



## Animal conflicts escalate in a warmer world

Niccolò Fattorini<sup>a,b,\*</sup>, Sandro Lovari<sup>a,c</sup>, Sara Franceschi<sup>d</sup>, Gianpasquale Chiatante<sup>b,e</sup>,  
Claudia Brunetti<sup>a</sup>, Carolina Baruzzi<sup>a,f</sup>, Francesco Ferretti<sup>a,b</sup>

<sup>a</sup> Department of Life Sciences, University of Siena, Via P.A. Mattioli 4, 53100 Siena, Italy

<sup>b</sup> NBFC, National Biodiversity Future Center, 90133 Palermo, Italy

<sup>c</sup> Maremma Natural History Museum, Strada Corsini 5, 58100 Grosseto, Italy

<sup>d</sup> Department of Economics and Statistics, University of Siena, Piazza San Francesco 8, 53100 Siena, Italy

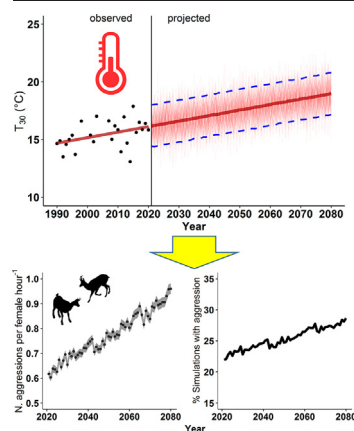
<sup>e</sup> Department of Biology, University of Florence, Via Madonna del Piano 6, 50019 Sesto Fiorentino, Italy

<sup>f</sup> Department of Wildlife Ecology and Conservation, North Florida Research and Education Center, University of Florida, 155 Research Rd., Quincy, FL 32351, USA

### HIGHLIGHTS

- Climate change influences animal behaviour, yet effects on aggression are unknown.
- We tested cumulative effects of warming/drought on aggression, in a wild herbivore.
- Warming/drought increased aggression at feeding through vegetation-mediated effect.
- Simulations predicted 50 % increase in aggression by 2080 due to accumulated warming.
- Climate change may exacerbate intraspecific conflicts within animal societies.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

Editor: Rafael Mateo Soria

#### Keywords:

Aggression  
Animal conflicts  
Climate change  
Drought  
Global warming  
Resource competition

### ABSTRACT

The potential for climate change to affect animal behaviour is widely recognized, yet its possible consequences on aggressiveness are still unclear. If warming and drought limit the availability of food resources, climate change may elicit an increase of intraspecific conflicts stemming from resource competition. By measuring aggressivity indices in a group-living, herbivorous mammal (the Apennine chamois *Rupicapra pyrenaica ornata*) in two sites differing in habitat quality, and coupling them with estimates of plant productivity, we investigated whether harsh climatic conditions accumulated during the growing season influenced agonistic contests at feeding via vegetation-mediated effects, and their interaction with the site-specific habitat quality. We focused on females, which exhibit intra-group contest competition to access nutritious food patches. Accounting for confounding variables, we found that (1) the aggression rate between foraging individuals increased with the warming accumulated over previous weeks; (2) the probability to deliver more aggressive behaviour patterns toward contestants increased with decreasing rainfall recorded in previous weeks; (3) the effects of cumulative warming and drought on aggressivity indices occurred at time windows spanning 15–30 days, matching those found on vegetation productivity; (4) the effects of unfavourable climatic conditions via vegetation growth on aggressivity were independent of the site-specific habitat quality. Simulations conducted on our model species predict a ~50 % increase in aggression rate following the warming projected over the next 60 years. Where primary productivity will be impacted by warming and drought, our findings suggest that the anticipated

\* Corresponding author.

E-mail address: [niccolo.fattorini@unisi.it](mailto:niccolo.fattorini@unisi.it) (N. Fattorini).

<http://dx.doi.org/10.1016/j.scitotenv.2023.161789>

Received 24 October 2022; Received in revised form 29 December 2022; Accepted 19 January 2023

Available online 28 January 2023

0048-9697/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

climate change scenarios may trigger bottom-up consequences on intraspecific animal conflicts. This study opens the doors for a better understanding of the multifactorial origin of aggression in group-living foragers, emphasising how the escalation of agonistic contests could emerge as a novel response of animal societies to ongoing global warming.

“As climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food.”

[C. Darwin, On the Origin of Species, 1859]

## 1. Introduction

Aggression is ubiquitous in the animal kingdom, primarily arising from competition for mates, food or shelter. Intraspecific social interactions govern coexistence patterns of group-living species, and underpin the origins, maintenance, and diversification of animal societies (Hardy and Briffa, 2013; Moss and While, 2021). Conspecifics usually interact via agonistic behaviours to establish dominance hierarchies leading to reciprocal rank assessment, thus reducing overt aggression and the risk of injurious fighting (Maynard Smith and Price, 1973; Clutton-Brock and Albon, 1979; Clutton-Brock et al., 1979). Aggressiveness is delivered through a continuum of behaviour patterns spanning dominance postures, threat displays, appeasements and avoidance, which rarely culminate into attacks due to cost of fighting. A plethora of eco-evolutionary processes is regulated by intraspecific agonistic interactions. Aggressive contests may impact on individual resource acquisition and body growth, can suppress reproduction as well as influence physiology, fitness and survival, ultimately affecting vital rates of animal populations (Potter et al., 1976; Clutton-Brock and Parker, 1995; Packer et al., 1995; Milner-Gulland et al., 2003).

