease allows the avoidance of feeding interference, thus stress response. However, protein content in diet decreased, while crude fibre levels increased, from summer to autumn. This would support the hypothesis of decreasing quality of forage throughout summer-autumn. If so, variation of abundance, quality and dispersion of resources could promote avoidance of feeding interference, through the decrease of group size.

Younger females appeared to be involved more frequently in aggressive interactions than older ones, but the age effect was not significant. Older females showed higher levels of crude protein and lower levels of crude fibre in their diet than younger ones. The former, thereby dominant individuals (Locati & Lovari 1991, Lovari & Rosto 1985), could have priority access to better quality forage compared to younger ones. Alternatively, they could benefit from a greater experience in searching for high quality pasture (e.g. De Roos et al. 2009).

My results support that feeding interference is stronger when females share highly nutritious resources, suggesting the importance of the access to adequate summer forage, to recover from births and face the high costs of motherhood. Therefore, local variation in food quality may influence the behavioural ecology of group-living species, potentially resulting in aggressive interactions.

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Javier Lazaro





## SUPPLEMENTARY MATERIALS

### Supplementary material Chapter 1

**Table S.1.1** Mating tactic (AMT: T = territorial, NT = non-territorial), year of birth (Birth), date of capture (Capture), age at capture (in months), month of death (Death), age at death (in months) for monitored male Alpine chamois (ID: individuals). Med: median; QR: quartiles range; Mn: mean; Sd: standard deviation.

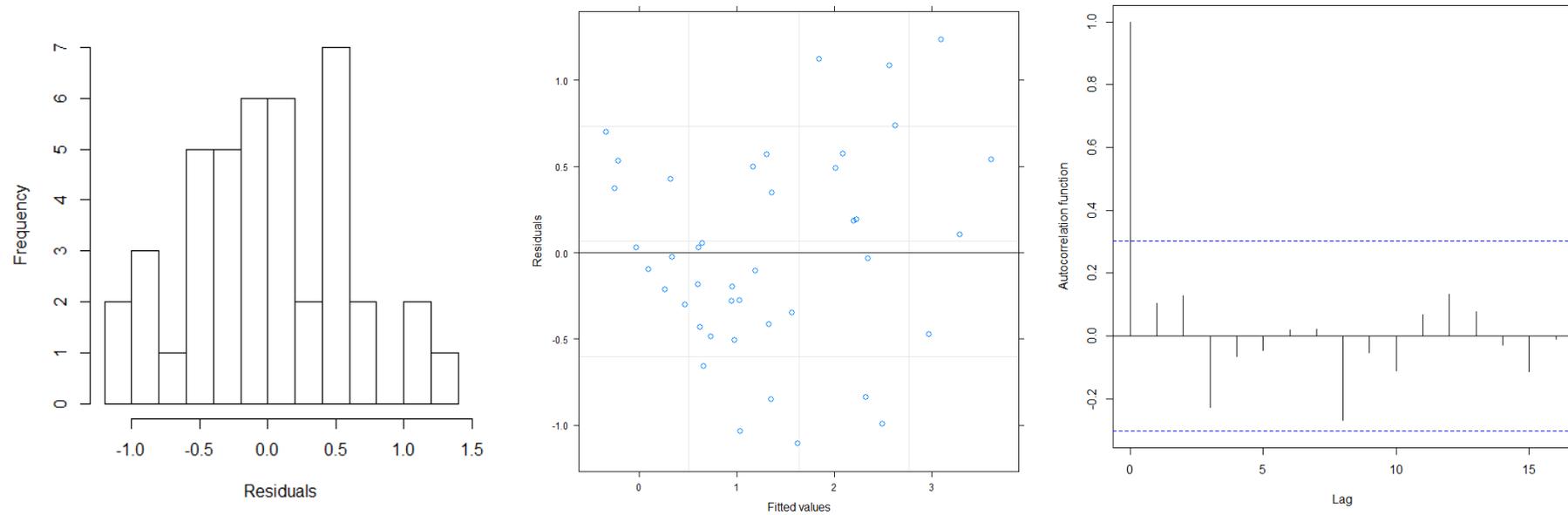
ID	AMT	Birth	Capture	Age capture	Death	Age death
<b>M1</b>	T	2005	12/02/2010	57	July 2012	86
<b>M4</b>	T	2003	02/04/2010	83	February 2018	177
<b>M5</b>	T	2004	12/05/2010	72	May 2018	168
<b>M11</b>	T	2003	10/11/2010	90		
<b>M13</b>	T	2006	11/11/2010	54		
<b>M14</b>	T	2002	17/11/2010	102		
<b>M16</b>	T	2004	23/11/2010	78		
<b>M17</b>	T	2004	02/12/2010	79	January 2018	164
<b>M19</b>	T	2002	14/12/2010	103		
<b>M25</b>	T	2005	14/12/2011	79	January 2018	152
<b>M31</b>	T	2004	07/12/2012	103	January 2017	152
<b>M34</b>	T	2010	25/11/2015	66	March 2017	82
<b>M36</b>	T	2011	25/11/2015	54		
<b>M41</b>	T	2007	23/12/2015	103		
<b>M42</b>	T	2011	23/12/2015	55	February 2017	69
	<b>T</b>			<b>Med= 79</b>		<b>Mn= 131</b>
				<b>QR= 61-96</b>		<b>Sd= ±44</b>
<b>M7</b>	NT	2004	31/05/2010	72		
<b>M8</b>	NT	2005	01/06/2010	61	March 2014	106
<b>M9</b>	NT	1999	26/10/2010	137	February 2012	153
<b>M12</b>	NT	2006	10/11/2010	54		
<b>M15</b>	NT	2004	17/11/2010	78	January 2013	104
<b>M18</b>	NT	2003	03/12/2010	91	February 2018	177
<b>M21</b>	NT	2003	22/12/2010	91		
<b>M22</b>	NT	2006	22/12/2010	55	March 2013	82
<b>M23</b>	NT	NA	28/01/2011	NA		
<b>M24</b>	NT	2005	10/03/2011	70	June 2017	145
<b>M26</b>	NT	2007	14/06/2012	61		
<b>M28</b>	NT	2008	14/11/2012	54	March 2017	106
<b>M29</b>	NT	2001	07/12/2012	139	January 2017	188
<b>M35</b>	NT	2003	25/11/2015	150	January 2017	164
<b>M40</b>	NT	NA	07/12/2015	NA		
<b>M43</b>	NT	2012	05/01/2016	44		
	<b>NT</b>			<b>Med= 71</b>		<b>Mn= 136</b>
				<b>QR= 56-91</b>		<b>Sd= ±37</b>

