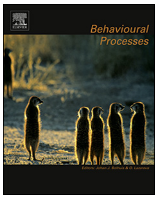
Behavioural Processes 167 (2019) 103909

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Temporal variation in foraging activity and grouping patterns in a mountain-dwelling herbivore: Environmental and endogenous drivers

Niccolò Fattorini[a,*], Claudia Brunetti[a], Carolina Baruzzi[a], Gianpasquale Chiatante[b], Sandro Lovari[a,c], Francesco Ferretti[a]

[a] Department of Life Sciences, University of Siena. Via P.A. Mattioli 4, 53100 Siena, Italy
[b] Department of Earth and Environmental Sciences, University of Pavia, Via Ferrata 1, 27100 Pavia, Italy
[c] Maremma Natural History Museum, Strada Corsini 5, 58100 Grosseto, Italy

ARTICLE INFO

Keywords:
Seasonality
Foraging Activity
Group size
Rupicapra
Chamois
Mountain herbivores

ABSTRACT

In temperate ecosystems, seasonality influences animal behaviour. Food availability, weather, photoperiod and endogenous factors relevant to the biological cycle of individuals have been shown as major drivers of temporal changes in activity rhythms and group size/structure of herbivorous species. We evaluated how diurnal female foraging activity and grouping patterns of a mountain herbivore, the Apennine chamois *Rupicapra pyrenaica ornata*, varied during a decreasing gradient of pasture availability along the summer-autumn progression (July–October), a crucial period for the life cycle of mountain ungulates.

Females increased diurnal foraging activity, possibly because of constrains elicited by variation in environmental factors. Size of mixed groups did not vary, in contrast with the hypothesis that groups should be smaller when pasture availability is lower. Proportion of females in groups increased, possibly suggesting that they concentrated on patchily distributed nutritious forbs. Occurrence of yearlings in groups decreased, which may have depended on dispersal of chamois in this age class. Presence of kids in groups did not show variation through summer-autumn, suggesting a close mother-juvenile relationship even at the end of weaning and/or, possibly, low summer mortality. Both endogenous and environmental factors contribute to shape variation in foraging activity and grouping behaviour in mountain-dwelling herbivores.

1. Introduction

In temperate ecosystems, seasonality is a major driver of changes in the biological cycle of individuals. Accordingly, changes in animal behaviour occur during the year in seasonal habitats (Paul et al., 2008, for a review). Amongst herbivorous species, intra-annual variations are common in foraging patterns (e.g. Brivio et al., 2016), spatial behaviour (e.g. van Beest et al., 2011) and social interactions (e.g. Fattorini et al., 2018b). The investigation of temporal changes in foraging activity and grouping patterns (e.g. group size/composition) of gregarious herbivores may help to understand their social dynamics and environmental-mediated behaviours. Recent studies have shown the importance of natural resource abundance, predators, weather and photoperiod as environmental determinants of activity and grouping patterns in herbivorous mammals (Mason et al., 2014; Chirichella et al., 2015; Brivio et al., 2016; Iranzo et al., 2018). Other studies have emphasised the relevance of endogenous factors concerning the biological cycle of individuals, such as social or reproductive requirements, in shaping activity and grouping patterns (Buuveibaatar et al., 2013). Yet, few studies have quantified the overall effect of seasonality *per se*, which reflects the joint effects of temporal changes in both environmental/physical parameters and the biological stage of individuals.

Daily activity rhythms of wild herbivores are synchronised with external inputs (*zeitgebers*: Pittendrigh, 1993). Owing to thermoregulation and predator avoidance as constrains, herbivores' major *zeitgebers* are temperature (Belovsky and Slade, 1986; Abáigar et al., 2017) and light (Harmsen et al., 2011; Palmer et al., 2017). In turn, temporal variation in those *zeitgebers*, determining temperature regime and photoperiod, can influence seasonal changes of activity rhythms (Owen-Smith and Goodall, 2014; Davimes et al., 2016). Most herbivorous mammals, especially those living in open habitats, are known to be crepuscular: they are more active at dusk/dawn than during the central parts of day/night (Georgii and Schröder, 1983; Alados, 1986; Pipia et al., 2008). Enhancing foraging at dusk-dawn allows them to avoid both heat (e.g. Mason et al., 2014) and encounters with nocturnal predators (e.g. Canidae: Torretta et al., 2017; Felidae: Harmsen et al.,

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[*] Corresponding author.
E-mail address: niccolo.fattorini@gmail.com (N. Fattorini).

https://doi.org/10.1016/j.beproc.2019.103909
Received 17 February 2019; Received in revised form 12 July 2019; Accepted 17 July 2019
Available online 19 July 2019

2011). Resource availability should not be a major determinant of daily activity rhythms, because pasture is evenly available around the clock for herbivores (but see Owen-Smith and Goodall, 2014, for digestive constrains). Conversely, seasonal variations in levels of activity may be expected according to intra-annual differences in food availability (Massé and Côté, 2013; Owen-Smith, 2013).