Although the potential for climate change to affect animal behaviour has been widely recognized (Tuomainen and Candolin, 2011; Wong and Candolin, 2015), the mechanistic pathways underlying its possible effects on aggression are poorly understood, and recent studies call for uncovering the consequences of anticipated warming scenarios on these pathways (Fisher et al., 2021). Surprisingly, few studies have explored the effects of temperature on aggressive behaviour, and relevant information is limited to direct effects of warming. Research conducted across various animal taxa has shown either increases, decreases, or nonlinear variations in agonistic contests with warmer temperatures, at both intra- and interspecific levels (spiders: Doering et al., 2018; insects: Nguyen and Stahlschmidt, 2019; crustaceans: Gherardi et al., 2013; fish: Kua et al., 2020; birds: Gudka et al., 2019; mammals: Xu et al., 2021). Most often, these proximate effects of temperature are intimately linked to species-specific energetic constraints depending on the interplay between heat stress, thermal balance and metabolic rate (Fisher et al., 2021). Conversely, we know little about how animals might alter their levels of aggression following second-order, indirect effects of temperature or other climatic variables upon the availability of food resources. Here, we address the lack of empirical evidence by investigating explicitly the effects of climatic variables on aggressive contests, a research direction that has been recommended to be prioritised to understand the consequences of future warming on animal societies (Fisher et al., 2021; Moss and While, 2021).

The resource competition hypothesis predicts that individuals will be more aggressive due to competition for limited food resources (Peiman and Robinson, 2010), contributing to explain between-species difference in aggressivity (Andrade et al., 2021). It thus offers a framework to investigate variation in agonistic contests with changing climatic conditions. A growing body of research is shedding light on the cumulative effects of climatic variables on vegetation productivity (Vicente-Serrano et al., 2013; Wen et al., 2019; Ding et al., 2020; Wei et al., 2022; Yuan et al., 2022; Zhang et al., 2022). Unlike instantaneous and lagged effects, cumulative effects do not ignore chronic and carryover effects of weather on plant growth, providing more insights about responses of vegetation to recent

climate change (Yuan et al., 2022). Indeed, ecologists have started to reveal how cumulative effects of weather underlie resource-dependent ecological responses of animal populations by driving food quality and availability (Ferretti et al., 2019; Hidalgo Aranzamendi et al., 2019). Amongst meteorological parameters, accumulated temperature and precipitation exert the strongest signatures on global patterns of vegetation growth, though with differences across seasons, biomes and geographic areas (Ding et al., 2020; Wei et al., 2022; Yuan et al., 2022; Zhang et al., 2022). Where cumulative warming and drought limit the availability of food resources for herbivorous species, climate change may trigger an increase in intraspecific conflicts stemming from the resource competition hypothesis.

Climate change effects are particularly severe for organisms adapted to strongly seasonal habitats such as mountain “specialists” (Pepin et al., 2015; Schmeller et al., 2022). In mountain ecosystems, global warming has altered the distribution of cold-adapted plant species, with elevational shifts and a general thermophilization of alpine vegetation across continents (Gottfried et al., 2012; Pauli et al., 2012; Zu et al., 2021). Warming temperatures reduce abundance and persistence of sensitive mountain vegetation (Nomoto and Alexander, 2021), decreasing the quality and availability of food resources for herbivores. Warming-induced habitat loss and seasonal mismatch of pasture availability can substantially affect resource allocation, population dynamics and viability of mountain herbivores (Pettorelli et al., 2007; White et al., 2019; Lovari et al., 2020). Here we consider a mountain-dwelling species, the Apennine chamois *Rupicapra pyrenaica ornata*, to test the prediction that warming temperature and drought increase intraspecific aggressiveness during feeding through cumulative effects of unfavourable climatic conditions on vegetation growth. The chamois is a group-living herbivore whose females are particularly dependent on high-quality, cold-adapted forbs to meet energetic demands during lactation (Lovari et al., 2020). Indeed our hypothesis has been focused on female chamois because, in summer, they forage together with yearlings and juveniles on alpine meadows, exhibiting intra-group contest competition to access nutritious food patches (Locati and Lovari, 1990; Fattorini et al., 2018a,b). Success in displacing contestants guarantees priority access to resources, with disputes increasing in frequency and intensity where resources are scarce (Fattorini et al., 2018b).

We took advantage of a quasi-experimental situation by measuring aggressivity indices coupled with remote-sensing estimates of plant productivity in two sites differing in habitat quality, particularly in terms of availability of high-quality vegetation and ensuing population viability, to investigate whether harsh climatic conditions during the growing season influenced agonistic contests via vegetation-mediated effects. Furthermore, we assessed how this relationship depended on site-specific habitat quality. Following the resource competition hypothesis, we predicted that chamois would increase aggressiveness following detrimental effects of accumulated warming and drought on vegetation productivity, and expected a stronger increase in aggressiveness in the food-restricted, lower-quality site.

## 2. Materials and methods

### 2.1. Study area and population

Our study was conducted within the Abruzzo Lazio and Molise National Park (central Apennines, Italy), a protected area with temperate oceanic bioclimate (Pesaresi et al., 2014). We worked in two sites of similar size, located ~6 km apart (food-restricted site: upper Val di Rose, 0.4 km<sup>2</sup>, 1800–1982 m; food-rich site: Mt. Meta, 0.3 km<sup>2</sup>, 2100–2242 m). Both sites were covered by alpine grasslands dominated by forbs and

graminoids, yet they markedly differed as to habitat quality, in terms of availability of nutritious vegetation for chamois and relevant effects on population viability. Patches of cold-adapted, protein-rich forbs, the most nutritious and selected food resource by chamois (Ferretti et al., 2014, 2015; Lovari et al., 2020), were ~40 % more abundant in the food-rich site (Ferretti et al., 2015, 2019); moreover patches dominated by unpalatable graminoids were ~10 times more widespread in the food-restricted site (Ferretti et al., 2015, 2019). Previous studies found lower feeding efficiency, poorer diet quality, higher endogenous stress levels, less maternal care by female chamois, and reduced overwinter survival of offspring, in the food-restricted site than in the food-rich one (Ferretti et al., 2015, 2019; Scornavacca et al., 2016; Fattorini et al., 2018b). The negative effects of resource depletion affected the chamois population, which collapsed by ~70 % in the food-restricted site during the last four decades (Lovari et al., 2014, 2020). Over the same period, the population increased in the food-rich, “refuge” site, at higher elevation, where chamois was absent a few decades ago (Lovari et al., 2020), emphasising the superior habitat quality of this site (sensu Rachlow, 2008; Stamps, 2008). In our study period, respectively in 2014 and 2015, the minimum number of chamois observed at the same time in mixed groups was 32 and 21 in the food-restricted site, and 68 and 69 in the food-rich site. Because female ungulates generally show strong philopatry (e.g. Loison et al., 1999, 2008, for Northern chamois *R. rupicapra*), we can reasonably assume that females did not move between the two study sites during our study period. This assumption is supported by preliminary data on females tracked in our same study sites through VHF and GPS telemetry, which showed local herd/site fidelity (Latini et al., 2013). Moreover we did not observe females with morphologically distinct features (e.g. broken horns, scars) moving between our study sites.

