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Age, seasonality, and correlates of aggression in female Apennine chamois

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Abstract

Intrinsic and environmental stressors, such as age and seasonality, may influence social behavior and endocrine levels in gregarious foragers, but little is known about how season and age affect both behavioral and physiological responses. We evaluated seasonal/age variation of aggression and vigilance, and seasonal/age variation of endocrine levels (fecal cortisol and testosterone metabolites), in a gregarious herbivore, the Apennine chamois *Rupicapra pyrenaica ornata*. We examined a period of decreasing resource abundance and maternal care from July to October, a key period for nursing, weaning, and early growth of offspring. Aggression rate, vigilance, and cortisol levels decreased throughout July–October, while aggression intensity showed the reverse. Aggression intensity peaked when chamois were on the most nutritious vegetation patches. Dominance increased with age, and prime-aged females (4–8 years old) showed higher cortisol and testosterone levels and were involved in aggressive interactions more often than subadult or older females. Our findings suggest that, in early summer, when nursing effort is the greatest, selection of nutritious food patches leads to frequent encounters between female chamois, enhancing aggression rate, vigilance, and endogenous stress response. The progressive decrease in food abundance throughout July–October triggers competition for scarce resources and increased intensity of aggression. Most likely, the energetic demands of lactation and offspring guarding were key determinants of behavioral and physiological stress of female chamois. Our results suggest a multi-factorial compromise between reproductive state and stress levels, in a group-living species.

Significance statement

The cost of motherhood: in female chamois, aggression, vigilance, and stress peak during lactation, despite abundant food resources. In females, aggression and dominance increase with age. A multi-factorial compromise between reproductive stage and stress may be necessary in a group-living animal. We suggest that motherhood is a stressful event for female chamois.

Keywords Aggression · Vigilance · Stress · Cortisol · Testosterone · Social dominance

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Introduction

The investigation of proximate physiological processes under- lying behavior may help to understand its evolution, because those processes may affect the relative fitness of individuals (Bonier et al. 2009; Boonstra 2013). In gregarious species, competition may involve a trade-off with safety (fish: Hoare et al. 2004; birds: Caraco 1979; mammals: Molvar and Bowyer 1994), and agonistic interactions between individuals are frequent. Various agonistic interactions, ranging from rit- ualized dominance displays to aggressive threats, are involved in establishing dominance, which, in turn, allows reducing dangerous fighting (Rowell 1974; Gauthereaux 1978; Syme and Syme 1979). In gregarious foragers, aggression is also driven by competion for food, reflecting feeding interference (fish: Noël et al. 2005; birds: Goldberg et al. 2001; mammals: Monaghan and Metcalfe 1985). An endogenous response to stress could be related to intraspecific aggression (DeVries et al. 2003), with a transient acute stress response related to ag- gressive events (Soma et al. 2000; Clement et al. 2005). Conversely, the long-term effects of competition (e.g., Krebs et al. 2001; but see Le Saout et al. 2016), social density/ crowding (e.g., Viblanc et al. 2014; but see Michelena et al. 2012) and establishment of dominance relations (e.g., Sapolsky 1983; but see Taillon and Côté 2008) can lead to a chronic increase of basal stress levels.

Aggressive behavior may also interfere with group dy- namics, by increasing vigilance to avoid attacks by con- specifics (Treves 2000; Favreau et al. 2010, 2018). Hence, although vigilance is mainly an antipredator behavior (Lima 1987; Frid 1997), it is also expected to reflect in- dividual responses to social stressors such as the presence or rank of competitors

(Beauchamp 2015a). If so, vigi- lance may reflect endogenous stress (Michelena et al. 2012; Voellmy et al. 2014; but see Thierry et al. 2014).

In vertebrates, a number of studies have related adre- nocortical activity to stress (Romero 2002, for a review) and have emphasized the role of androgens in promoting aggressive behavior (Adkins-Regan 1981, for a review). Patterns of endocrine levels are species-specific (Adkins- Regan 1981; Reeder and Krämer 2005; Keay et al. 2006) and vary greatly according to endogenous and environ- mental factors (e.g., Finch and Rose 1995; Wingfield et al. 1997; Romero 2002; Millspaugh and Washburn 2004; Wingfield 2005; Keay et al. 2006). Short-term production of glucocorticoids and androgens is adaptive, because it mediates behavioral adjustments to the environment (Wingfield et al. 1998), whereas the effect of a prolonged increase of endocrine levels remains uncertain. A long- term increase of glucocorticoids/androgens may underlie chronic stress and/or immunosuppression, potentially re- ducing survival and reproductive success (Folstad and Karter 1992; Sapolsky 1992; Möstl and Palme 2002; Bonier et al. 2009). Alternatively, chronic stress may also underlie adaptive mechanisms (Boonstra 2013). Studies considering both hormonal and behavioral responses to environmental determinants could increase our under- standing of their effects on animal populations.

In temperate ecosystems, seasonality is a major deter- minant of variation in social behavior and activity of individuals, because it affects availability of resources (e.g., Albon and Langvatn 1992). As competitive inter- actions between individuals are influenced by resource abundance (Sirot 2000), aggression and vigilance should also vary seasonally (Stokes 1962; Taillon and Côté 2007; Favreau et al. 2018). In addition, endocrine levels can be driven by seasonal mechanisms/events such asfood availability (Kitaysky et al. 1999) or reproduction (Pavitt et al. 2015, 2016).

Aspects of social behavior such as aggression and vigi- lance, and their endocrine correlates, are also expected to change according to age and/or social status of individuals (DeVries et al. 2003; Reeder and Krämer 2005; Bartoš et al. 2010; Beauchamp 2015b). Among various *taxa*, dominance is positively correlated with both age and androgen level (fish: Taves et al. 2009; birds: Searcy and Wingfield 1980; mam- mals: Pelletier et al. 2003; but see also Wingfield et al. 1990, for the challenge hypothesis). It is unclear, however, how so- cial rank affects the response to stress: glucocorticoid secre- tion can be higher either in subordinate individuals or in dom- inant ones (reviews: Creel 2001; Goyman and Wingfield 2004; Koolhaas et al. 2011).

The assessment of endocrine and behavioral re- sponses to both intrinsic and environmental stressors such as age and seasonality should increase our under- standing of adaptations of wild species, especially those living in highly seasonal ecosystems. Yet, few studies have examined both behavior and physiology in wild animal populations.

We evaluated how season and age affected key aspects of social behavior and endocrine levels in a mountain-dwelling herbivore, the Apennine chamois *Rupicapra pyrenaica ornata*, in the central Apennines (Italy). In these strongly sea- sonal mountainous environments, cold and snow cover limit the availability of food for herbivores during the long winter. High-quality forage is only available during the short 3–4- month green-up season and usually decreases from summer to autumn (Pettorelli et al. 2007; Villamuelas et al. 2016). In summer, access to high-quality food is essential, especially for juveniles that have to grow and store fat reserves for winter survival (Festa-Bianchet 1988; Lenihan and Van Vuren 1996; Côté and Festa-Bianchet 2001a; Pettorelli et al. 2007). Lactation creates a significant energy cost for adult females, who also have to recover from gestation (Gittleman and Thompson 1988; Therrien et al. 2007). The best food re- sources for Apennine chamois are vegetation patches domi- nated by *Trifolium thalii* and other forbs (Ferrari et al. 1988; Ferretti et al. 2015). Depletion of these patches can reduce offspring survival (Lovari et al. 2014; Ferretti et al. 2015), with negative effects on population dynamics (Ferretti et al. 2015; Scornavacca et al. 2016). The phenology of forbs in the high grasslands of the Apennines shows the typical seasonal trend of vegetation growth in temperate habitats: pasture qual- ity increases from the green-up after snow melt, in late May– early June, to a peak in July, and then decreases from late August to autumn/early winter (Ferrari et al. 1988; Primi et al. 2016). Accordingly, maternal care by female chamois peaks in early summer and decreases with approaching au- tumn (Scornavacca et al. 2016, 2018; see also Ruckstuhl and Ingold 1994, for Northern chamois *R. rupicapra*).