In group-living herbivores, the level of gregariousness is determined by the trade-off between foraging competition and predation risk. Thus, group size tends to limit feeding interference while maximising safety within groups (Molvar and Bowyer, 1994; Isvaran, 2007). Furthermore, amongst polygynous ungulates, segregation between sexes and age classes is common (Jarman, 1974; Ruckstuhl, 2007; Main, 2008). Usually adult males live solitarily or in unisexual ("bachelor") groups throughout the year, except during the rut, when they join mixed groups of females and immature individuals. Conversely, adult females are usually phylopatric and live in larger groups with offspring and immatures (Bovidae: e.g. chamois *Rupicapra* spp., Loison et al., 1999b; Cervidae: e.g. mule deer *Odocoileus hemionus*, Bowyer, 1984). This pattern may differ in species with continuous territorial behaviour, where a dominant male holds a group of females and juveniles outside of the rut (Antilocapridae: e.g. pronghorn *Antilocapra americana*, Kitchen, 1974; Camelidae: e.g. vicuna *Vicugna vicugna*, Koford, 1957).

Assessing the seasonal progression of foraging activity levels and grouping patterns of gregarious ungulates may provide insights into herbivore responses to potential seasonal shifts occurring in temperate habitats under changing environmental conditions (e.g. Walther et al., 2002). We examined temporal variation of diurnal female foraging activity and diurnal grouping patterns in the Apennine chamois *R. pyrenaica ornata*, throughout July–October. We focused our investigation in summer-early autumn, because the warm months are particularly important to nursing females and weaning kids, in mountain-dwelling herbivores (Ferretti et al., 2015; Scornavacca et al., 2016, for our study population). In mountain ecosystems of temperate habitats, the availability of nutritious pasture for herbivores peaks in early summer and decreases as approaching autumn (Ferrari et al., 1988; Primi et al., 2016; Villamuelas et al., 2016). Accordingly, intensity of maternal care provided by mothers to offspring decreases over this period (Ruckstuhl and Ingold, 1994; Scornavacca et al., 2018). Physical variables such as temperature and daylight duration also change throughout summer-autumn at temperate latitudes, with seasonality of temperature being further intensified in mountain ecosystems. In turn, variations in activity rhythms and grouping dynamics could be expected because of the overall contribution of the factors above.

Seasonality may affect foraging activity of herbivorous mammals, but different effects of seasonal variation in resource availability have been shown. Herbivores seem to be more active when availability of resources is greater (Massé and Côté, 2013; Brivio et al., 2016; Pagon et al., 2017). Conversely, other studies have shown that individuals exhibit compensation mechanisms through which activity increases when resources are scarce (Pérez-Barbería et al., 1997, 1998; Owen-Smith and Cain, 2007; Carnevali et al., 2016). Also, no variation in activity has been shown along the gradient of resource availability, during the warm months (Bruno and Lovari, 1989). There are two periods across seasons when female chamois should retain high energy. The first is after the birth season, in early summer, when food availability peaks and females have to cope with lactation; the second is in autumn, when winter rigours approach, food is less nutritious, and females have to cope with future food shortage and gestation effort. In turn, an increase in diurnal foraging activity by female chamois could be expected from summer to autumn, to compensate for the decreasing forage availability and quality.

A lower food availability has been suggested to support smaller groups of ungulates, because individuals should avoid feeding competition (Bon et al., 1990; Fryxell, 1991; Isvaran, 2007; Marino and Baldi, 2014). Thus, one could expect that group size of chamois would decrease throughout summer-autumn, when availability and quality of pasture become lower (in *Rupicapra* spp.: Bruno and Lovari, 1989; Richard and Pépin, 1990; Pérez-Barbería and Nores, 1994; Chirichella et al., 2015; but see Herrero et al., 2002). Group structure of social herbivores, reflected by occurrence of different age-sex classes in mixed groups, is influenced by sexual segregation, and differs according to the phase of the biological cycle itself (Blank et al., 2012; Buuveibaatar et al., 2013). In Apennine chamois, an increase — albeit with a different absolute extent (Lovari and Cosentino, 1986) — in proportions of males and females in mixed groups can be expected from summer to the pre-rut (October), as males have to join groups of females to perform courtship (Lovari and Locati, 1991), and also because of yearling dispersal and/or potential kid mortality after weaning. In fact, a greater proportion of kids in groups is expected at the onset of nursing activities, in early summer (in *Rupicapra* spp.: Shank, 1985; Lovari and Cosentino, 1986; Herrero et al., 2002).

According to our hypotheses, we predicted that, from July to October: diurnal foraging activity of females would increase (*prediction i*); size of mixed groups would decrease (*prediction ii*), with increasing proportions of males and females (*prediction iii*) and decreasing proportions of kids and yearlings (*prediction iv*).

2. Methods

2.1. Study area

Our study was conducted in the upper meadows of Mt. Meta (2100–2240 m a.s.l.), in the Abruzzo, Lazio and Molise National Park (ALMNP; Central Apennines, Italy). Several vegetation communities occur in this area: forb-dominated patches (*c.* 24%, e.g. *Trifolium* spp. and *Anthillys vulneraria*), palatable graminoids (*c.* 39%, mainly *Festuca* spp.), unpalatable graminoids (*c.* 1%, *Brachypodium genuense*), and sparse vegetation on rocks/screes (*c.* 36%) (Ferretti et al., 2015). The population of chamois inhabiting the area of Mt. Meta has increased during the last decades (*cf.* Ferretti et al., 2015), and included at least 80 chamois in our study years (see Results). Whilst mixed groups of females and immatures graze on upper meadows throughout summer-autumn, sightings of males are rare events in this period, because male Apennine chamois live solitarily outside the rut, at lower altitudes (Lovari and Cosentino, 1986). In ALMNP, potential predators of chamois are wolf *Canis lupus*, Apennine brown bear *Ursusarctos marsicanus* and golden eagle *Aquila chrysaetos*, although predation on chamois is negligible (for wolf: Grottoli, 2011; for Apennine brown bear: Ciucci et al., 2014; for golden eagle: Scornavacca and Brunetti, 2015).