Potential terrestrial predators of chamois move across both sites, but predation on chamois is negligible (wolf *Canis lupus*: 1.6 % in diet; brown bear *Ursus arctos*: <0.05 % in diet; Ciucci et al., 2014, 2020). Predation on juvenile chamois by golden eagle *Aquila chrysaetos* is also rare (Scornavacca and Brunetti, 2016). Additionally, predator attacks do not appear to influence aggressive behaviour in female chamois (Baruzzi et al., 2017). For further details on study areas, see Ferretti et al. (2015).

## 2.2. Behavioural data collection

We collected data on chamois aggressive behaviour between 1<sup>st</sup> July and 31<sup>st</sup> August 2014 and 2015, corresponding to the main nursing stage, when mixed groups of females, yearlings and juveniles gather on alpine meadows to forage on high-quality vegetation (Lovari and Cosentino, 1986; Fattorini et al., 2019). Male chamois, by contrast, tend to live in forests at lower elevations (Lovari and Cosentino, 1986), segregating from females and escaping regular observation. Animals were observed from dawn to dusk, using binoculars or spotting scopes, at a distance of 50–200 m, depending on terrain and range of vision. We avoided recording data whenever chamois appeared to react to our presence. Sexually mature ( $\geq 2$  years old) female chamois can be distinguished from males and age classes can be discriminated visually (Lovari, 1985). We recorded data on foraging groups of females, considering a group as at least two mature females in sight of each other and <40 m apart (Bruno and Lovari, 1989). The focal group was selected immediately after detection and observed continuously, for at least 30 min and up to a maximum of ~6 h, depending on its movements and visibility. We used 5-minute sampling bouts to record the number of aggressive contests between females, through continuous focal-group sampling, and group size and structure, through instantaneous scan sampling (Altmann, 1974). In both years, we conducted 6–8 observation hours day<sup>-1</sup>, during at least 7–8 days at each site every month.

Aggressive contests while feeding can occur either as a single aggressive behaviour pattern displayed by the attacker followed by immediate submission or escape of the recipient (Supplementary Content 1) or as escalated encounters, including a series of consecutive behaviour patterns displayed by both opponents for a few seconds until one (the ‘loser’) is displaced, implying that the attacked individual reacted to the aggressor. For ~98 % contests ( $n = 740$ ), we were able to record opponents' age classes and

behaviour patterns displayed during the interaction. Only aggressive patterns delivered by ‘winners’ were considered for analysis, as ‘losers’ performed a negligible proportion (~3 %,  $n = 1015$ ) of the aggressive patterns recorded, mainly exhibiting submissive patterns or escaping. Female chamois deliver indirect or direct forms of aggressiveness to displace rivals (ungulates: Walther, 1974; Schaller, 1977; chamois: Locati and Lovari, 1990; Lovari and Locati, 1993), and this categorisation has been used to evaluate the intensity of feeding contests in this mammal (Fattorini et al., 2018a,b). Indirect forms involve ritualized behaviours such as dominance postures/displays and are considered to be less aggressive. Direct forms, encompassing overt threats such as approaches and chases (Supplementary Content 1), are more intense, less ritualized forms of aggression and may include attempts at physical contact.

## 2.3. Vegetation productivity

Remote-sensing indices are commonly implemented to assess ecological responses of animal populations to vegetation (Pettorelli et al., 2005). We used the Enhanced Vegetation Index (EVI) as a proxy for assessing accumulated weather effects on vegetation productivity (see Villamuelas et al., 2016; Lovari et al., 2020, for chamois). We obtained EVI data from the MOD13Q1 product of the MODIS sensor (Moderate Resolution Imaging Spectroradiometer) from the TERRA satellite of NASA accessible from the United States Geological Survey (USGS; <https://earthexplorer.usgs.gov>), at temporal resolution of 16 days and spatial resolution of 250 m. Daily EVI in both study sites and years was obtained by linearly interpolating 16-days MODIS scenes obtained over the study period (each scene was made by 46 images from which the EVI was averaged). For each site and year, daily EVI was standardized by the maximum value recorded, making it comparable across our study sites and years to identify the relationship between relative vegetation productivity and climatic conditions recorded at a fixed location. Such normalization is recommended to better compare vegetation productivity anomalies between different areas and years (Pettorelli et al., 2005; Meroni et al., 2019).

## 2.4. Meteorological variables

Mean daily temperatures (°C) and daily amounts of rainfall (kg m<sup>-2</sup>) were derived by 10-minute resolution data recorded at a weather station ~10 km from both study sites (Passo Godi station, 1570 m elevation). Because our study sites differed slightly in elevation, temperature recorded from a fixed altitude location allows testing site-specific effects without being confounded by decreasing ambient temperature with increasing elevation (Mason et al., 2014a). We calculated the mean daily temperature and the total amount of rainfall over various time windows prior to each observation day to test indirect effects of weather (Ferretti et al., 2019, for chamois in our study sites). At the planetary scale, sensitivity of vegetation to cumulative effects of climatic conditions during the growing season has been reported to occur mostly at time-lags between 15 and 40 days (Ding et al., 2020). In our study area, snowmelt occurs in late spring, and the ground is snow-free from late-May/early-June (Bruno and Lovari, 1989). Time windows beginning >30 days prior to 1<sup>st</sup> July, our first observation day, are therefore unlikely to be relevant to accumulated weather effects on aggressive behaviour if the latter is mediated by vegetation, because of the masking effect of snow cover on vegetation growth (Ferretti et al., 2019). Moreover considering long time-lags would increase the risk of false positive climatic signals due to spurious effects (Hidalgo Aranzamendi et al., 2019). For analysis, we thus used arbitrarily defined time windows of 15, 20, 25, and 30 days.