To assess the effects of seasonality and age, we examined intraspecific aggression and vigilance behavior of female chamois throughout summer–autumn, during the temporal de- crease of resource abundance and nursing effort, and in rela- tion to age. To evaluate seasonal/age variation of proximate determinants of behavior, we also determined levels of fecal cortisol and fecal testosterone metabolites of females, as phys- iological indicators related to basal stress levels (Zwijacz-Kozica et al. 2013; Corlatti et al. 2014) and, possibly, to ag- gressiveness (Corlatti et al. 2012).

The seasonal decrease in quantity and quality of food could be the major determinant of social behavior and of endocrine correlates in female chamois. As competitive interactions be- tween individuals are expected to increase when resources are limited (Sirot 2000), intraspecific aggression could increase from summer through autumn, leading to greater vigilance and higher endocrine levels (hypothesis 1). If so, we predicted that, from July to October, chamois would show the follow- ing: (1a) an increasing rate and intensity of aggressive inter- actions among females; (1b) an increasing rate and duration of vigilance behavior; (1c) increasing levels of fecal testosterone and cortisol metabolites. Alternatively, the seasonal decrease in nursing behavior could be the major driver of behavior and endocrine levels in females (Pavitt et al. 2016). As females should maximize access to resource because of high energetic demands of lactation, feeding interference could decrease from summer through autumn (hypothesis 2). If so, we pre- dicted that, from July to October, chamois would show the following: (2a) a decreasing rate and intensity of aggressive interactions between females; (2b) a decreasing rate and dura- tion of vigilance

behavior; (2c) decreasing levels of fecal tes- tosterone and cortisol metabolites.

Social behavior and endocrine correlates are also expected to be influenced by social rank, which increases with age in female chamois (Lovari and Rosto 1985; Locati and Lovari 1991), leading to two sets of alternative predictions (Bstress of dominants^ versus Bstress of subordinates^ hypotheses; Creel 2001). Dominant, adult females, could afford potentially cost- lier aggression rather than ritualized patterns (Lovari 1985), to assert or reinforce their rank (Eccles and Shackleton 1986; Lovari et al. 2015), as well as higher androgen levels (Searcy and Wingfield 1980; Pelletier et al. 2003). They could also increase vigilance to monitor potential competitors, be- cause of increased aggression to maintain their status (Hall 1960; Stahl et al. 2001). In turn, they could tolerate the greatest endogenous stress, revealing the cost of dominance (hypothesis 3; Creel 2001). If so, we predicted that adult fe- male chamois would show the following: (3a) the greatest use of direct forms of aggression, i.e., threats; (3b) the greatest rate and duration of vigilance; (3c) the highest fecal testosterone and fecal cortisol levels. Alternatively, dominant, adult fe- males could show lower androgen levels (Wingfield et al. 1990; Taillon and Côté 2008) and/or lower aggressiveness

(Fairbanks 1994; Côté 2000) than subadult, lower-ranking females. However, displacements by dominant individuals could lead to increased vigilance (Keverne et al. 1978; Waite 1987) and endogenous stress for subadults, thus revealing costs of subordination (hypothesis 4; Creel 2001). If so, we predicted that adult female chamois would show the following: (4a) the lowest use of direct forms of aggression, i.e., threats; (4b) the lowest rate and duration of vigilance; (4c) the lowest fecal testosterone and fecal cortisol levels.

Methods

Study area and population

Our study was conducted in alpine meadows of Mt. Meta (*c*. 30 ha, *c*. 2100–2242 m asl), in the Abruzzo, Lazio and Molise National Park (ALMNP; Central Apennines, Italy), through- out July–October 2014 and 2015. This area lies in the temper- ate oceanic bioclimate, lower orotemperate thermotype, and lower/upper humid ombrotype (Pesaresi et al. 2014). There is no dry season and snow cover usually lasts from late November to May–June (Bruno and Lovari 1989). Vegetation cover includes forb-dominated patches (*c*. 24%, e.g., *Trifolium* spp. and *Anthyllis vulneraria*), palatable graminoids (*c*. 39%, mainly *Festuca* spp.), unpalatable graminoids (*c*. 1%, *Brachypodium genuense*), and rocks/ screes with sparse vegetation (*c*. 36%) (Ferretti et al. 2015).

Female chamois give birth in May (Lovari 1977). Mixed group of chamois with adult females, yearlings, and juveniles graze on alpine meadows from late spring–early summer (af- ter parturition and snowmelt) to late autumn–early winter (Lovari and Cosentino 1986; Bruno and Lovari 1989). Nursing lasts until October, at least (Scornavacca et al. 2016, 2018). Male chamois are solitary outside the rut, mainly living in forests, at lower altitudes (Lovari and Cosentino 1986). Previous observations reported that only 4–5 solitary males inhabited our study area in 1970s–1980s, with no mixed groups of chamois (SL, personal observations). Nowadays, a substantial chamois herd is present (Ferretti et al. 2015). For groups of females, yearlings, and juveniles, the maximum number of individuals observed at the same time was 69 and 78 in 2014 and 2015, respectively.

Red deer *Cervus elaphus* occasionally move through the area, but overlap little with the chamois altitudinal range (Ferretti et al. 2015). Potential predators in our study area are gray wolf *Canis lupus*, brown bear *Ursus arctos*, and golden eagle *Aquila chrysaetos* (which may prey on juve- niles), although predation on chamois is negligible (Patalano and Lovari 1993; Ciucci et al. 2014; Scornavacca and Brunetti 2015; Baruzzi et al. 2017). For further details of our study area, see Ferretti et al. (2015).

Behavioral data

Behavioral observations were conducted from July through October, in 2014 and 2015, from dawn to dusk (05:00–20:00). We performed *c*. 7 h of observations/day, for at least 7 days/month. We attempted to balance behavioral sampling across months (July: 63 h, August: 62 h, September: 50 h, October: 51 h) and across periods of the day (dawn to midday: 120 h, midday to dusk: 96 h). Chamois were observed using binoculars (Nikon 10x30, Zeiss 15x70) or spotting scopes (Nikon 20-60x), at distances of at least 200 m, depending on terrain and range of vision. In our study area, chamois were habituated and could be approached to within a few meters without moving away from the observer or showing alert be- havior (staring in the direction of the observer or orientating their ears to him/her, or raising the tail; Lovari 1985). We avoided recording data whenever we felt that the animals were reacting to our presence (cf. Winnie Jr and Creel 2007). It was not possible to record data blind because our study involved focal animals in the field.