2.2. Data collection

We recorded female activity and grouping patterns of chamois from July to October (2014–2015), through focal-group sampling (Altmann, 1974). We performed on average *c.* 4 h of diurnal (from dawn to dusk) observations/day, for a total of *c.* 6 days/month. Sampling was balanced across months and time of the day. We observed chamois using 10 × 30 and 15 × 70 binoculars and a 20–60 × spotting scope, at distances of 100–200 m, depending on terrain and range of vision. In ALMNP, chamois were habituated to human presence and could be approached at a short distance without moving away from the observer (flight distance: 10–20 m, Patterson, 1988). However, we avoided recording data whenever we felt that the animals were reacting to our presence (*cf.* Winnie and Creel, 2007).

The focal group of chamois was selected on-site immediately after detection, irrespective of its size. A group was considered as "at least 2 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). Whenever possible, when more than one group was present in the study site, 2–3 observers contemporarily performed separate observations on different groups. We observed each focal group continuously, 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. We recorded group size, group structure (no. of kids, no. of yearlings, no. of females, no. of males) and the number of foraging females through instantaneous scan sampling (Altmann, 1974), in 5-min sampling intervals. We also recorded time (hh:mm) of each scan. Sex/age classes of chamois were assessed following Lovari (1985). In each scan, the proportion of foraging females was calculated over the total no. of females in group, while the proportion of each sex/age classes in group was calculated over the total no. chamois in group. Overall, we recorded 2212 scans (*c.* 184 h of observations) on 77 focal sightings of chamois groups (mean ± S.E.: 2.4 ± 0.1 h of observation/group).

2.3. Statistical analyses

We analysed female foraging activity and grouping patterns of chamois using generalised linear mixed models (GLMMs; Zuur et al., 2009). We modelled six response variables separately, one to assess foraging activity of females (proportion of foraging females), and five to assess grouping patters (group size, proportions of females, males, kids and yearlings in group). Proportions, being continuous variables in 0–1 range, were modelled with beta errors (link function: logit). When proportions where equal to 0 and 1, as these values are not allowed in beta regression, they were converted to 0.0000001 and 0.9999999, not altering the biological meaning of our result. Group size, being a positive integer, was modelled with zero-truncated negative binomial errors (link function: log).

To evaluate the effect of summer-autumn progression on our response variables, we included as predictor the linear effect of Julian day (continuous, as no. of days from 1st of January; mean ± S.E.: 236.4 ± 36.9), because explorative analysis of our response variables confirmed the absence of nonlinear trends over Julian days. We also included several control predictors: group size (continuous; mean ± S.E.: 24.0 ± 0.3; only when modelling foraging activity and proportions of sex/age classes in group), year (categorical, 2014 or 2015; reference category: year 2014) and time of day (continuous, as decimal hours from midnight; mean ± S.E.: 11.5 ± 2.7; both linear and quadratic, in order to account for bimodal diurnal pattern: e.g. Mason et al., 2014). We did not consider environmental parameters themselves as predictors, since they vary according to the Julian day, which was our test predictor. Therefore, we rather assessed the summer-autumn changes of environmental parameters in our study area (see Supplementary Material). However, any potentially influencing inter-annual variation of weather (e.g. Loison et al., 1999a) as well as the bimodal, daily variation of temperature (e.g. Mason et al., 2014) were accounted for by the relevant control predictors, i.e. year and time of day, respectively. As our aim was to evaluate changes according to the Julian day, we were not interested to assess any interaction of Julian day with such control predictors; moreover including interactions may elicit multicollinearity in our models. Multicollinearity among predictors was tested for each full model by calculating the variance inflation factor (VIF), for all predictors. All VIF values were < 2, indicating no multicollinearity between the explanatory variables (Zuur et al., 2009). VIFs were calculated through the R package car (Fox and Weisberg, 2011).

We treated the focal-group of chamois as a random intercept, to account for repeated observations carried out on the same group, on the same day. Although we could not control any potential pseudoreplication of observations across days due to unmarked animals possibly moving between groups, our response variables should have not been affected because they were recorded at the group level, with no indicators concerning individual chamois. Random intercepts should also allow to handle potential spatial autocorrelation of our response variables (Zuur et al., 2009) recorded on a feeding patch, at least at the scale of each focal-group observation bout. Furthermore, we treated each scan sampling interval as a random intercept nested within the relevant observation bout. We took this precaution to avoid potential temporal autocorrelation of our response variables, as they were recorded subsequently within the same focal-group bout (*cf.* Fattorini et al., 2018a).