**Table S.1.2** Mating tactic (AMT: T = territorial, NT = non-territorial) and mating opportunities index (mean number females/observation hours) for each male Alpine chamois monitored (ID: individuals) in each rutting period (2011, 2012, 2015, 2016, 2017). Med: median; QR: quartiles range; Mn: mean; Sd: standard deviation.

ID	AMT	2011	2012	2015	2016	2017
M1	T	4.15				
M4	T	7.25	2.31	0.75	0.75	
M5	T	0.92	1.67	0.00	0.19	0.17
M11	T	0.52	1.88	0.05		
M13	T	3.39	4.33	0.70	2.38	2.50
M14	T	2.42	0.00			
M16	T	3.36	2.50	0.76	0.64	1.48
M17	T	3.65	1.50	0.36	0.12	0.50
M19	T	NA	0.67			
M25	T		0.25	0.31	0.42	1.22
M31	T			0.32	0.00	
M34	T				0.00	
M36	T				0.47	2.97
M41	T				1.71	2.66
M42	T				1.09	
	<b>T</b>	<b>Med= 3.4</b> <b>QR= 2.0-3.8</b>	<b>Med= 1.7</b> <b>QR= 0.7-2.3</b>	<b>Med= 0.3</b> <b>QR= 0.2-0.7</b>	<b>Med= 0.5</b> <b>QR= 0.1-0.9</b>	<b>Mn= 1.6</b> <b>Sd= ±1.1</b>
M4	NT					1.19
M7	NT	0.43				
M8	NT	0.48	0.08			
M9	NT	0.28				
M12	NT	0.68	0.75	0.00		
M15	NT	0.83	0.50			
M18	NT	0.94	0.33	0.00	0.00	0.91
M21	NT	NA	0.17			
M22	NT	0.39	0.00			
M23	NT	NA				
M24	NT	NA	0.50	0.14	0.21	
M26	NT		1.33			
M28	NT		0.25	0.29	0.04	
M29	NT			0.00	0.04	
M35	NT				0.00	
M40	NT				1.34	1.64
M43	NT					0.46
	<b>NT</b>	<b>Med= 0.5</b> <b>QR= 0.4-0.7</b>	<b>Med= 0.3</b> <b>QR= 0.2-0.5</b>	<b>Med= 0.0</b> <b>QR= 0.0-0.1</b>	<b>Med= 0.0</b> <b>QR= 0.0-0.2</b>	<b>Mn= 1.0</b> <b>Sd= ±0.5</b>