Intraspecific aggression

Aggressive interactions among females (≥ 2 years old) were assessed through continuous focal-group sampling (Altmann 1974) by 2–3 observers, on foraging groups of females, year- lings, and juveniles. Among group-living species, aggressive interactions should be relatively rare events within the overall time budget (e.g., birds: Caraco 1979; mammals: Molvar and Bowyer 1994). Dawkins (2007, p. 93) suggests longer sam- pling bouts to record infrequent events. Thus, we observed each focal group for at least 30 min, depending on group movements and visibility. Whenever possible, when the group did not split, we continued observing the focal group up to a maximum of *c*. 6 h. During focal-group observations, we re- corded group size/structure (number of adult and subadult females; number of yearling; number of juveniles; number of males) and number of foraging females (percentage of ac- tive females) every 5 min (sampling periods), through instan- taneous scan sampling (Altmann 1974). We considered a group as Bat least two animals staying in sight and less than 40 m apart from each other at the time of observation^ (e.g., Krämer 1969; Bruno and Lovari 1989). We recorded all oc- currences of interactions between females during each 5-min sampling interval, in a portable dictaphone. For each aggres- sion event, we also recorded date and time (hh:mm), behavior patterns used by each individual during the interaction, age class of dominant and subordinate chamois, type of interaction (see below), and the type of vegetation (forbs; palatable graminoids; sparse vegetation on cliff/scree) where the inter- action occurred. Four age classes were assessed according to Lovari (1985) by estimating the ratio between horn height and ear length (subadult, i.e., 2–3 years old; 4–5 years old; 6–8 years old; ≥ 9 years old). This procedure has been validated on individuals of known age (Lovari 1985). The dominant individual was defined as the female who performed the last dominance pattern and/or did not withdraw (Locati and Lovari 1991; Corlatti et al. 2012). Conversely, the subordinate was considered as the female who escaped and/or responded with a submissive pattern (Locati and Lovari 1991; Corlatti et al. 2012). As the aggressor was not always dominant, we also recorded who initiated the interaction. The type of interaction was defined as a single aggression (a dominance pattern followed by an immediate submission/escape by the oppo- nent), or sequence (a series of consecutive dominance behav- ior patterns performed by both opponents). The latter case implied that the attacked individual reacted to the aggressor; thus, we considered it as an escalation. Dominance and sub- missive behavior patterns performed by female chamois were recorded following Lovari (1985). Dominance patterns in- clude both indirect and direct forms of aggression to intimidate/displace rivals (Lovari 1985). Indirect forms in- volve visual dominance postures (Lovari 1985). Direct threats such as approaches/chases are the least ritualized and may include attempts at physical contact, although this is rare (Locati and Lovari 1990). Submissive patterns include with- drawal and several ritualized, subordinate postures, e.g., low stretch and reactive urination (Lovari 1985). We did not record vocal-based patterns because of the complexity in their detec- tion and interpretation (Lovari 1985). Dominance behavior patterns performed by female chamois were divided into di- rect and indirect forms of aggression (hereafter *threats* and *displays*, respectively; e.g., Schaller 1977; Walther 1974), to evaluate the intensity of interactions. Threats were considered more aggressive than displays (Walther 1974; Schaller 1977; Lovari et al. 2015; in Apennine chamois: Lovari 1985).

Vigilance behavior

Vigilance behavior of foraging females was assessed by con- tinuous focal-animal sampling (Altmann 1974), by 2–3 ob- servers. As vigilance events are more frequent than agonistic events (e.g., birds: Caraco 1979; mammals: Molvar and Bowyer 1994), we used shorter sampling periods to record them (Dawkins 2007, p. 93). Observations were conducted in 10-min bouts (e.g., Favreau et al. 2018), and each bout was divided into 1-min sampling intervals, to record variation of group size/structure. Group size and structure (number of adult and subadult females; number of yearlings; number of juveniles; number of males) as well as distance to the nearest cliff (i.e., distance from escape terrain, to account for preda- tion risk: 0–25 m; 25–75 m; > 75 m) were assessed by instan- taneous scan sampling (Altmann 1974). We recorded the number of head lifts performed by a female chamois during each 1-min sampling interval. We considered a head lift when a female interrupted grazing and raised her head above her

shoulders while scanning (e.g., Lipetz and Bekoff 1982). For each head lift, we recorded date, time (hh:mm), duration (sec- onds), and type (*chewing*: the individual keeps on chewing while scanning; *no chewing*: the individual does not chew while scanning; *indeterminate*: we could not see the mouth of the individual). Chewing was used to evaluate the cost of vigilance: head lifts where individuals did not keep on chewing are expected to interfere with foraging processes more than those where chewing continues (e.g., Underwood 1982; Fortin et al. 2004; McDougall and Ruckstuhl 2018). We avoided recording vigilance behavior on the same individual in the same day: whenever possible, we observed chamois that could be distinguished by their respective positions on the slope (Frid 1997), while another observer helped to follow those who had already been sampled. Morphological details (horn patterns, e.g., broken horns; coat/color features, e.g., scars/spots; Lovari and Rolando 2004, p. 78), visible at close range, helped to further decrease the probability of recording data from the same individual repeatedly in the same day (Ferretti et al. 2014, 2015; Lovari et al. 2014).

Endocrine data

The assessment of fecal hormone metabolites can provide unbiased results as it does not involve stressing the animal (Millspaugh and Washburn 2004; Sheriff et al. 2011). Furthermore, this non-invasive tool provides information on long-

term hormonal levels of wild species (Millspaugh and Washburn 2004; Sheriff et al. 2010).

We collected fresh fecal samples from subadult and adult female chamois to measure the concentrations of fecal androgen (FAMs) and cortisol (FCMs) metabolites as hormonal indicators of aggressiveness and stress, re- spectively (cf. Southern chamois: Dalmau et al. 2007; Northern chamois: Corlatti et al. 2012, 2014; Zwijacz- Kozica et al. 2013; Hadinger et al. 2015). Fresh fecal samples were collected from July to October 2015, imme- diately after we observed defecation. We stored samples in a portable freezer box, which prevented changes be- cause of air temperature and immunoreaction of metabo- lites (Möstl et al. 1999). We recorded date, time (hh:mm), and age class of female chamois. Fecal samples were fro- zen at − 20 °C as soon as back from the field, no later than 10 h from collection (Corlatti et al. 2012, 2014; Ezenwa et al. 2012). We tried to balance fecal sample collection by month, time of day, and chamois age class. We avoided collecting samples from the same individual in the same day (see above). However, anonymized sam- pling of feces should still provide robust estimates of en- docrine levels of chamois, especially during the non- mating season (Corlatti 2018, for Northern chamois).

Extraction and determination of fecal steroids were con- ducted as previously reported by Pecorella et al. (2016), for fallow deer *Dama dama*. FCMs and FAMs were determined respectively using a multi-species cortisol enzyme immuno- assay kit (K003; Arbor Assays, Ann Arbor, MI) and a multi- species testosterone enzyme immunoassay kit (K032; Arbor Assays, Ann Arbor, MI) both designed to quantitatively mea- sure cortisol and testosterone in dried fecal extracts.