For each response variable, we performed a model selection according to the information-theoretic approach (Burnham and Anderson, 2002). Previous studies on foraging activity and grouping patterns of ungulates allowed us to evaluate all the possible combinations of biologically meaningful predictors (Table S1; Supplementary Material). Each model evaluated, including a different combination of predictors, could represent a different *a priori* hypothesis. The null model was also evaluated, to allow for an assessment of model performance relative to a fixed baseline (Mac Nally et al., 2018). In turn, all the possible combinations between predictors were ranked and weighted from each global model. Following a conservative approach (Burnham and Anderson, 2002: 131; Richards, 2008; Richards et al., 2011), we did not select models with ΔAICc ≥6 in respect to the best model (the model with the lowest AICc value), as well as models with an AICc value

Table 1

Result of models selection: selected models with ΔAICc < 6 while accounting for nesting, each with k, AICc value, ΔAICc and weight. Nested random effects are shown in parentheses. For those response variables in which only a single best model was selected within ΔAICc < 6, the first not retained-model is also reported (in square brackets). The effect of Julian day is shown in bold.

Response variable	Models retained	k	AIC_c	ΔAIC_c	Weight
a. Proportion of active females	**Julian day** + time + time^2 + (focal group/sampling interval)	7	−16003.6	0	1
	[time + time^2 + (focal group/sampling interval)	6	−15997.5	6.10	0]
b. Group size	year + (focal group/sampling interval)	5	15881.8	0	0.801
	(focal group/sampling interval)	4	15884.6	2.80	0.199
c. Proportion of females	**Julian day** + time + time^2 + year + group size + (focal group/sampling interval)	9	−3028.6	0	0.508
	Julian day + time + time^2 + group size + (focal group/sampling interval)	8	−3027.7	0.95	0.317
	time + time^2 + year + group size + (focal group/sampling interval)	8	−3024.9	3.74	0.078
	time + time^2 + group size + (focal group/sampling interval)	7	−3024.2	4.42	0.055
	Julian day + group size + (focal group/sampling interval)	6	−3023.6	5.03	0.042
d. Proportion of males	group size + (focal group/sampling interval)	5	−46456.2	0	1
	[(focal group/sampling interval)	4	−46428.5	27.72	0]
e. Proportion of kids	time + time^2 + group size + (focal group/sampling interval)	7	−4303.8	0	1
	[time + group size + + (focal group/sampling interval)	6	−4289.3	14.49	0]
f. Proportion of yearlings	**Julian day** + time + year + group size + (focal group/sampling interval)	8	−13185.8	0	0.447
	Julian day + time^2 + year + group size + (focal group/sampling interval)	8	−13185.5	0.35	0.377
	Julian day + year + group size + (focal group/sampling interval)	7	−13182.0	3.80	0.067
	Julian day + time + group size + (focal group/sampling interval)	7	−13181.3	4.56	0.045
	Julian day + time^2 + group size + (focal group/sampling interval)	7	−13180.9	4.89	0.039
	time + year + group size + (focal group/sampling interval)	7	−13180.0	5.85	0.025

Table 2
Coefficients (B) and 95% confidence intervals (95% CIs) estimated for the top-ranked models of female foraging activity and grouping patterns. Variance of random factors is also shown. Asterisk marks the confidence intervals which does not include 0. The effect of Julian day, when present, is shown in bold.

Response variable	Predictor	B	95% CI
a. Proportion of active females	intercept	8.4576	5.9339; 10.9812 *
(sampling interval:focal group) variance = 1.5660	**Julian day**	**0.0117**	**0.0038; 0.0197** *
(focal group) variance = 1.7130	time	−1.7679	−2.0756; −1.4601 *
	time^2	0.0753	0.0622; 0.0884 *
b. Group size	intercept	3.0221	2.7700; 3.2741 *
(sampling interval:focal group) variance = 0.0114	year (2015)	−0.3594	−0.6767; −0.0421 *
(focal group) variance = 0.4522			
c. Proportion of females	intercept	0.4416	−0.8721; 1.7554
(sampling interval:focal group) variance = 0.1182	**Julian day**	**0.0058**	**0.0011; 0.0105** *
(focal group) variance = 0.6413	time	−0.1600	−0.2719; −0.0480 *
	time^2	0.0067	0.0019; 0.0114 *
	year (2015)	−0.3390	−0.7193; 0.0412
	group size	−0.0168	−0.0198; −0.0138 *
d. Proportion of males	intercept	−5.2450	−5.4590; −5.0311 *
(sampling interval:focal group) variance < 0.0001	group size	0.0126	0.0081; 0.0172 *
(focal group) variance = 0.3752			
e. Proportion of kids	intercept	−3.8997	−4.8351; −2.9642 *
(sampling interval:focal group) variance = 0.2563	time	0.3434	0.1882; 0.4985 *
(focal group) variance = 1.0490	time^2	−0.0136	−0.0202; −0.0070 *
	group size	0.0355	0.0313; 0.0397 *
f. Proportion of yearlings	intercept	−0.4531	−2.2173; 1.3110
(sampling interval:focal group) variance < 0.0001	Julian day	**−0.0101**	**−0.0171; −0.0032** *
(focal group) variance = 1.4250	time	−0.0364	−0.0660; −0.0068 *
	year (2015)	0.7592	0.1941; 1.3243 *
	group size	0.0118	0.0078; 0.0157 *

greater than that of any simpler alternative, thus achieving either a set of top-ranked models or a single best model for each response variable while accounting for nesting (Table 1).