## 2.5. Statistical analysis

The principal aim of our study was to test explicitly the potential link between accumulated climatic conditions and animal aggression, to understand how the anticipated climate change scenarios may drive aggressive contests. Because we hypothesised that cumulative effects of weather

would be the *ultimate* determinant of aggression between foraging individuals (Fig. 1), the logic of our analytical approach was primarily aimed at investigating whether accumulated temperature and rainfall during the growing season influenced aggression indices. Separately, we also investigated cumulative effects of weather on vegetation growth, which is expected to be the *proximate* determinant of aggression according to the resource competition hypothesis (Fig. 1). Analyses were run and presented first by considering meteorological parameters accumulated within the time window spanning 30 days prior to the focal observation day (see below), but then they were repeated by considering the other time windows to explore the appropriate timescales at which climatic signals on aggression may occur. We hypothesised cumulative, i.e. indirect, effects of weather on aggression, but previous studies also show potentially direct effects of temperature on aggression (see Introduction). Thus, we also repeated the analyses by using the temperature recorded in each 5-minute observation bout. Direct effects of rainfall were not considered because we could not record behavioural data during rainy hours, due to limited visibility. Eventually, to support the occurrence of proximate effects of vegetation productivity on aggression indices, we conducted a separate analysis where we replaced meteorological predictors with the standardized EVI.

We analysed the effects of temperature and rainfall on aggression indices using generalized linear mixed models (GLMMs; Zuur et al., 2009). Intra-group aggression rate, the number of aggressions between females recorded in 5-minute sampling bouts, was standardized by the corresponding number of females in the group to index the number of aggression per female, hereafter defined as the *pro capite* aggression rate, and modelled with tweedie errors (log link function) to handle continuous,  $0^+$  values ( $n = 2479$  data-points). Aggression intensity, defined as the probability to display a threat toward the recipient during an aggressive contest, was modelled with binomial errors (logit link function) to handle presence/absence data ( $n = 982$  data-points). For both aggression indices, we included as fixed effects mean daily temperature,  $T_{30}$  (continuous, in  $^{\circ}\text{C}$ ), and total amount of precipitation,  $P_{30}$  (continuous, as  $\text{kg m}^{-2}$ ), recorded over 30 days prior to each focal observation, as well as their interactions with the study site (factor; reference level: food-rich site) to investigate site-specific, habitat quality effects of cumulative climatic conditions in influencing animal aggressiveness. We also considered a set of fixed effects to account for confounding variables known to influence female aggression in chamois. We included the linear and the quadratic effects of time of day

(continuous, standardized as negative or positive decimal hours from solar noon), as aggression indices tend to increase or decrease while departing from noon (Fattorini et al., 2018a,b); Julian date (integer, as days elapsed from 1<sup>st</sup> January), to control for the linear variation in female aggressiveness over the nursing stage (Fattorini et al., 2018b). For aggression intensity we also included as fixed effects whether the contest was escalated (factor; reference level: no escalation), the opponent's relative age class (factor; reference level: same age class), and the age class of the actor of each aggressive behaviour delivered (factor; reference level: subadult), because these variables may influence the probability of displaying more or less intense aggressions in chamois (Locati and Lovari, 1990, 1991; Fattorini et al., 2018b). For both aggression indices, we included group identity as a random intercept to control for repeated observations of the same chamois group.

Cumulative effects of weather on vegetation productivity were analysed through GLMMs, by modelling the standardized daily EVI through beta errors (logit link function), as customarily done when handling continuous proportions (standardized EVI = 1 was considered equivalent to  $1-10^{-10}$ , to enable the use of beta errors without altering its biological meaning). We included as fixed effects  $T_{30}$ ,  $P_{30}$ , and their interactions with the study site, as well as the linear effect of Julian date to consider the general decreasing trend of EVI throughout the study period (Fattorini et al., 2019, for our study area). We included the year as a random intercept to account for repeated measurements of EVI recorded in the same year. Preliminary exploration of model residuals also suggested heterogeneity of variance between observed and interpolated EVI values, as well as in relation to the interaction between accumulated temperature and study site, which we accounted for by modelling the dispersion against these variables.

In all models, we scaled covariates and found no multicollinearity amongst them ( $r < |0.5|$ ; VIFs  $< 2$ ). For each full model specified as above, we conducted a model selection to determine the top-ranked model(s) best supporting our data. Model selection was performed by comparing all possible candidate models, including the null model, because each of them could represent an alternative, plausible hypothesis. We used the Akaike's Information Criterion corrected for small samples (AICc) to rank models, a metric trading-off model complexity with goodness of fit (Aho et al., 2014). We followed the 'nesting rule' to avoid retaining overly complex models (Harrison et al., 2018): models with  $\Delta\text{AICc} \geq 2$  with respect to the best model (i.e., the model with the lowest AICc value), as well as models with an AICc value greater than that of any simpler alternative were not selected. Model weight, reflecting the probability that a given model is the best model, was thus standardized within each subset of selected models. Results of model selections are reported in Appendices 1–5 (Supporting information). For each response variable, we used the best model to make inference on the effects of predictors by assessing whether 95 % confidence intervals of coefficients overlapped 0. Best models were validated via inspection of residuals and assessment of model fit (Appendix 6, Supporting information). GLMMs and model selections were conducted respectively through the R packages *glmmTMB* (Brooks et al., 2017) and *MuMIn* (Bartoń, 2020).