## Supplementary material Chapter 2

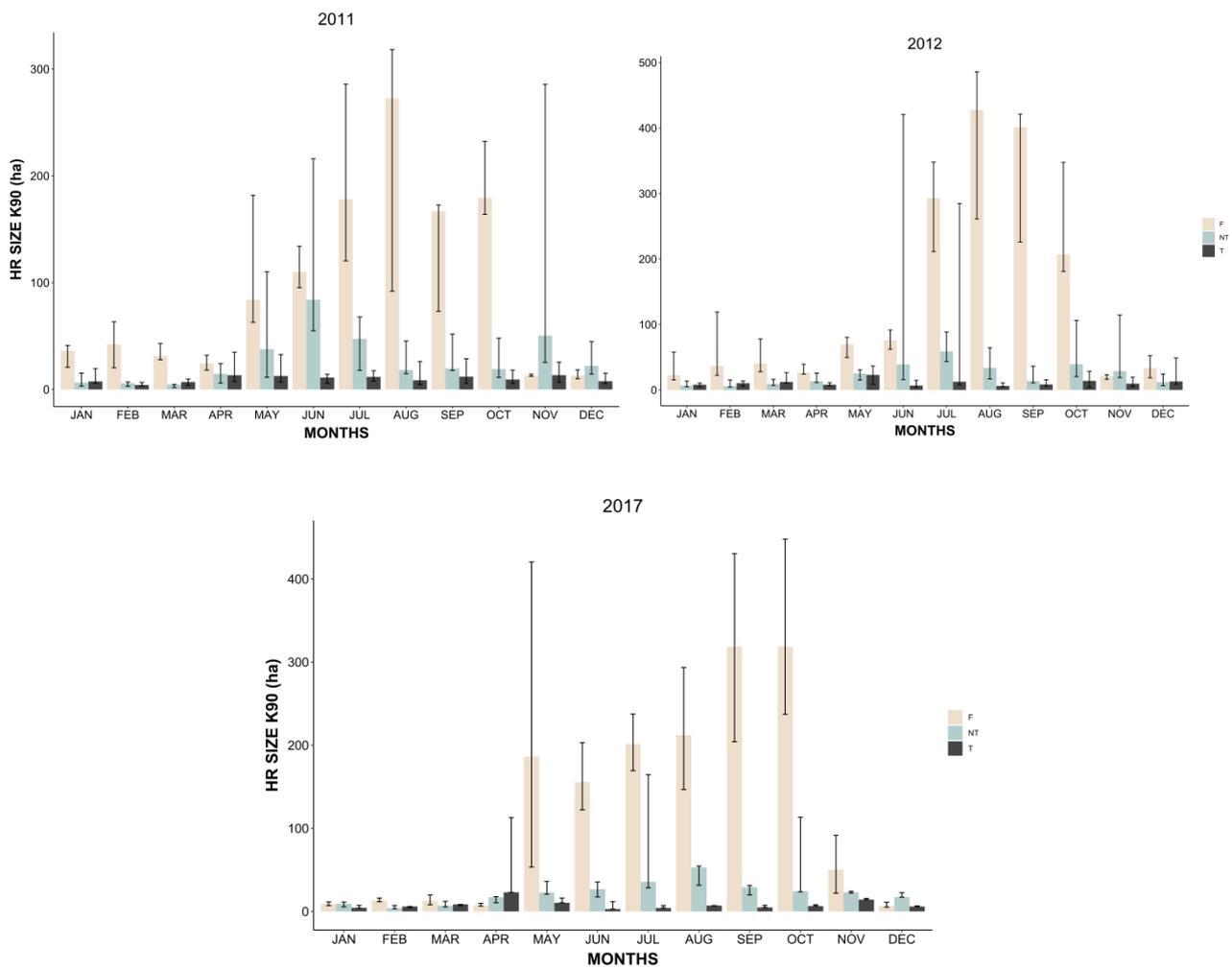
**Fig. S.2.1** Model checking plots for the best model (Table. 1a; response variable: mating opportunities index) showing, from left to right, frequency distribution of residuals, residuals against fitted values and autocorrelation functions, with horizontal dashed lines providing an approximate 95% confidence interval for the autocorrelation estimate at each lag. Conditional  $r^2$  was 0.78; regression between predicted and observed values was highly significant ( $B: 0.72, s.e. = 0.06, p = <0.001$ ).