According to Richards et al. (2011), we based inference on selected models. For each response variable and from each selected model, we estimated coefficients of predictors, 95% confidence intervals and variance of random effects. Estimates for the best models are reported in Table 2, whilst those for alternative top-ranked models, when present, are reported in Table S2 (Supplementary Material). The effects of predictors were assessed by checking whether 95% confidence intervals of coefficients overlapped 0. Models were validated through visual inspection of residual patterns (Zuur et al., 2009). All the analyses were performed in R (R Core Team, 2013), through the packages *MuMIn* (for model selection; Bartoń, 2012) and *glmmTMB* (for GLMMs; Brooks et al., 2017).

3. Results

Diurnal foraging activity of females increased from July to October (Fig. 1a; Table 2a) and peaked at crepuscular periods (proportion of foraging females increased by *c.* 88% at dawn/dusk in respect to the central part of the day, in summer, and by *c.* 17% in autumn; Fig. 1b; Table 2a).

The maximum number of females, yearlings and kids observed at the same time was 69 (in 2014) and 78 (in 2015), whilst the maximum number of males observed at the same time was 9 (in 2014) and 3 (in 2015). Mean group size of chamois was 24.0 individuals (S.E.: 0.3; median: 21; interquartile range: 23; N = 2212 scans), and did not vary from July to October (Fig. 2a; Table 2b). Proportion of females in groups increased by *c.* 24% (Fig. 2b; Table 2c) in July-October, whereas that of males was not influenced by Julian day (Fig. 2c; Table 2d). Proportion of kids in groups did not vary over July-October (Fig. 2d; Table 2e), whereas that of yearlings decreased by *c.* 64% (Fig. 2e; Table 2f). Grouping patterns of chamois were also influenced by control predictors, depending on the response variable (Table 2; Figures S1, S2 and S3, Supplementary Material).

4. Discussion

Amongst herbivores, both behavioural and physiological patterns vary seasonally (Paul et al., 2008, for a review). Our findings suggest how the summer-autumn transition shapes variation in both foraging

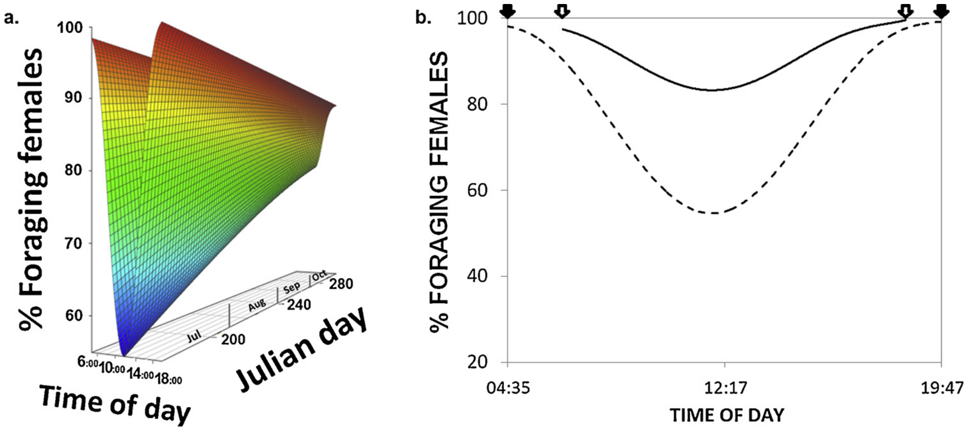

Fig. 1. Predicted proportion of foraging females (over the no. of females in group) in relation to (a) Julian day and time of day (within the relevant civil dawn/dusk time in the study area) and (b) time of day, at the beginning (1st of July: dotted line) and at the end (31st of October: continuous line) of the study period, within dawn/dusk time (1st of July: black arrows; 31st of October: white arrows). Time of day is expressed as hh:mm (Central European Time, winter time, UTC + 01:00).