## 2.6. Predicting future aggression rate

Accumulated summer temperatures varied significantly in our study area during the last decades, while cumulative summer precipitation remained relatively stable (Appendix 7, Supporting information). Therefore, for 2021–2080, we simulated changes only in the aggressivity index of chamois influenced by temperature, i.e. the aggression rate (see Results). Simulations of aggression rate were based on future trajectories of  $T_{30}$  specifically projected by considering the past summer temperatures occurred in our study area (Appendix 7, Supporting information). During the last decades, linear/exponential increases of global temperatures have occurred (Hegerl et al., 2018). Thus, our projection assumed no major variation in the trend of temperature increase until 2080. We used temperature over 30 days prior to 1<sup>st</sup> August to allow comparison of our locally-calibrated

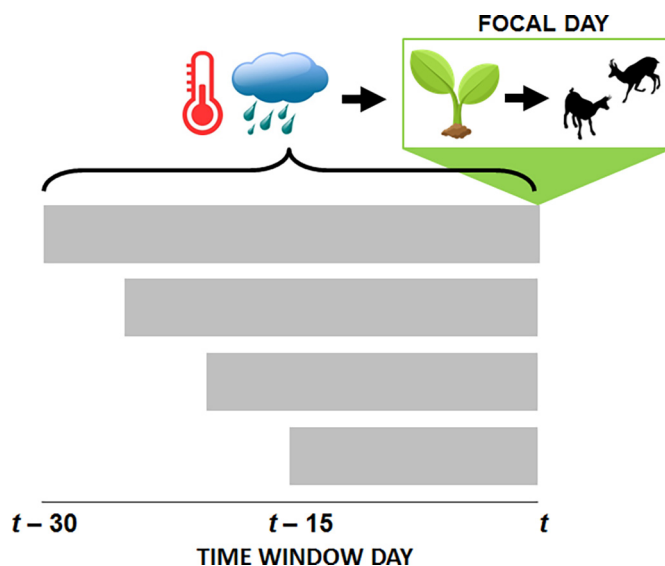


Fig. 1. Schematic representation illustrating the logic behind our investigation. Cumulative effects of temperature and rainfall, considered over various time windows (grey bars) prior to focal observation day ( $t$ ), determines vegetation growth at day  $t$ , which in turn drives frequency and intensity of feeding contests between female chamois at day  $t$ .

projections at the median date of the study period to those forecasted by global models and available at the monthly scale. Indeed, our projections of summer climatic conditions over a month prior to 1<sup>st</sup> August in 2021–2080 were consistent with those forecasted in the study area in July through the ensemble of 84 CMIP6 scenarios (21 Global Circulation Models coupled with four Shared Socioeconomic Pathways of climate policy) encompassing the likely range of future radiative forcing (Appendix 8, Supporting information).

For every simulated trajectory of  $T_{30}$ , say  $\{T_{30,t,i}\}$  with  $t = 2021, \dots, 2080$  and  $i = 1, \dots, 10,000$ , and for each of the three arbitrary time periods separately (Time = -5, 0, 5 h from noon), we generated the corresponding trajectory of the *pro capite* intra-group aggression rate at a fixed date (Julian day = 212, i.e. 1<sup>st</sup> August). Hence, we simulated 10,000 trajectories according to the model where the *pro capite* intra-group aggression rate in the  $i$ -th trajectory for the year  $t$ , say  $\{Y_{t,i}\}$ , was a random variable generated from a Tweedie distribution  $TW_p(\mu_{t,i}, \Phi)$  with expectation

$$E(Y_{t,i}) = \mu_{t,i} = g^{-1}(\beta_0 + u + \beta_1 T_{30,t,i} + \beta_2 \text{Time} + \beta_3 \text{Time}^2 + \beta_4 \text{Julian day})$$

and variance

$$V(Y_{t,i}) = \Phi \mu_{t,i}^p,$$

where the link function  $g$  was the natural logarithm,  $\beta_0, \beta_1, \beta_2, \beta_3$  and  $\beta_4$  were the coefficients estimated from the top-ranked model, the random intercept  $u$  was generated from a normal distribution with 0 expectation and variance  $\sigma^2$  estimated from the top-ranked model, and  $\Phi$  and  $p$  were the parameters of the Tweedie distribution estimated from the top-ranked model. For simulations, we used parameters of the top-ranked model fitted with unstandardized covariates. Finally, as the simulated aggression rate reflected the *pro capite* frequency of agonistic contests in 5-minute sampling bouts, we hour-normalized it so that the *pro capite* intra-group aggressions hour<sup>-1</sup> was  $12 Y_{t,i}$ .

### 3. Results

Overall, we recorded 1607 animal-hours of observations (i.e., 2479 bouts on 71 focal groups; mean  $\pm$  S.E.:  $34.9 \pm 2.35$  bouts group<sup>-1</sup>;  $2.9 \pm 0.19$  observation hours group<sup>-1</sup>;  $7.8 \pm 0.12$  females bout<sup>-1</sup>), observing a total of 740 aggressive contests (mean  $\pm$  S.E. number of aggressions per female hour<sup>-1</sup> and percentage of threats delivered to contestants, respectively: food-restricted site,  $0.6 \pm 0.1$  and  $87.2\% \pm 2.88\%$ ; food-rich site,  $0.6 \pm 0.1$  and  $84.7\% \pm 2.89\%$ ). Neither the best model predicting aggression rate nor that explaining aggression intensity supported the effect of site-specific habitat quality or its interaction with climatic conditions, yet both best models supported cumulative effects of weather on aggressivity indices (Appendices 1–2, Supporting information).

The *pro capite* aggression rate was positively influenced by the temperature accumulated over the previous 30 days: independently of confounding variables, as average temperature rose from 12.1 to 17.7 °C, aggression frequency increased by ~120% (Table 1a; Fig. 2a). Sensitivity analyses confirmed this result for time windows of 15, 20 and 25 days preceding focal observations (Appendix 1, Supporting information). Conversely, aggression rate was not influenced by the direct effect of temperature (Appendix 4, Supporting information). Rainfall was not selected as an influential predictor of aggression rate at any time window (Table 1a and Appendix 1, Supporting information).

We found that the probability to deliver more aggressive behaviour patterns to contestants increased with decreasing rainfall over the previous 30 days: accounting for confounders, as rainfall decreased from 134.6 to 20 kg m<sup>-2</sup>, threat delivering probability increased by ~25% (Table 1b; Fig. 2b). We obtained the same result considering time windows of 15, 20 and 25 days (Appendix 2, Supporting information). In all cases, temperature was never supported as a predictor driving the probability of delivering more or less aggressive behaviour patterns to contestants (Table 1b and Appendix 2, Supporting information).