### Supplementary material Chapter 3

**Table S.3.1** Parameters estimated from the best models on effects of temporal variation (Month) and sex/mating tactic (female, territorial male T, non-territorial male NT) on monthly home range size (HR Kernel 90%) of female and male Alpine chamois in 2011, 2012 and 2017 ( $\beta$ : coefficient, SE: standard error, p-value). Reference categories for categorical predictors = Month: Jan; Tactic: female.

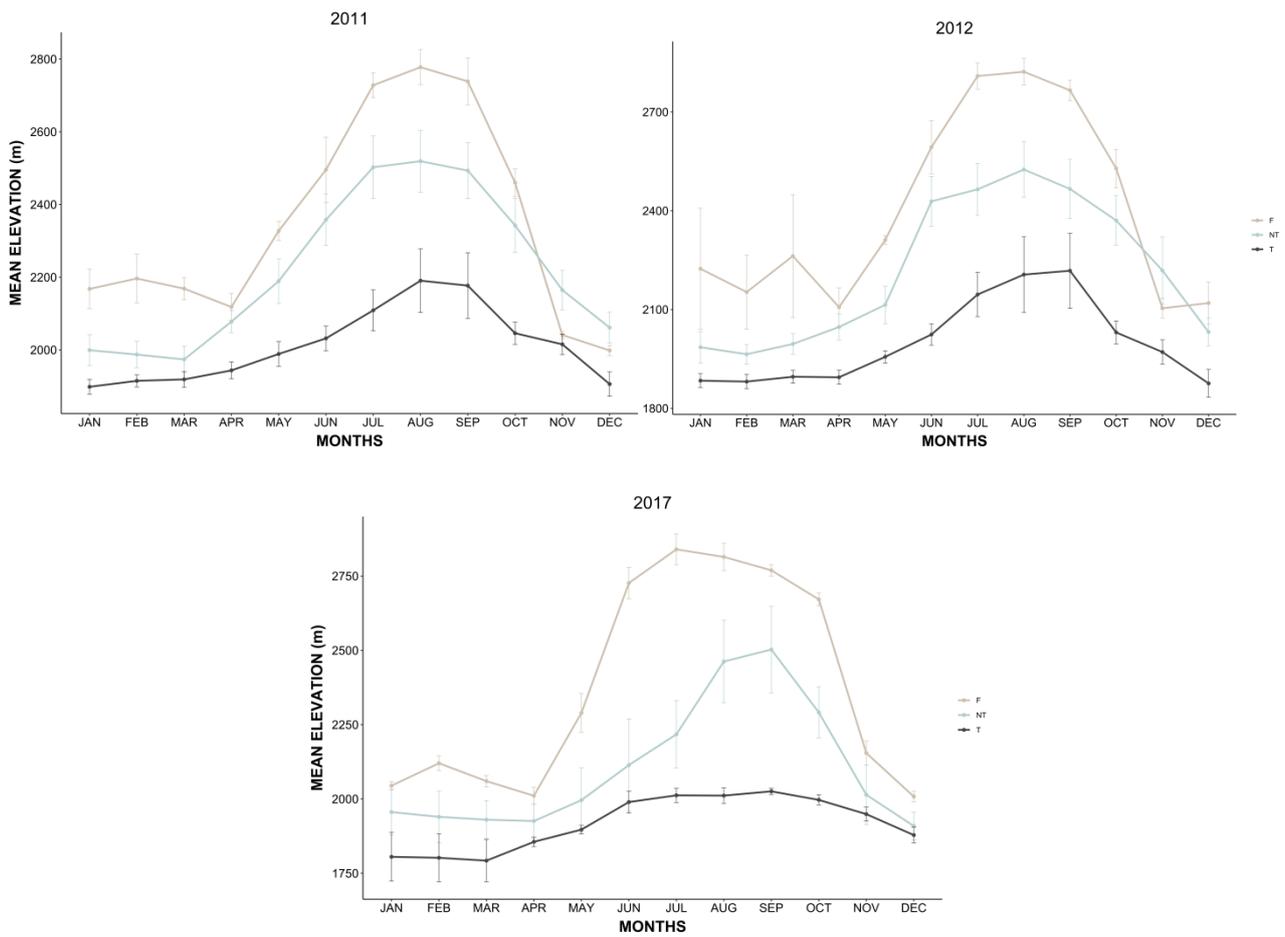
Model	Variables	$\beta$	SE	p-value	Variables	$\beta$	SE	p-value
HR	Intercept	3.13	0.37	<0.001***	Feb×TactT	-0.80	0.44	0.07
	Feb	0.36	0.34	0.30	Mar×TactT	-0.13	0.44	0.76
	Mar	0.26	0.35	0.45	Apr×TactT	1.24	0.46	<0.01**
	Apr	-0.19	0.35	0.59	May×TactT	-0.97	0.46	<0.05*
	May	2.04	0.35	<0.001***	Jun×TactT	-1.67	0.45	<0.001***
	Jun	2.02	0.35	<0.001***	Jul×TactT	-0.72	0.46	0.12
	Jul	2.41	0.35	<0.001***	Aug×TactT	-2.17	0.46	<0.001***
	Aug	2.56	0.35	<0.001***	Sep×TactT	-2.42	0.45	<0.001***
	Sep	2.55	0.35	<0.001***	Oct×TactT	-2.31	0.46	<0.001***
	Oct	2.66	0.35	<0.001***	Nov×TactT	0.14	0.47	0.76
	Nov	0.60	0.36	0.10	Dec×TactT	0.54	0.46	0.23
	Dec	-0.21	0.35	0.55				
	TactNT	-0.97	0.43	<0.05*				
	TactT	-0.79	0.44	0.07				
	Feb×TactNT	-0.44	0.44	0.32				
	Mar×TactNT	-0.37	0.44	0.41				
	Apr×TactNT	0.91	0.44	<0.05*				
	May×TactNT	-0.36	0.45	0.41				
	Jun×TactNT	0.53	0.45	0.23				
	Jul×TactNT	-0.58	0.44	0.19				
	Aug×TactNT	-0.95	0.46	<0.05*				
	Sep×TactNT	-1.38	0.45	<0.01**				
	Oct×TactNT	-0.98	0.45	<0.05*				
	Nov×TactNT	1.74	0.47	<0.001***				
	Dec×TactNT	1.62	0.45	<0.001***				