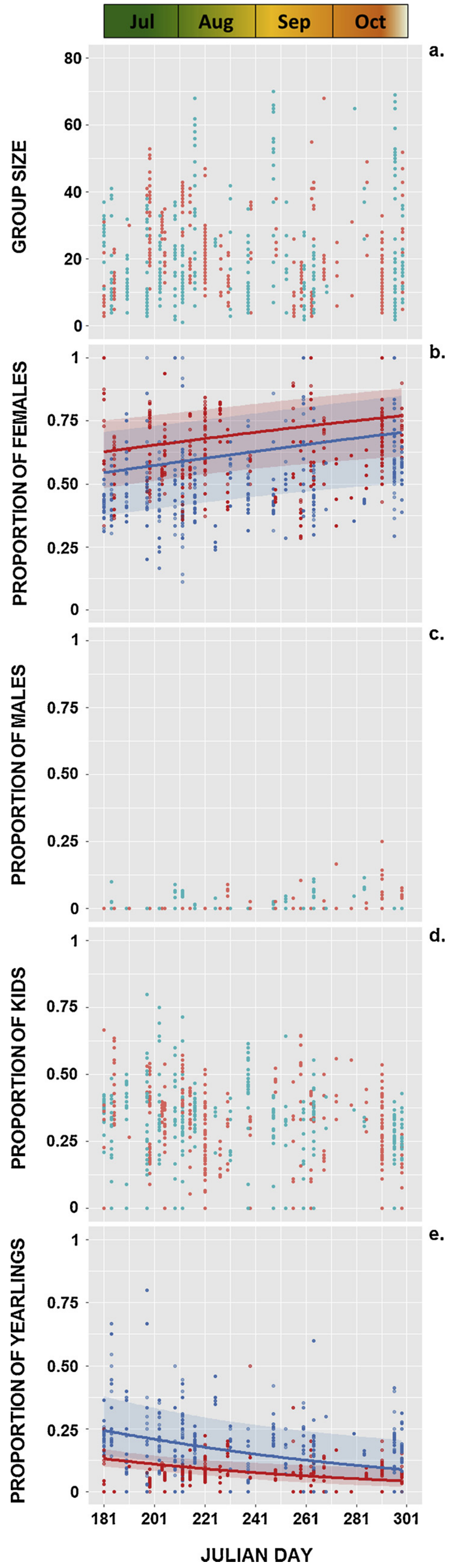

Fig. 2. Observed group size (a) and proportion of females (b), males (c), kids (d) and yearlings (e) in mixed groups of chamois in relation to Julian day (2014: red dots; 2015: blue dots). Predicted values and 95% confidence intervals (lines and bands, 2014: red; 2015: blue) are added when variation through Julian days is supported by GLMMs.

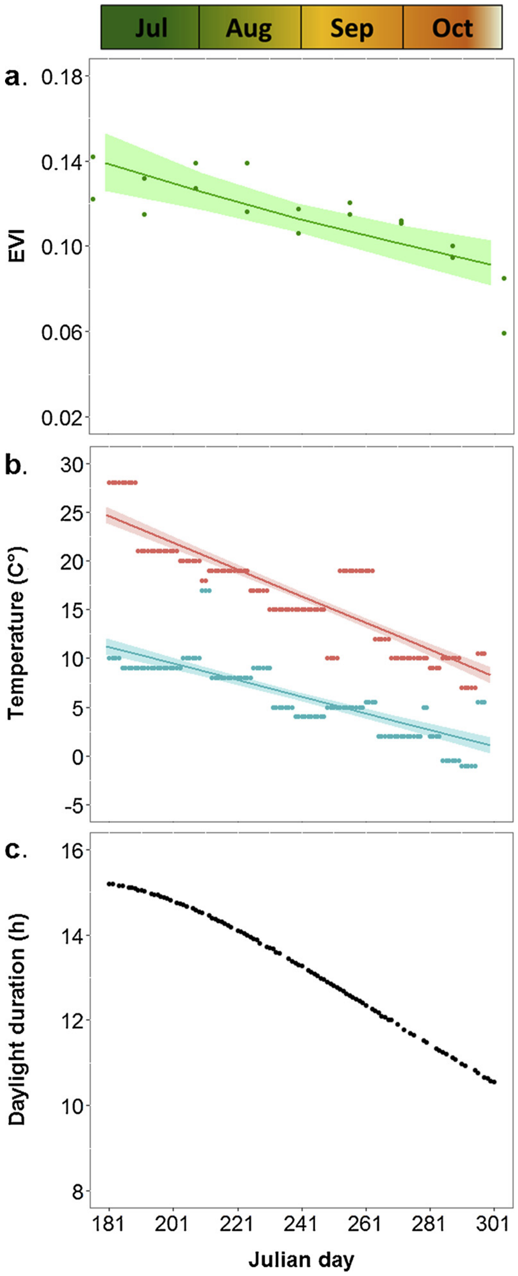

Fig. 3. Temporal trend of environmental parameters in our study area: (a) vegetation productivity, indexed by mean EVI; (b) maximum (red items) and minimum (blue items) ambient daily temperature; (c) observed daylight duration. Continuous lines: predicted values; bands: 95% confidence intervals; dots: observed values. Analyses are reported in Supplementary Material.

activity and grouping patterns of a mountain-dwelling herbivore.

Previous studies on foraging activity rhythms of chamois have provided contradictory evidences on their variation in July-October, with female activity being either greater (e.g. Carnevali et al., 2016) or lower (e.g. Brivio et al., 2016; Grignolio et al., 2018) when resources are scarce. Also, no overall variation of female activity through the summer-autumn gradient of food resources has been detected (Bruno and Lovari, 1989). Accounting for time of day, foraging activity increased through months, as vegetation productivity decreased (Fig. 3a). Our result supports *prediction* (*i*) and agrees with previous studies suggesting that female chamois increased time allocated in feeding activities to compensate for the lower availability of high-quality resources (Pyrenean chamois *R. pyrenaica pyrenaica*: Pépin et al., 1991; Cantabrian chamois *R. pyrenaica parva*: Pérez-Barbería and Nores, 1996; Pérez-Barbería et al., 1997, 1998; Alpine chamois *R. rupicapra rupicapra*: Carnevali et al., 2016). Apennine chamois may have also increased bite rate to compensate for a lower food availability (*cf.* Puorger et al., 2018, for Alpine chamois), but previous research in our study area does not suggest it, as the bite rate of females did not increase across summer-autumn (Ferretti et al., 2015). In addition to our explanation, two further hypotheses may help to explain summer-autumn increase of female foraging activity.