**Table 1**

Parameters estimated from the best GLMM predicting (a) aggression rate and (b) aggression intensity of foraging female chamois *Rupicapra pyrenaica ornata*: variance of random intercepts ( $\sigma^2$ ), dispersion parameter ( $\Phi$ ), power parameter ( $p$ ), predictors' coefficient estimates ( $\beta$ ) and their 95% confidence intervals (CIs). An asterisk marks coefficients whose CIs do not include '0'. Cumulative effects of mean temperature ( $T_{30}$ ) and total amount of rainfall ( $P_{30}$ ) over the previous 30 days on aggression indices are bolded. Reference levels for 'Opponent's relative age' and 'Contest type' are 'younger' and 'not escalated'. All covariates are scaled. For measurement units of explanatory variables, see text.

Aggression index	Predictor	$\beta$ coefficient	95 % CI	
a. <i>Pro capite</i> intra-group aggression rate $\sigma^2_{\text{GroupID}} = 0.344$ $\Phi = 0.755$ $p = 1.328$	Intercept	-3.295	-3.481; -3.109	*
	$T_{30}$	<b>0.257</b>	<b>0.043; 0.471</b>	*
	Julian day	-0.189	-0.410; 0.032	
	Time of day	0.282	0.098; 0.465	*
	Time of day <sup>2</sup>	0.176	0.022; 0.331	*
	b. Aggression intensity $\sigma^2_{\text{GroupID}} = 0.418$	Intercept	2.150	1.757; 2.542
$P_{30}$		<b>-0.314</b>	<b>-0.569; -0.059</b>	*
Julian day		0.429	0.150; 0.708	*
Opponent's relative age (same)		0.542	0.086; 0.998	*
Opponent's relative age (older)		-0.369	-0.912; 0.174	
Contest type (escalated)		-0.806	-1.189; -0.422	*

Best models of relative vegetation productivity provided support to a general effect of the site-specific habitat-quality on standardized EVI for all time windows, with greater productivity in the food-rich, higher-quality site (Appendix 3, Supporting information). Standardized EVI increased with lower temperature and increased rainfall accumulated over time windows of 15, 20, 25 and 30 days, though for most time windows the increase in productivity with decreasing temperature appeared to be weaker in the food-rich site (Appendix 3, Supporting information).

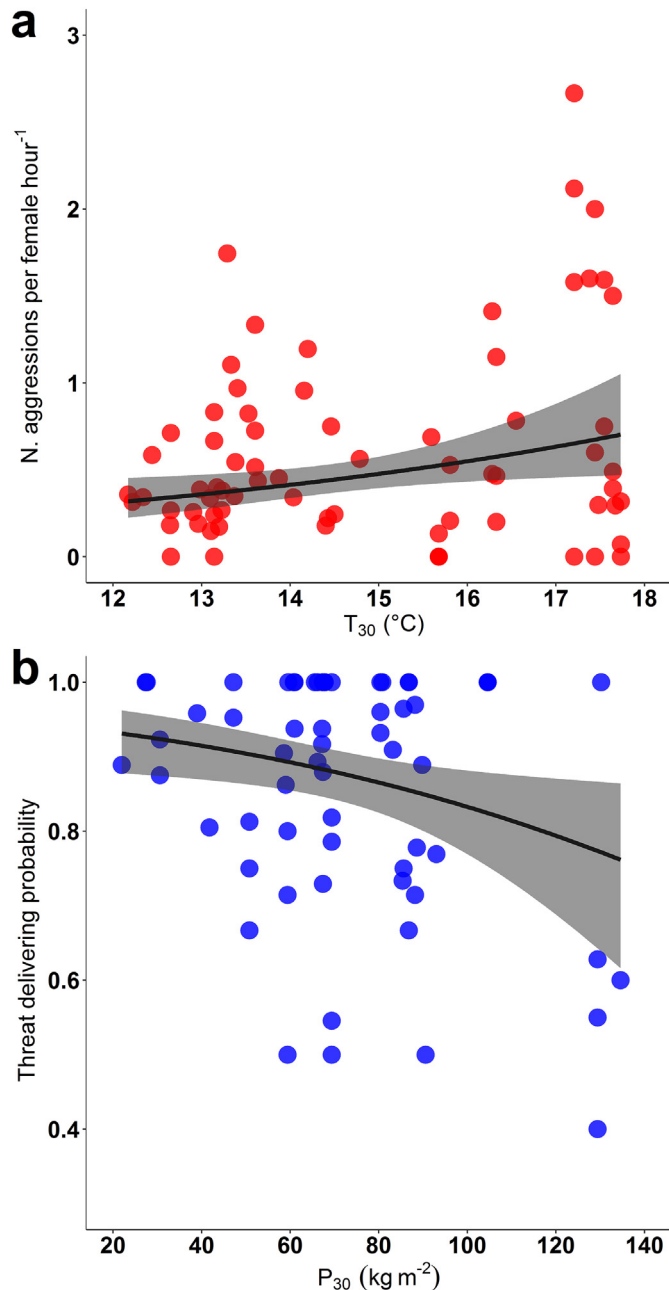
Following an accumulated summer warming of ~2.8 °C in the study area (Fig. 3a), our simulations predicted that the *pro capite* intra-group aggression rate of chamois would increase by 43–56% over the next 60 years, depending on the daily period (Fig. 3b and Appendix 9, Supporting information). The proportion of simulations where chamois engage in agonistic contests at feeding was also predicted to increase by 17–28%, depending on day time (Fig. 3b and Appendix 9, Supporting information).

### 4. Discussion

As the Earth's climate has warmed at an unprecedented rate, profound consequences on animal behaviour have emerged at multiple spatiotemporal scales (Tuomainen and Candolin, 2011; Wong and Candolin, 2015). Despite alarming effects of increasing temperature on foraging, reproductive, and spatiotemporal behaviour have been identified across the animal kingdom, potential consequences on aggressiveness are still obscure. Our study provides the first direct evidence that warmer temperatures may exacerbate animal feeding contests through indirect effects mediated by food resources.