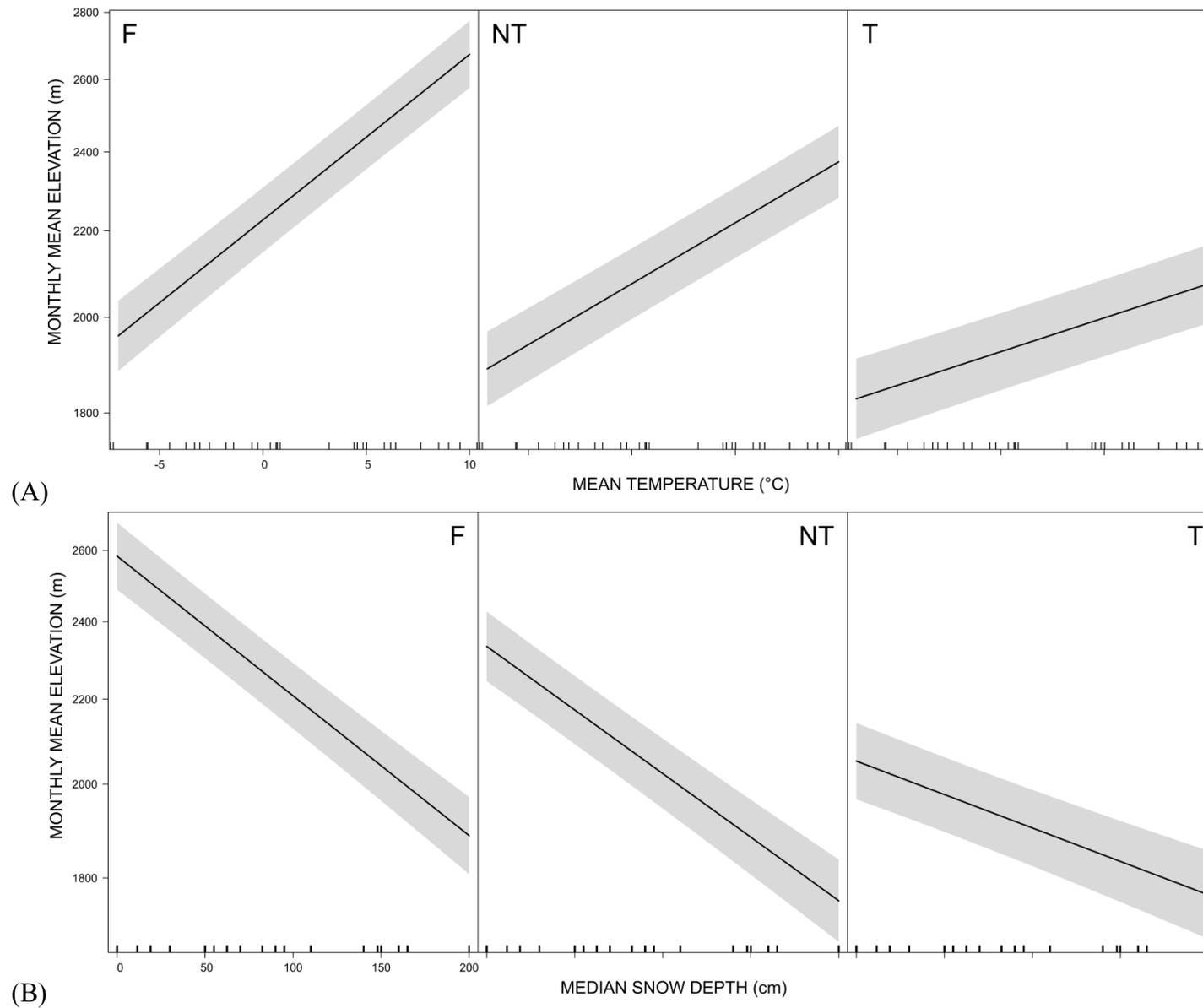
**Fig. S.3.1** Monthly variation of home range size (K90%, ha) of female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in single years 2011-2012-2017. Median values and 25%-75% quartiles are shown.