Inter- and intra-assay coefficients of variation were 11.7% and 9.9%, respectively. The FCMs and FAMs test sensitivities were determined by measuring the least amount of hormone standard consistently distinguishable from the zero concentration of standard and were calcu- lated to be 17.3 ng/g feces and 9.92 pg/g feces respective- ly. The mean recovery rates of cortisol and testosterone added to dried feces were 96.7% and 107.6% respectively (N = 8). All fecal samples were analyzed at multiple dilu- tions (1:4, 1:8, 1:16, and 1:32) and all regression slopes were parallel to the standard curve (r^2 = 0.985). According to the manufacturer, the cortisol antibody used to quantify FCM cross reacts 100% with cortisol, 18.8% with dexa- methasone, 7.8% with prednisolone, 1.2% with corticoste- rone, and 1.2% with cortisone. The testosterone antibody cross reacts 100% with testosterone, 56.8% with 5α-dihy- drotestosterone, and 0.27% with androstenedione.

Statistical analyses

We discarded focal-group bouts that lasted less than 15 min from the analysis of aggressive interactions and focal-animal bouts that lasted less than 5 min from the analysis of vigilance. A short bout occurred when the focal group/individual moved away from our sight, or when poor weather limited our range of vision. Overall, we analyzed 77 focal-group bouts to assess female-female aggression (mean ± SE: 2.4 ± 0.2 h of observation/group), 316 focal-animal bouts to assess female vigilance (mean ± SE: 8.1 ± 0.1 min of observation/individual), and 76 fecal samples to assess endocrine correlates.

We investigated seasonal/age variation of female cham- ois social behavior (aggression, vigilance) and hormone levels through generalized linear models and generalized linear mixed models (GLMs and GLMMs, respectively; Bolker et al. 2009). Statistical analyses were conducted ac- cording to the information-theoretic approach (Burnham and Anderson 2002), by evaluating multiple competing a priori hypotheses, for each indicator. Beside seasonality and age, previous studies identified further influencing fac- tors of aggression, vigilance, and hormone levels (Table S1). We could not discard, in advance, any combination of these variables, because all the relevant hypotheses could be biologically meaningful. We performed a model selection to rank all possible models, as each of them could represent a different plausible a priori hypothesis. We modeled nine response variables separately: three indicators concerning aggression, four indicators concerning vigilance, and two endocrine indicators (Table S2). For each indicator, the rel- evant global model included some biologically meaningful fixed effects, which could influence the response variable (Table S2).

We expected that female social behavior and endocrine correlates would be affected by the decreasing gradient of food availability and/or investment in maternal care through summer–autumn, which decrease linearly from July through October (food availability: Ferrari et al. 1988; maternal care: Scornavacca et al. 2016, 2018). A preliminary explorative analysis did not support quadratic variations of our response variables through summer–au- tumn. In turn, to evaluate the role of seasonality, we in- cluded the linear effect of Julian day (i.e., the no. of days elapsed from the first of January) as numeric predictor. The effect of age on aggression, vigilance, and hormones was assessed by including age class as categorical predic- tor (reference category: subadult, i.e., 2–3 years old). The use of actual age as a continuous variable would have been a better predictor than age class, but we used age class to further reduce the probability of a mistake in age assessment.

As feeding interference is influenced by number (Sirot 2000) and activity (Kortet and Hedrick 2007) of competitors, we considered the number of females in a group and the per- centage of active females as numeric predictors of aggression rate. The intensity and outcome of aggression between two opponents can vary with both the type of aggression event (e.g., whether the fight is escalated: e.g., Clutton-Brock et al. 1979) and the resource value (e.g., food quality: Sirot 2000). Consequently, models to assess the intensity/outcome of an aggression also included the aggression type (reference cate- gory: sequence) and the vegetation patch where female cham- ois interacted (reference category: graminoids) as categorical

predictors.

Vigilance is affected by predation risk (Lima 1987; Frid 1997) and mountain ungulates use rocky cliffs/ridges to es- cape from predators (cf. Baruzzi et al. 2017, for Apennine chamois). Vigilance also varies greatly according to group size (Beauchamp 2008). Therefore, models on vigilance be- havior included distance to the nearest cliff (Frid 1997) as categorical predictor (reference category: 25–75 m), and group size as numeric predictor.

Daily activity rhythms of herbivores are bimodal, peaking at dusk/dawn (in *Rupicapra* spp.: Bruno and Lovari 1989; Rüttimann et al. 2008; Darmon et al. 2014; Mason et al. 2014; Brivio et al. 2016; Carnevali et al. 2016; but see Šprem et al. 2015, for forest-dwelling chamois). In addition, potential ecological drivers such as predation risk could vary over the day and further influence behavior. Hormone levels also show circadian rhythms (Breuner et al. 1999; Romero and Remage-Healey 2000; Touma et al. 2003; Millspaugh and Washburn 2004; Reeder and Krämer 2005). In turn, to account for bimodal daily variation of behavioral/endocrine indicators, all global models included both linear and quadratic effects of time of day as numeric predictors. Time of day (hh:mm) was included as hours from midnight. For all the behavioral indi- cators, as they were recorded in two sampling years, we in- cluded year as a categorical predictor (reference category: year 2014), to account for potential inter-annual differences.

When required by the recording procedure, random effects were included. In models of aggression rate, we treated the focal group of chamois as a random intercept, to account for repeated observations conducted on the same group and po- tential unbalanced sampling among groups (van de Pol and Wright 2009, p. 794). In models concerning the outcome and the intensity of aggressions between female chamois, as both response variables were recorded as repeated mea- sures on the same aggressive event, we treated each event as a random intercept. In models on vigilance behavior, we considered the focal female chamois as a random in- tercept, to account for repeated observations conducted on the same individual.

Numeric predictors were standardized according to Gelman (2008), to compare effect size of predictors (i.e., their relative importance). Multicollinearity among predictors was tested for each full model by calculating the variance inflation factor (VIF) for all predictors. All VIF values were < 2, indi- cating no multicollinearity between the explanatory variables (Zuur et al. 2009). VIFs were calculated through the R pack- age *car* (Fox and Weisberg 2011).

Model selection was performed following the minimum Akaike's information criterion, corrected for small samples (AICc: Burnham and Anderson 2002). For each response var- iable, all alternative models, each one representing a plausible, a priori hypothesis, were ranked and weighted from the global model (Table S2). Despite the large number of models evalu- ated (sensu Freedman and Pee 1989), the ratio between the number of variables and the number of observations was small (Table S2). Models with ΔAICc ≥ 4 of the best model, as well as models with an AICc value greater than that of any simpler, nested alternative, were not selected (Table S3).

For each response variable, standardized coefficients of predictors, standard errors, 95% confidence intervals, and var- iance of random effects were estimated for the top-ranked model (Table S3). The significance of predictors was assessed by checking whether 95% confidence intervals included 0. Model selection, GLMs, and GLMMs were performed through the R packages *MuMIn* (Bartoń 2012), *stats* (R Core Team 2013), *VGAM* (Yee 2015), and *glmmADMB* (Bolker et al. 2012).

Data availability

The datasets analyzed during the current study are available from the corresponding author on rea- sonable request.

Results

Intraspecific aggression

All the indices of aggressive behavior varied throughout the study period, although the effect of Julian day was smaller compared to other predictors (Table 1). Female-female aggres- sion rate decreased over summer–autumn (Fig. 1a; Table 1a). Aggression rate increased with increasing number of females in the group, which had the greatest effect size, and with the proportion of active females (Table 1a). Time of day did not influence the frequency of aggression.