#### 4.1. Increased aggression under climate change: a plastic response to resource-mediated effects of weather

After perturbations in food availability, plasticity in aggressive responses should be adaptive, since aggressiveness is predicted to increase as an evolutionary stable strategy when food resources become scarce (Siro, 2000). Warmer temperatures and drought often limit water and nutrient supply to plants, augmenting fibre and reducing digestible protein contents for wild herbivores (Jonasson et al., 1986; Craine et al., 2009). Moreover, warming and drought directly affect viability of cold-adapted plant communities through effects on their physiology (Nomoto and



**Fig. 2.** Effects of (a) mean temperature ( $T_{30}$ ) and (b) total amount of rainfall ( $P_{30}$ ) accumulated over 30 days prior to focal observation day on (a) the hour-normalized, *pro capite* intra-group aggression rate and (b) the occurrence probability of delivering more aggressive behaviour patterns, while feeding, by female chamois *Rupicapra pyrenaica ornata*. Lines and shading: values predicted while averaging the effects of other confounding variables and 95 % confidence intervals. Dots: observed values averaged by chamois focal-group (a: number of aggression per female hour<sup>-1</sup>; b: proportion of threats over the total amount of aggressive behaviour patterns delivered).

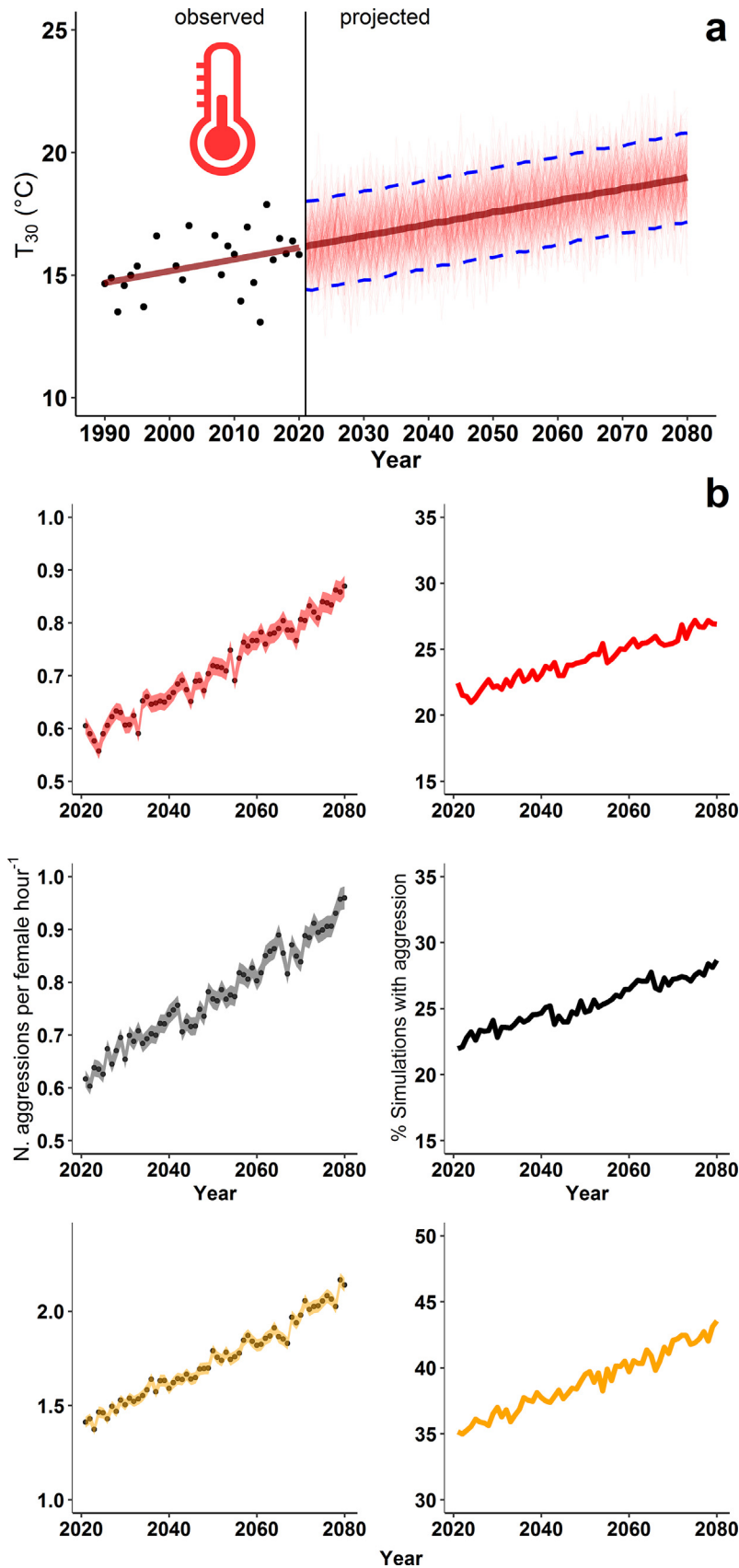
Alexander, 2021), thus shrinking food patches available to herbivores (Lovari et al., 2020). Chamois experiencing hotter and drier conditions over the sensitive period of vegetation growth not only responded by reducing feeding efficiency, as shown in our same study sites (Ferretti et al., 2019), but also increased aggression rate and escalated the intensity of aggressive contests to displace potential competitors, likely securing access to food patches. In mountain herbivores, increased warming during the growing season appears to reduce mass gain either through heat stress or perturbations in food availability (Rughetti and Festa-Bianchet, 2012;