**Table S.3.2** Parameters estimated from the best models of effects of temporal variation (Month) and sex/mating tactic (female, territorial male T, non-territorial male NT) on monthly elevations (Elev.) of female and male Alpine chamois in 2011, 2012 and 2017 ( $\beta$ : coefficient, SE: standard error, p-value). Reference categories for categorical predictors = Month: Jan; Tactic: female.

Model	Variables	$\beta$	SE	p-value	Variables	$\beta$	SE	p-value
Elev.	Intercept	7.66	0.02	<0.001***	Feb×TactT	-0.01	0.02	0.66
	Feb	0.01	0.02	0.46	Mar×TactT	< -0.01	0.02	0.97
	Mar	0.01	0.02	0.70	Apr×TactT	0.04	0.02	0.08
	Apr	-0.03	0.02	0.17	May×TactT	-0.04	0.02	0.12
	May	0.08	0.02	<0.001***	Jun×TactT	-0.13	0.02	<0.001***
	Jun	0.21	0.02	<0.001***	Jul×TactT	-0.16	0.02	<0.001***
	Jul	0.27	0.02	<0.001***	Aug×TactT	-0.14	0.02	<0.001***
	Aug	0.28	0.02	<0.001***	Sep×TactT	-0.12	0.02	<0.001***
	Sep	0.26	0.02	<0.001***	Oct×TactT	-0.11	0.02	<0.001***
	Oct	0.19	0.02	<0.001***	Nov×TactT	0.06	0.02	<0.05*
	Nov	-0.01	0.02	0.65	Dec×TactT	0.05	0.02	<0.05*
	Dec	-0.04	0.02	<0.05*				
	TactNT	-0.09	0.03	<0.01**				
	TactT	-0.13	0.03	<0.001***				
	Feb×TactNT	-0.02	0.02	0.39				
	Mar×TactNT	-0.01	0.02	0.59				
	Apr×TactNT	0.05	0.02	<0.05*				
	May×TactNT	-0.01	0.02	0.56				
	Jun×TactNT	-0.04	0.02	0.11				
	Jul×TactNT	-0.07	0.02	<0.01**				
	Aug×TactNT	-0.04	0.02	0.09				
	Sep×TactNT	-0.04	0.02	0.12				
	Oct×TactNT	-0.02	0.02	0.31				
	Nov×TactNT	0.09	0.02	<0.001***				
	Dec×TactNT	0.07	0.02	<0.01**				



**Fig. S.3.2** Monthly variation of elevations (m) occupied by female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in single years 2011-2012-2017. Mean values and standard errors are shown.



**Fig. S.3.3** (A) Effects of monthly mean temperature (°C) on monthly elevations (m) occupied by female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in 2011-2012-2017. (B) Effects of median snow depth (cm) on monthly elevations (m) occupied by female (F), non-territorial male (NT) and territorial male (T) Alpine chamois in 2011-2012-2017.

**Table S.3.3** (a) Effects of monthly mean temperature (T°C) and sex/mating tactic (female, territorial male, non-territorial male) on monthly mean elevations (Elev.month); (b) effects of monthly median snow depth (snow) and sex/mating tactic on monthly mean elevations; (c-e) effects of monthly variation on NDVI values of locations of female, territorial male (T) and non-territorial male (NT) Alpine chamois in 2011, 2012 and 2017. Random effects in each model = Id: individual identities; Year: 2011, 2012, 2017. Results of model selection: variables retained, degrees of freedom, logLikelihood, AICc,  $\Delta$ AICc values and model weight are shown.