The proportion of threats increased over summer–autumn (Fig. 1b; Table 1b). Time of day had the greatest effect on the intensity of aggression: the probability to perform a threat peaked in the central part of the day. Vegetation type influ- enced aggression intensity: female chamois used more often threats when on patches of forbs rather than on palatable graminoids or cliffs with sparse vegetation (Table 1b). Threats were more likely to be performed in single aggression events, while displays were the most used when an opponent reacted to the attacking individual. Age class of the sender greatly influenced the intensity of aggression, but relative age of the recipient did not: subadult females sent threats as often as displays, whereas adult females performed more threats than subadults (Fig. 2a; Table 1b).

For an individual, the outcome of an aggression was only influenced by age class: the older the female, the greater the probability to win (Fig. 2b; Table 1c), which increased from individuals aged 2–3 and 4–5 years (*c*. 20% of won interac- tions, with no difference between these age classes) to those aged 6–8 years (*c*. 50%) and to ≥ 9-year-old females (*c*. 80%). Age class affected the probability of being involved in ag- gressive interactions: females aged 6–8 years were observed in significantly more aggressions than expected from their relative occurrence in the population (Table S4a) and interacted more often than expected with females aged ≥8 years (Table S4b).

Vigilance behavior

All vigilance indicators but one were influenced by Julian day, but not by age class (Table 2). Head lift rate decreased from July through October (Fig. 1c; Table 2a) and did not differ among age classes (Fig. 2c; Table 2a). Time of day had the greatest effect on head lift rate, which peaked at crepuscular periods. The frequency of head lifts decreased as group size increased, and it was lower in 2015.

In the majority of cases (*c*. 90%; $N = 929$ head lifts), we could assess whether the female was chewing or not. The probability to stop chewing during scans decreased through- out July–October and was positively affected by group size. (Table 2b). Year of sampling had the greatest effect size on this indicator: the occurrence of non-chewing vigilance was great- er in 2015.

Table 1 Parameters estimated from the top-ranked models on aggres- sive behavior (β: standardized coefficient, SE: standard error; CI: confi- dence interval). Variance of random factors is also shown. Asterisks mark the confidence intervals which do not include 0. Effect of Julian day and age class, when present, is shown in italic. The reference categories of categorical predictors are: single aggression (for aggression type), 2– 3 years (for age class); graminoids (for vegetation patch)

Indicator	Predictor	β	SE	95% CI
(a) Aggression rate (focal group) variance = 0.36770	Intercept	− 1.37896	0.09555	− 1.56623; − 1.19168 *
	Julian day	*− 0.00031*	*0.00013*	*− 0.00056; − 0.00005* *
	Time	0.28199	0.14516	− 0.00252; 0.56650
	No. females in group	0.01380	0.00205	0.00978; 0.01782 *
	% active females	0.00105	0.00013	0.00079; 0.00130 *
(b) Aggression intensity (aggression event) variance = 0.00747	Intercept	0.65244	0.05117	0.55215; 0.75273 *
	Julian day	*0.00004*	*0.00001*	*0.00002; 0.00006* *
	Time	0.38675	0.18155	0.03091; 0.74259 *
	$Time^2$	− 0.39879	0.17847	− 0.74859; − 0.04899 *
	Aggression type (sequence)	− 0.11440	0.02058	− 0.15474; − 0.07406 *
	Sender age class (4–5 years)	*0.31203*	*0.05811*	*0.19813; 0.42592* *
	Sender age class (6–8 years)	*0.29726*	*0.05211*	*0.19512; 0.39939* *
	Sender age class (≥ 9 years)	*0.28351*	*0.05181*	*0.18196; 0.38506* *
	Vegetation patch (forbs)	0.04595	0.02259	0.00167; 0.09023 *
	Vegetation patch (rocks)	− 0.00094	0.02751	− 0.05486; 0.05298 *
(c) Aggression outcome (aggression event) variance < 0.0000	Intercept	0.13881	0.03750	0.06531; 0.21231 *
	Winner age class (4–5 years)	*0.01028*	*0.04705*	*− 0.08194; 0.10250*
	Winner age class (6–8 years)	*0.38450*	*0.04717*	*0.29204; 0.47695* *
	Winner age class (≥ 9 years)	*0.74041*	*0.04469*	*0.65282; 0.82800* *

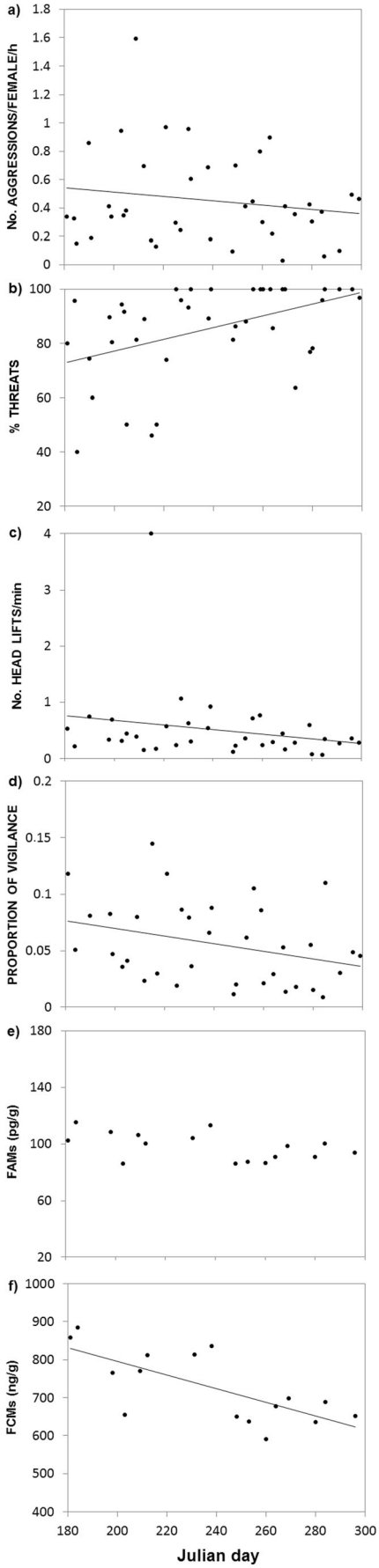
a)
No. AGGRESSIONS/FEMALE/h
b)
% THREATS
c)
No. HEAD LIFTS/min
d)
PROPORTION OF VIGILANCE
e)
FAMs (pg/g)
f)
FCMs (ng/g)
Julian day

Fig. 1 Seasonal variation in daily a aggression rate between chamois, b proportion of threats performed by a female, c female vigilance rate, d proportion of time spent vigilant by a female, e female FAMs concentration, and f female FCMs concentration. A regression line was added when variation through Julian days was supported by GLMMs

The duration of head lifts did not vary with season (Table 2c). The proportion of costly head lifts performed in vigilance bouts had the greatest effect on this indicator: the greater the percentage of non-chewing head lifts, the greater the mean duration of vigilance. Group size did not influence this index, which peaked at dusk. The duration of head lifts was affected nonlinearly by distance from escape terrain: it did not vary between 0 and 75 m, but increased on grazing patches at least 75 m from the nearest cliff.