(*I*) In mountain ungulates, activity plays a key role in modulating thermoregulatory requirements (e.g. Mason et al., 2014). Enhanced foraging activity in autumn may result from the decreasing trend of daily temperature through months. Different findings from previous studies could be explained by geographical and climatic variations. In an area of central-eastern Alps, female chamois were more active in summer than in autumn, when resources were more abundant (Brivio et al., 2016; Grignolio et al., 2018). Our study area was located at a lower altitude (*c.* 2200 m a.s.l.) than that of those studies (*c.* 3000 m a.s.l.; Brivio et al., 2016; Grignolio et al., 2018). On the central Apennines, our chamois population could have been exposed to higher daily temperatures than that on the Alps, especially in the warmest months, while not being able to move to upper altitude (*sensu* Mason et al., 2014). Our results also differed from those found in a neighbouring area, on the Apennines, where Bruno and Lovari (1989) did not show any variation of female Apennine chamois activity throughout summer-autumn, in 1980s. Over the last decades, growing temperatures in upper mountain meadows (e.g. Gottfried et al., 2012) may have led Apennine chamois to decrease their summer activity in the central part of the day. Suggestively, Bruno and Lovari (1989) reported a third peak of diurnal summer female activity in the central part of the day, in which we observed the lowest activity. Nowadays, the summer-autumn decrease of maximum daily temperature may be stronger than that concerning the minimum ones (Fig. 3b and Table S4, Supplementary Material, for our study area) supporting that, in summer, potential heat anomalies (i.e., extreme maximum daily values, thus in the central part of the day) may have occurred (*cf.* Amendola et al., 2019). Because of the greatest temperature in July–August, Apennine chamois presumably tended to reduce summer diurnal activity. One could further speculate that summer nocturnal feeding (which has been so far reported in predator-free areas: e.g. Brivio et al., 2016; Carnevali et al., 2016; Grignolio et al., 2018) might have allowed to compensate it. In any case, this hypothesis would suggest that heat avoidance as thermoregulatory behaviour would be the key determinant of chamois activity rhythms (Mason et al., 2014).

(*II*) Alternatively, female chamois may have increased diurnal foraging activity through days to compensate for the decreasing daily availability to forage under sunlight, in autumn. If so, avoiding nocturnal foraging could be more important than avoiding heat, in our study population (because being active during the night would increase the risk of encounters with predators such as largely nocturnal wolves: Mancinelli et al., 2018, in our study site). At the latitude of our study area, photoperiod is nearly halved from July to October (Fig. 3c). Thus, females may have had to compensate their food supply through the increase of diurnal activity. This hypothesis would suggest that darkness avoidance as an antipredatory ploy (*cf.* Šprem et al., 2015) may be an important determinant of chamois activity.

As to the effect of time of day, Hofmann (1989: 445) suggested that chamois may require six daily cycles of pasture/ruminant activity (including four diurnal cycles) because of physiological requirements. Nevertheless, the "dawn-dusk" bimodal rhythm of diurnal activity of female Apennine chamois we found is in agreement with previous studies on *Rupicapra* spp. (Brivio et al., 2016; Bruno and Lovari, 1989; Carnevali et al., 2016; Darmon et al., 2014; Mason et al., 2014; Rüttimann et al., 2008; but see: Šprem et al., 2015, for forest-dwelling chamois; Pęksa and Ciach, 2018, for chamois affected by human disturbance). Presumably, foraging rhythms may partly depend on adaptations to local nutritional conditions, although experimental data from different areas would be necessary to test it.

In gregarious herbivores, phenology of grouping patterns is mainly influenced by food availability (Fryxell, 1991) and age-sexual segregation (Main, 2008). In contrast to our prediction (*ii*), group size of chamois did not decrease as pasture availability became lower, which militates against an increase of fission events throughout a temporal, decreasing gradient of food availability. Although the productivity of vegetation in upper grasslands decreases from July to October (Primi et al., 2016: 125, for ALMNP; Fig. 3a and Table S4, Supplementary Material, for our study area), the proportion of nutritious forbs in diet of female chamois in our study area has been shown to be relatively high from summer to autumn, suggesting a great availability of nutritious pasture for chamois and therefore the possibility to select the best food (Ferretti et al., 2015). In turn, group size may have not shown the expected decrease through months: group splitting to avoid foraging interference would be unnecessary, if the best food is available.

Apart from the decreasing proportion of yearlings in group, the increasing proportion of females in groups from July to October (our prediction, *iii*) could have been also triggered by food dispersion. In autumn, female chamois concentrate on nutritious forbs (*Leguminosae*), which are patchily distributed (Ferrari et al., 1988), thus influencing group size and cohesion (Lovari and Cosentino, 1986). In spite of the approaching mating season, proportion of males did not increase, not supporting our prediction (*iii*). The rut of Apennine chamois is highly synchronised in November–early December (Lovari and Locati, 1991), with males herding females to perform courtship. Most likely, our study period did not allow us to detect males joining mixed group of females and juveniles, as males live solitary, at lower altitudes, outside the rutting season (Lovari and Cosentino, 1986). In addition, even a slight increase in proportion of males in October may have not been detected because of their very low absolute occurrence in mixed group compared to other sex-age classes (see Results).