Model	Variables retained	df	logLik	AICc	$\Delta$ AICc	Weight
(a) Elev.month	T°C + Tactic + T°C×Tactic + (1 Id) + (1 Year)	9	-4294.0	8606.2	0.00	1.00
(b) Elev. month	Snow + Tactic + Snow×Tactic + (1 Id) + (1 Year)	9	-4380.5	8779.4	0.00	1.00
(c) Females	Month + (1 Id) + (1 Year)	15	-888.2	1810.9	0.00	1.00
(d) T males	Month + (1 Id) + (1 Year)	15	-1109.1	2252.0	0.00	1.00
(e) NT males	Month + (1 Id) + (1 Year)	15	-1206.5	2446.6	0.00	1.00

**Table S.3.4** Parameters estimated from the best models on (a) effects of monthly mean temperature (T°C) and sex/mating tactic (female, territorial male T, non-territorial male NT) on monthly mean elevations (Elev.month); (b) effects of monthly median snow depth (snow) and sex/mating tactic on monthly mean elevations, for female and male Alpine chamois in 2011, 2012 and 2017 ( $\beta$ : coefficient, SE: standard error, p-value). Reference category for categorical predictor Tactic: female.

	Model	Variables	$\beta$	SE	p-value
(a)	Elev.month	Intercept	7.71	0.02	<0.001***
		T°C	0.02	<0.01	<0.001***
		TacticNT	-0.07	0.02	<0.01**
		TacticT	-0.14	0.02	<0.001***
		T°C×TacticNT	< -0.01	<0.01	<0.001***
		T°C×TacticT	-0.01	<0.01	<0.001***
		(b)	Elev.month	Intercept	7.86
	Snow	-1.57		8.65	<0.001***
	TacticNT	-1.01		2.61	<0.001***
	TacticT	-2.30		2.77	<0.001***
	Snow×TacticNT	1.41		1.22	0.25
	Snow×TacticT	8.18		1.25	<0.001***

**Table S.3.5** Parameters estimated from the best models of the effects of monthly variation of NDVI values of the locations used by female, territorial male (T) and non-territorial male (NT) Alpine chamois, in 2011-2012-2017 ( $\beta$ : coefficient, SE: standard error, p-value). Reference category for categorical predictor Month: May.

Model	Variables	$\beta$	SE	p-value	Model	Variables	$\beta$	SE	p-value
Females	Intercept	1730.07	269.90	<0.001***	T males	Intercept	3395.05	344.86	<0.001***
	Jan	-1689.98	333.97	<0.001***		Jan	-3174.54	432.98	<0.001***
	Feb	-2089.44	417.05	<0.001***		Feb	-3009.37	468.66	<0.001***
	Mar	-1807.81	359.91	<0.001***		Mar	-3063.62	520.27	<0.001***
	Apr	205.06	318.83	0.52		Apr	-1964.31	447.72	<0.001***
	Jun	1222.50	307.14	<0.001***		Jun	2076.02	432.98	<0.001***
	Jul	1970.83	317.76	<0.001***		Jul	2441.09	439.80	<0.001***
	Aug	1361.31	311.63	<0.001***		Aug	1547.96	457.09	<0.001***
	Sep	833.73	307.14	<0.01**		Sep	1268.79	432.98	<0.01**
	Oct	732.74	311.63	<0.05*		Oct	241.59	457.09	0.60
	Nov	-1222.78	316.89	<0.001***		Nov	-2919.45	457.79	<0.001***
	Dec	-1329.59	316.89	<0.001***		Dec	-3049.07	432.98	<0.001***
NT males	Intercept	2967.70	313.04	<0.001***					
	Jan	-2935.37	404.50	<0.001***					
	Feb	-2612.69	423.14	<0.001***					
	Mar	-3094.37	514.64	<0.001***					
	Apr	-1780.84	397.28	<0.001***					
	Jun	1508.84	405.02	<0.001***					
	Jul	1631.06	397.28	<0.001***					
	Aug	891.08	404.38	<0.05*					
	Sep	675.39	390.52	0.09					
	Oct	-159.79	404.38	0.69					
	Nov	-2788.68	390.52	<0.001***					
	Dec	-2778.90	396.68	<0.001***					