Time spent in vigilance decreased throughout summer–au- tumn (Fig. 1d; Table 2d) and did not differ between age classes (Fig. 2d; Table 2d). Time of day had the greatest effect on this indicator, which peaked at crepuscular periods and was lower in 2015.

Hormone levels

Levels of fecal androgen metabolites (FAMs) did not vary throughout the study period (Fig. 1e; Table 3a), whereas those of fecal cortisol metabolites (FCMs) decreased from July through October (Fig. 1f; Table 3b).

Age class showed the greatest effect size on fecal hormone metabolites (Table 3). Four-to-five and 6–8-year-old females showed both the highest FAMs and FCMs, whereas subadult and older females showed lower levels of both endocrine in- dices (Fig. 2e, f; Table 3). Time of day had no effect on fecal metabolites.

FAMs and FCMs measured on the same sample were pos- itively correlated (Fig. 3; two-tailed t test: $N = 76$; $t = 14.885$; df = 74; $r = 0.86$; $p < 0.0001$).

Discussion

Our results show that social behavior of chamois and its endocrine correlates differed both throughout the sum- mer–autumn progression and between age classes, although the effect size of seasonality and age depended on the indi- cator and varied according to other influencing factors. The frequency of aggression between grazing females mainly increased both with the number and activity of potential competitors, suggesting the occurrence of feeding interfer- ence over resources. In contrast to our prediction (1a), the rate of aggression between females decreased throughout summer–autumn, but intensity of aggression showed the opposite pattern (our prediction, 1a). Thus, aggressions were more frequent when both quality and quantity of re- sources were the highest (Ferrari et al. 1988; Ferretti et al. 2015), but females performed a greater proportion of threats than dominance displays, when resources became poorer. The best food resources for Apennine chamois include snowbed vegetation dominated by *Trifolium thalii* and other nutritious forbs, which grow in patches, on slightly acidic terrain with prolonged snow cover (Ferrari et al. 1988). Lactation peaks in summer (Scornavacca et al. 2016, 2018), which imposes heavy energetic demands upon fe- males (Gross et al. 1995; Ruckstuhl et al. 2003; Froy et al. 2016; Pavitt et al. 2016). In summer, females select high- quality foraging sites (Ferrari et al. 1988), which may in- crease the probability of having to challenge a lactating conspecific over a rich food resource (Boness et al. 1982; McDonough 1994). Subordinate individuals could quickly withdraw to other nutritious patches, possibly explaining the lower occurrence of threats in summer than in autumn. Conversely, after nursing/weaning and before the winter rigors, females could escalate to direct forms of aggression over a scarcer resource, explaining the increase in aggres- sion intensity throughout summer–autumn. Accordingly, Bruno and Lovari (1989) observed that female chamois in- creased the rate of steps caused by social displacements in autumn compared to summer, which may reflect a response to more intense aggressive interactions. These results sug- gest that investment in maternal care and seasonal variation of food availability may have contributed to shape different aspects of female aggressiveness, providing partial support to both our predictions (1a, 1b). Another explanation for the higher rate of aggression when food was more abundant might be that some vegetation patches were closer to anti- predator escape terrain such as cliffs, thus reducing preda- tion risk. Aggression rate between females might have in- creased in summer, when newborns were more vulnerable, to access safer food patches (Kim et al. 2004).

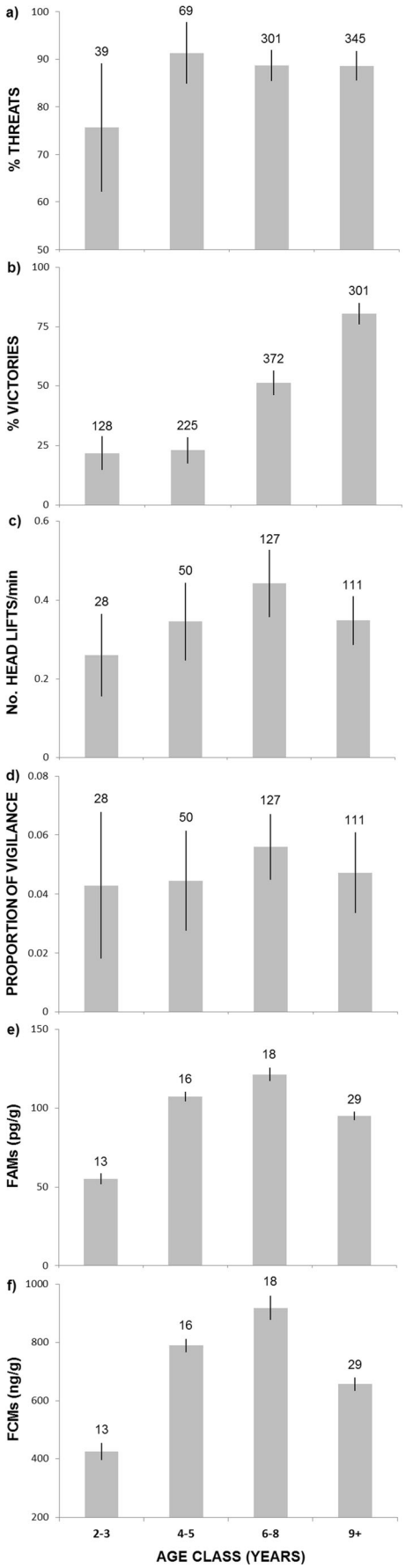
a)
% THREATS
100
90
80
70
60
50
39
69
301
345
b)
% VICTORIES
100
75
50
25
0
128
225
372
301
c)
No. HEAD LIFTS/min
0.6
0.4
0.2
0
28
50
127
111
d)
PROPORTION OF VIGILANCE
0.08
0.06
0.04
0.02
0
28
50
127
111
e)
FAMs (pg/g)
150
100
50
0
13
16
18
29
f)
FCMs (ng/g)
1000
800
600
400
200
13
16
18
29
2-3
4-5
6-8
9+
AGE CLASS (YEARS)

Fig. 2 Age-related variation of a proportion of victories in interactions between female chamois, b proportion of threats performed by a female, c female vigilance rate, d proportion of time spent vigilant by a female, e female FAMs concentration, and f female FCMs concentration. Error bars/numbers indicate the bootstrapped 95% confidence intervals and sample size, respectively

In contrast to our prediction (1b), vigilance behavior of female chamois decreased throughout summer–autumn. Among ungulates, vigilance is usually greater in females than in males, mainly as an antipredatory strategy to protect off-spring (Lipetz and Bekoff 1982; Alados 1985; Ferretti et al. 2014). If so, females may have been particularly wary in sum- mer because of the high vulnerability of newborns (Ruckstuhl and Ingold 1999, for Northern chamois), leading to a greater scanning rate than in autumn. The greater vigilance rate/effort showed by females in the crepuscular periods, as well as the greater probability to perform less intense aggression, may have resulted from the higher perception of predation risk as darkness approached. In fact, wolves are mainly nocturnal in our study area (Mancinelli et al. 2018). Predators may have also played a role in the observed inter-annual differences on vigilance behavior.