Apennine chamois give births in May-early June, making the newborn kids more vulnerable at the onset of summer. One could have expected that kids would tend to stay closer to their mothers during early summer than in autumn, mainly to be protected against potential predators (accordingly, in this population, female vigilance decreased throughout July-October: Fattorini et al., 2018b). Nevertheless, in contrast to our prediction (*iv*), occurrence of kids in mixed groups did not change from summer to autumn, suggesting that females were still accompanied by kids after weaning (Richard-Hansen and Campan, 1992; Pérez-Barbería and Nores, 1996; Ruckstuhl and Ingold, 1999). Also, an even occurrence of kids in group through months may indicate a low mortality throughout weaning. Conversely, the decrease of yearlings in groups through days (our prediction, *iv*) suggests that they may leave mixed groups after one year from birth, when mothers start to raise the newborn kids (*cf.* Hutchins, 1984, for mountain goat *Oreamnos americanus*). As in other mountain ungulates (e.g. Festa-Bianchet, 1991; Romeo et al., 1997), previous works on chamois have shown that yearlings and subadult males are the main dispersers (Loison et al., 1999b, 2008), which supports our results. Alternatively, the decreasing occurrence of yearlings in groups might also be due to a higher predation pressure on this age class (Cote et al., 1997; Baruzzi et al., 2017), not kept under mother protection as kids.

Summer-autumn group structure of Apennine chamois was consistent with the typical pattern of sexual-age segregation shown by mountain ungulates. In mountain-dwelling species, sexual segregation usually reflects the spatial/habitat ones, i.e. the different use of space/habitat across sex-age classes (see also Ruckstuhl, 2007; Biggerstaff et al., 2017, for temporal segregation). Mixed groups of females and juveniles tend to select sites located at higher altitudes and/or closer to escape terrain than males (e.g. upper grasslands: Shank, 1985; Lovari and Cosentino, 1986; Bleich et al., 1997; Ciuti et al., 2009). Their habitat selection is influenced not only by antipredatory ploys (e.g. rugged/steep terrain: Mooring et al., 2003; shorter distance to rocky cliffs/ridges: Baruzzi et al., 2017), but also by their great energy requirements during nursing/weaning, leading to selection of sites providing high-quality vegetation patches (Shank, 1985; Lovari and Cosentino, 1986; Bourgoin et al., 2018; but see Bleich et al., 1997; Ciuti et al., 2009). Several hypotheses have been proposed to explain the adaptive significance of sexual/spatial segregation, in ungulates (Main et al., 1996; Bleich et al., 1997; Ruckstuhl and Neuhaus, 2002; Ruckstuhl, 2007). Most likely, the ultimate, adaptive determinant of segregation is an increase of reproductive success for both sexes (Main, 2008, for a review). Accordingly, a larger number of females living in the same group can provide offspring with additional benefits, such as collective protection against predators (dilution of risk: Pipia et al., 2009; vigilance: Lashley et al., 2014; active defence: Lingle, 2001) and alloparental cares (e.g. allosuckling: Plesner Jensen et al., 1999). Similarly, solitary males can maximise their energy gain, thus reproductive investment, e.g. through feeding more efficiently (Bleich et al., 1997). These predictions seems to be supported for Apennine chamois, as females showed allonursing (Scornavacca et al., 2018) and males showed a greater foraging efficiency than females (Ferretti et al., 2014).

Our findings suggest that summer-autumn variation of activity and grouping patterns are ultimately driven by the interplay of different temporal mechanisms such as constrains of biological cycle (e.g. approaching the rut) and those of environmental factors (e.g. food availability, temperature, daylight duration). In a relatively “rich” area, as in our study site (see Ferretti et al., 2015, for comparison with other neighbouring areas), the temporal gradient of pasture availability may have not been a major determinant for grouping phenology. Nevertheless, in poorer habitats, where competition between conspecifics increases (Fattorini et al., 2018a), these patterns might be different. The predictability of seasonal transitions have helped individuals to synchronise behaviour during their life-history. In turn, potential unpredictable seasonality shifts such as those elicited by current environmental changes (e.g. Walther et al., 2002) and/or food depletion could further influence the timing of activity and grouping dynamics of individuals. To this end, effects on these behaviours should be uncovered through long-term studies on herbivores living in altered habitats.

Acknowledgements

We are indebted to D. Febbo, G. Rossi and A. Carrara for their continuous support, and to the ALMNP staff for logistic support. D. Scornavacca, S. Bernardini, A. Cotza and V. Pietrocini helped with data collection in 2014 and N. Pallari in 2015. Special thanks go to L. Corlatti and two anonymous reviewers who provided valuable comments and improved the manuscript.

S. Lovari and F. Ferretti planned this study; N. Fattorini participated in study planning, conducted most data collection and data analyses, wrote the first draft and participated in writing all drafts; F. Ferretti participated in data collection and analyses, as well as in writing up all drafts. S. Lovari supervised all stages of this study and participated in writing up all drafts; C. Brunetti participated in data collection and helped in data analysis; C. Baruzzi participated in data collection and in writing up the last draft; G. Chiatante conducted EVI analyses and wrote the relevant text.

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Our work followed the ARRIVE guidelines, the U.K. Animals (Scientific Procedures) Act, 1986 and associated guidelines, the EU Directive 2010/63/EU for animal experiments and the National Institutes of Health guide for the care and use of Laboratory animals (NIH Publications No. 8023, revised 1978).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2019.103909.

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