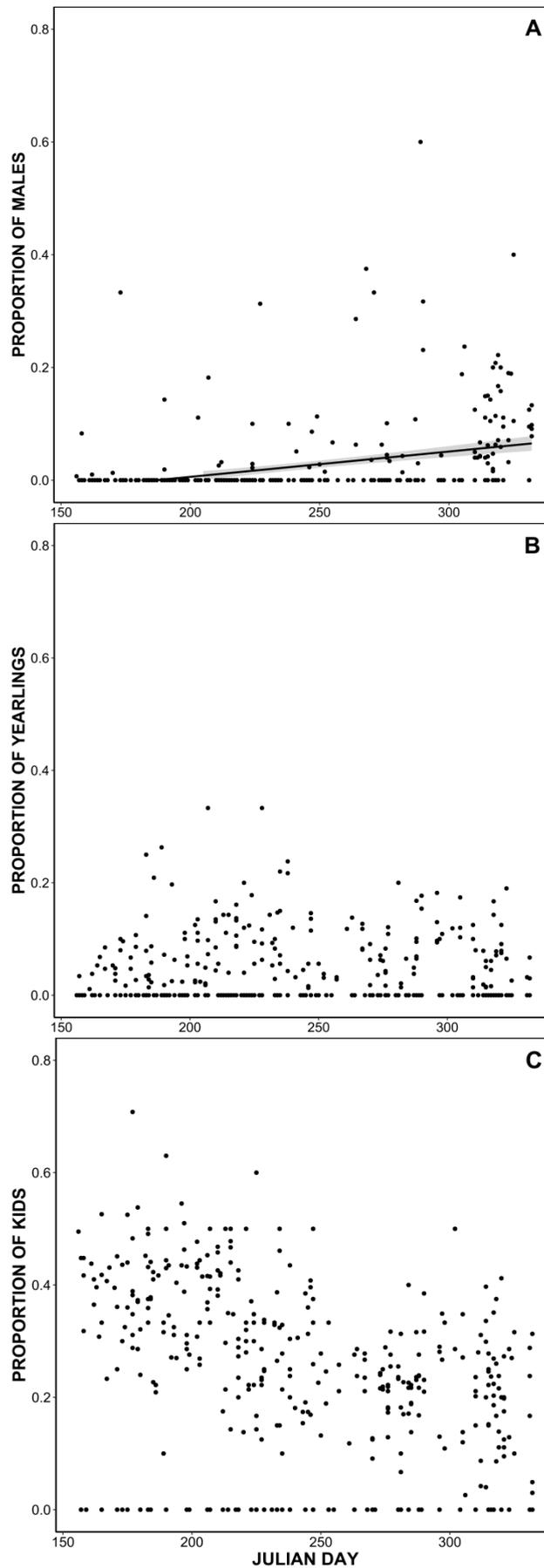
## Supplementary material Chapter 4

**Table S.4.1** Effects of seasonality on grouping pattern in adult female Alpine chamois: summaries of selected models of effects of Julian day and mean group size on proportion of males, yearlings and kids in the group, of female Alpine chamois, in 2017-2018. Random effects in each model = Id: individual identities, Year: 2017, 2018, Month. Result of model selection: variables retained, degrees of freedom, logLikelihood, AICc,  $\Delta$ AICc values and model weight are shown.

Model	Variables retained	df	logLik	AICc	$\Delta$ AICc	Weight
proportion of males	julian day + (1 Id) + (1 Year) + (1 Month)	6	4438.3	-8864.3	0.00	1.00
proportion of yearlings	group + (1 Id) + (1 Year) + (1 Month)	6	3047.4	-6082.6	0.00	1.00
proportion of kids	group + (1 Id) + (1 Year) + (1 Month)	6	897.6	-1783.1	0.00	1.00

**Table S.4.2** Parameters estimated from the best models on the effects of Julian day and mean group size on proportion of males, yearlings and kids in the group, of female Alpine chamois, in 2017-2018 ( $\beta$ : coefficient, SE: standard error, p-value).

Model	Variables	$\beta$	SE	p-value
proportion of males	intercept	-5.09	0.48	<0.001***
	julian day	<0.01	<0.01	<0.01**
proportion of yearlings	intercept	-3.57	0.17	<0.001***
	group	0.02	<0.01	<0.001***
proportion of kids	intercept	-2.27	0.27	<0.001***
	group	0.07	<0.01	<0.001***



**Fig. S.4.1** Proportion of males (a), yearlings (b) and kids (c) in groups of female Alpine chamois, in 2017-2018, in relation to Julian day. The black line and the shaded grey area indicate the predicted relationship and its standard error, when the variation through Julian day was supported by the model.



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