Table 2 Parameters estimated from the top-ranked models on vigilance behavior (β: standardized coefficient, SE: standard error; CI: confidence interval). For GLMMs, variance of random factors is also shown. Asterisks mark the confidence intervals which do not include 0. Effect of Julian day and age class, when present, is shown in italic. The reference categories of categorical predictors are: year 2014 (for year); 25–75 m (for cliff distance); 2–3 years (for age class)

Indicator	Predictor	β	SE	95% CI
(a) Vigilance rate (focal individual) variance = 0.37180	Intercept	− 0.82141	0.07765	− 0.97360; − 0.66922 *
	Julian day	*− 0.22624*	*0.10975*	*− 0.44135; − 0.01113* *
	Time	− 2.01460	0.96854	− 3.91294; − 0.11626 *
	Time^2	2.17659	0.96144	0.29217; 4.06101 *
	Year (2015)	− 0.73945	0.10298	− 0.94129; − 0.53761 *
	Group size	− 0.29676	0.11164	− 0.51557; − 0.07794 *
(b) Vigilance cost (focal individual) variance = 0.08195	Intercept	0.49810	0.15816	0.18811; 0.80809 *
	Julian day	*− 0.00194*	*0.00067*	*− 0.00325; − 0.00063* *
	Year (2015)	0.28000	0.04666	0.18855; 0.37145 *
	Group size	0.00432	0.00134	0.00169; 0.00695 *
(c) Vigilance duration	Intercept	1.89464	0.09645	1.70560; 2.08368 *
	Julian day	*− 0.22248*	*0.11550*	*− 0.65854; 0.00390*
	Time^2	0.33912	0.09394	0.15500; 0.52324 *
	Cliff distance (0–25 m)	0.15573	0.11838	− 0.07629; 0.38775
	Cliff distance (> 75 m)	0.38416	0.14135	0.10711; 0.66121 *
	Group size	0.16205	0.10267	− 0.03918; 0.36328
	% costly head lifts	0.53859	0.10023	0.34214; 0.73504 *
(d) Vigilance effort	Intercept	− 2.69503	0.22418	− 3.13442; − 2.25564 *
	Julian day	*− 0.60598*	*0.13085*	*− 0.86245; − 0.34951* *
	Time	− 2.96122	1.19209	− 5.29772; − 0.62472 *
	Time^2	3.39001	1.17750	1.08211; 5.69791 *
	Year (2015)	− 0.85061	0.12486	− 1.09533; − 0.60588 *
	Age class (4–5 years)	*0.38147*	*0.23898*	*− 0.08693; 0.84987*
	Age class (6–8 years)	*0.06220*	*0.21350*	*− 0.35626; 0.48066*
	Age class (≥ 9 years)	*− 0.18405*	*0.21395*	*− 0.60339; 0.23529*

Table 3 Parameters estimated from the top-ranked models on hormone levels (β: standardized coefficient, SE: standard error; CI: confidence interval).
Asterisks mark the confidence intervals which do not include 0. Effect of Julian day and age class, when present, is shown in italic. The reference category for age class is 2–3 years

Indicator	Predictor	β	SE	95% CI
(a) FAMs (pg/g)	Intercept	55.46374	1.08423	53.33865; 57.58883 *
	Time	− 24.02011	13.87170	− 51.20864; 3.16842
	Time^2	26.60420	14.00297	− 0.84162; 54.05002
	Age class (4–5 years)	*51.31064*	*2.76611*	*45.88906; 56.73221 **
	Age class (6–8 years)	*65.31186*	*3.09296*	*59.24966; 71.37406 **
	Age class (≥ 9 years)	*40.14460*	*1.92932*	*36.36313; 43.92607 **
(b) FCMs (ng/g)	Intercept	432.95764	18.02165	397.63521; 468.28007 *
	Julian day	*− 30.86646*	*15.25049*	*−60.75742; −0.97550 **
	Time	− 18.69168	15.45082	− 48.97529; 11.59193
	Age class (4–5 years)	*353.53687*	*24.47397*	*305.5679; 401.50585 **
	Age class (6–8 years)	*485.18387*	*23.76984*	*438.59498; 531.77276 **
	Age class (≥ 9 years)	*222.11726*	*21.78588*	*179.41693; 264.81758 **

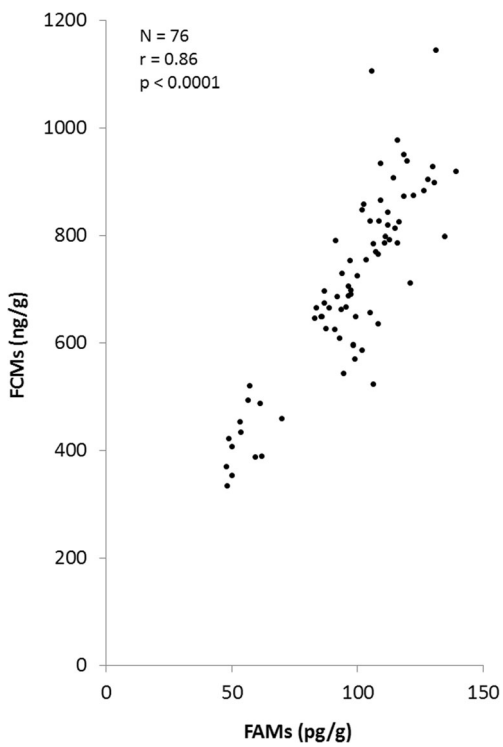

Fig. 3 Relationship between FAMs and FCMs concentrations of female chamois

A further confirmation of the antipredatory function of female vigilance was the increased head lift duration at a distance greater than 75 m from the nearest cliff (Frid 1997).

Although head lift rate decreased with increasing group size (Bmany-eye or detection effect^; Barnard and Thompson 1985; Elgar 1989; Lima 1995), occurrence of no chewing vigilance showed an opposite trend. Feeding interference also increased with increasing group size. Among foraging individuals, the risk of an aggression can elicit social monitoring of conspecifics, thus resulting in increased cost of vigilance (Treves 2000; Fortin et al. 2004; Favreau et al. 2010). We suggest that, in summer, both the greater offspring vulnerability and feeding inter- ference could lead to greater vigilance levels of female chamois, compared to autumn (our prediction, 2b).

The evaluation of FAMs and FCMs as hormonal indi- cators of aggressiveness and stress, respectively, has been used widely among mammals (primates: Barrett et al. 2002; carnivores: Dloniak et al. 2006; ungulates: Pavitt et al. 2016), with limitations (Touma and Palme 2005). FAMs of female chamois showed no seasonal variation, whereas FCMs

decreased from July through October, thus partially supporting our prediction (2c). Seasonal decrease of FCMs accompanied that of vigilance behavior. In lac- tating females, glucocorticoid secretion is associated with higher frequency and intensity of suckling stimuli (Walker et al. 1992; Pavitt et al. 2016). Accordingly, frequency of suckling events decreased from July to October, in our study population (Scornavacca et al. 2016, 2018). Romero (2002) reported that Bthe seasonal variation of basal glucocorticoid concentration is species/sex-specific and depends on the relative energetic costs of the different seasons for each species and on life-history patterns^. We suggest that three factors could explain the higher level of FCMs in summer than in autumn: (a) greater offspring vulnerability, (b) higher aggression rate, and/or (c) greater costs of lactation. If so, seasonal variation of nursing be- havior may be more important than seasonality of food resources per se in determining response to stress of fe- male chamois, supporting our hypothesis 2.

In addition to seasonality, variation in behavior and endocrine levels was related to age. In most mammals, social dominance is positively associated to age and/or androgens (Anderson 1986; Creel et al. 1992; Coltman et al. 2002; Pelletier and Festa-Bianchet 2006; Martin et al. 2013). Accordingly, probability to win a challenge in- creased with age in female chamois (Lovari and Locati 1991). Aggression intensity and androgens were related to age: both the use of threats and FAMs levels were higher in adult than in subadult females, supporting our predictions (3a, 3c). Although we cannot rule out that adult females showed higher FAMs levels because of the age-dependent sexual maturation (Murray et al. 1998; Vendola et al. 1998), higher androgens may have helped them to establish social dominance by promoting aggres- sion (Floody 1983; Giammanco et al. 2005). Threats were more likely to lead the opponent to withdraw than dis- plays, as the latter were used more often when the attacked female reacted. Also, the attacking individual won 99.9% of aggressions ($N = 1912$ aggressive events) (see also Lovari and Locati 1991). Thus, female chamois initiated interactions when they had a high probability of winning, suggesting that their age-based dominance relied on both experience and fighting ability/physical clues such as body mass, leading the oldest, heaviest females to dominate other age classes (Locati and Lovari 1991; Jennings et al. 2004). The establishment of a dominance hierarchy is common in polygynous male mammals, mainly to achieve mating advantages (Clutton-Brock and Huchard 2013). Yet, the adaptive significance of female dominance in polygynous species is less clear, ranging from Bmale choice^ to resource defense (for reviews: Rosvall 2011; Stockley and Bro-Jørgensen 2011; Clutton-Brock and Huchard 2013; Stockley and Campbell 2013). Gaining advantages for male choice may not play a major role in explaining dominance among female chamois, at least in our study period, not inclusive of the mating season (November: Lovari and Locati 1991). As the intensity of female aggression peaked on the most nutritious forb patches, we suggest that social dominance in female chamois may have devel- oped to establish priority access to crucial resources (Boness et al. 1982; Hutchins and Geist 1987; Locati and Lovari 1990; McDonough 1994; Ceacero et al. 2012). Access to better pasture is likely to provide advan- tages in terms of a better production of milk (Festa- Bianchet and Jorgenson 1998; Min et al. 2005; Therrien et al. 2007). If so, female dominance may ultimately en- hance growth and survival of offspring (Côté and Festa- Bianchet 2001b).

In contrast to both our predictions (3b, 4b), vigilance was not associated to age. This is in apparent contrast to what reported by Lovari and Rosto (1985) who found that subadult females showed greater vigilance than adult ones, in another area of the Apennine chamois range. The area where Lovari and Rosto (1985) conducted their observations had richer, concentrated patches of vegetation dominated by *Trifolium thalii* and other forbs, than our study area (Ferrari et al. 1988). Larger, closely knit groups form on rich, concentrated food resources (Bruno and Lovari 1989), which may promote a greater feeding interference where subadults are disadvan- taged, thereby more vigilant.

Adult females, in particular those 4–8 years old, were the most stressed, showing the greatest FCMs concentration. No data are available on the age-related breeding success of female Apennine chamois. In this study, the ratio of ju- veniles to adult females was 24:30 in 2014 and 28:31 in 2015. As chamois gives birth to 1 offspring/year (Lovari and Bruno 2003), these ratios may support the view that subadult females of Apennine chamois do not reproduce (Tettamanti et al. 2015; Morin et al. 2016, for Northern chamois). In the closely-related Northern chamois, female breeding peaks between 4 and 8 years, and decreases in older individuals (Tettamanti et al. 2015; Morin et al. 2016). Thus, our results suggest that motherhood is stressful for female chamois, likely because of the high metabolic costs of lactation (Walker et al. 1992; Kenagy and Place 2000; Goymann et al. 2001; Pavitt et al. 2016). Feeding interference may have played an additional role in influenc- ing stress levels among females, because 6–8 years old in- dividuals were involved in more aggressions than the other age classes and showed the highest FAMs levels.

Overall, as adult females were more aggressive and more stressed than subadult ones, our results provided a stronger support to our hypothesis 3, suggesting a greater response to stress in high-ranking individuals (Creel 2001). However, as the 4–8 years old, middle-ranking females were the most stressed of adult age classes, our results ultimately support neither the Bstress of dominants^, nor the Bstress of subordinates^ hypotheses (Creel 2001). Rather, they suggest that reproduction and feeding interference were key determinants of stress in female chamois (sensu Goymann and Wingfield 2004).

Previous studies reported contradictory relationships be- tween androgens and glucocorticoids (positive relationship: Mooring et al. 2006; negative relationship: Bartoš et al. 2010; no relationship: Pavitt et al. 2016). A high level of circulating androgens could result in significant costs to indi- viduals (Folstad and Karter 1992). Accordingly, female cham- ois with greater level of FAMs also showed higher FCMs, suggesting physiological stress from increased individual ag- gressiveness, which is energetically demanding (Mooring et al. 2006; Taillon and Côté 2008; Pavitt et al. 2015). To this end,

the adaptive significance of retaining greater androgen levels should reflect a further advantage to females (e.g. Dantzer et al. 2011). Androgens are commonly associated with the development of male characteristics (Fletcher 1978). Yet, in mammals, androgens may be converted to es- trogens (Adkins-Regan 1981), which promote feminine traits and/or behavior (Trainor and Marler 2001, 2002). The greater levels of FAMs showed by 4–8-year-old females might be ultimately associated—via conversion to estrogens—to devel- opment of maternal care, e.g., milk production. If so, 4–8- year-old females would additionally benefit from increased levels of FAMs in achieving a greater reproductive success. Androgens can inhibit glucocorticoids, whereas estrogen can enhance them (Handa et al. 1994); as stressed females also retained greater androgen levels, the occurrence of androgen- estrogen conversion in female chamois may be supported.

Although long-term evaluation of fitness is required to assess female reproductive success, our results show that seasonal and age-related variation underlies the phenology of social behavior and response to stress, suggesting com- plex trade-offs between access to food, dominance, and nursing behavior, for females. Adult females were the most aggressive and the most dominant, with higher endocrine levels. We suggest that their higher stress was ultimately linked to the costs of maternal care, emphasizing the key importance of summer months for the life cycle of mountain herbivores (Festa-Bianchet 1988; Ruckstuhl and Ingold 1994; Pettorelli et al. 2007; Therrien et al. 2007). Individual-level studies could further clarify relationships between nursing-related costs (Froy et al. 2016), hormonal mechanisms such as testosterone-estrogen conversion and potential reproductive benefits.

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Authors' contributions SL and FF planned this study; NF participated in study planning, conducted most data collection and data analyses, wrote the first draft, and participated in writing all drafts; FF participated in data collection and analyses, as well as in writing up all drafts. SL supervised all stage of this study and participated in writing up all drafts; CB partic- ipated in data collection and analyses; CB and AC participated in data collection; EM carried out hormone assays and wrote the relevant text; MCP provided statistical advice and participated in data analyses.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval We received the appropriate permissions for conducting the study in Abruzzo, Lazio and Molise National Park from the responsible authorities. All applicable international, national, and/or institutional guidelines for the use of animals were followed. Ethical approval from ethics committee for involving animals was not required.

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