Mason et al., 2014b), and drier conditions have been shown to trigger forage quality-mediated endogenous stress response (Anderwald et al., 2021). In our study areas, the decrease in relative vegetation productivity with warmer temperatures and reduced rainfall matched the temporal scales of climatic signals found on aggressive behaviour, between 15 and 30 days, conforming to findings at the global scale (Ding et al., 2020). Conversely, we did not find direct effects of weather on aggressivity indices. Furthermore, models replacing the cumulative effects of weather with the proximate effect of vegetation growth confirmed that aggression rate and intensity between chamois increased with reduced plant productivity (Appendix 5, Supporting information). These results strongly suggest that the increase in aggressiveness was driven ultimately by cumulative weather effects on vegetation growth. A hot growing season may increase atmospheric demand for evapotranspiration, inhibiting vegetation growth (Ding et al., 2020). Cumulative water deficit can suppress plant photosynthesis and desiccate soil moisture, reducing nutrient uptake by vegetation (Querejeta et al., 2021). Grasslands are especially sensitive and respond relatively quickly to drought because herbaceous plants have low water storage capacity, mainly obtaining water from topsoil (Wei et al., 2022). Previous data indeed have confirmed worsening feeding conditions of female chamois experiencing accumulated warming and drought in summer (Ferretti et al., 2019). Most likely, cumulative effects of harsh climatic conditions during the growing season thus increased the resource value, that is the motivation for chamois to escalate aggressive contests when feeding.

Effects of other ecological processes, such as interspecific competition, have been suggested to overlap and potentially exceed those of climate in shaping animal behaviour (Mason et al., 2014a; Herfindal et al., 2019, for mammals). Resource exploitation by a large competitor, the red deer *Cervus elaphus*, has been identified as a critical, additive player further reducing pasture quality and foraging efficiency of chamois in our food-restricted, lower-quality site (Lovari et al., 2014; Ferretti et al., 2015, 2019). In fact, relative vegetation productivity was greater in our food-rich site, where the effect of the accumulated warming on plant growth also appeared to be weaker. In contrast to our expectation, however, chamois responded consistently to cumulative climatic conditions at both sites. This result suggests that cumulative effects of harsh climatic conditions on vegetation could raise animal aggressiveness independently of habitat quality, emphasising the potential for climate change to elicit an increase in contest competition even in high-quality habitats, like areas with better resource availability and more viable populations.

#### 4.2. Increased aggression under climate change: potential evolutionary implications

Presently, we know little about how plasticity in aggressive responses could affect fitness, and whether it may translate into selective adaptations. Recent research has provided evidence that aggressive phenotypes are selected in animal populations experiencing extreme climatic events (Little et al., 2019), and that aggression may evolve rapidly through a positive feedback loop on the social environment (Wilson et al., 2009). In other circumstances, whenever intraspecific fighting implies lethal effects, the loss of aggression should be favoured by natural selection (Holway et al., 1998). In this case, climate warming would be expected to lower the fitness of individuals involved in lethal fighting (Andrade et al., 2021). However, in wild herbivores, maintaining access to high-quality food resources is of paramount importance during the favourable season as it promotes – via resource allocation – both individual and offspring survival, increasing lifetime reproductive success (Festa-Bianchet and Jorgenson, 1998; Gaillard et al., 2000; Therrien et al., 2007; McLoughlin et al., 2007; Hamel et al., 2009). Although long-term, individual-specific information on reproductive fitness would be needed to provide evidence of selective advantages in raising aggressiveness, we found that chamois initiating agonistic contests were more likely to displace opponents over food patches (99 % events;  $n = 740$ ), and that delivering more aggressive behaviour patterns elicited an earlier withdraw of contestants (Table 1b). This suggests that



**Fig. 3.** (a) Observed and forecasted cumulative summer warming in our study area following locally-calibrated projections of accumulated temperatures ( $T_{30}$ ) at the median date of our study period (Appendix 7, Supporting information, for details); for projection, the median (solid line), 5<sup>th</sup> and 95<sup>th</sup> percentiles (dashed lines), and 250 randomly selected trajectories (hollow lines) of  $T_{30}$  are shown. (b) Simulations conducted at three different daily periods (– 5, 0 and 5 h from solar noon, from top to bottom) predicting (left panel) the mean annual, hour-normalized, *pro capite* intra-group aggression rate of chamois *Rupicapra pyrenaica ornata* (shading: standard error) and (right panel) the percentage of simulations where individuals are engaged in agonistic contests at feeding, in the period 2021–2080.

the pay-off of food acquisition may exceed energetic costs of intraspecific disputes. Therefore, in absence of lethal conflicts, a temporary transition from plastic increases in aggressiveness to actual selection for more aggressive individuals may be hypothesised if global warming will reduce quality and quantity of food resources.

#### 4.3. Increased aggression under climate change: a widespread response?

Previous studies have found that animal aggression can be shaped by anthropogenic environmental alterations such as pollution (Sorvari and Eeva, 2010; Nabinger et al., 2018; McClelland et al., 2019; Xu et al., 2021; but see also Grunst et al., 2018). If primary productivity will be negatively impacted by warming and drought, indirect effects of anthropogenic climate change on behavioural responses could be more important than previously expected, potentially triggering bottom-up consequences on intraspecific animal conflicts. Despite uncertainty in the evolution of selective advantages, our study on a wild herbivorous mammal predicts an average ~ 50 % increase of the *pro capite* intra-group aggression rate over the next 60 years, following a projected accumulated warming of ~2.8 °C in summer. Suggestively, retrospective analyses of human behaviour report an increase in civil conflicts as global warming progresses, possibly explained by a ‘war over resources’ similar to that we suggest here for animal societies (e.g. Burke et al., 2009; Hsiang et al., 2011, 2013; Miles-Novelo and Anderson, 2019; but see also Adams et al., 2018). Clearly, generalizing our conclusions depends on whether, and how, animal responses involve individual variation of non-aggressive behavioural traits to avoid increasing intraspecific contests after a decrease in food resources. For example, ecological flexibility may allow species to shift their temporal activity or habitat use, which would mitigate the deteriorating effects of global warming on resource allocation (see e.g. thermal shelters- or climate change refugia-effects; Dobrowski, 2011; Mason et al., 2014a; Melin et al., 2014; Elsen and Tingley, 2015; Morelli et al., 2016; Billman et al., 2021; Reiner et al., 2021; Semenzato et al., 2021). However, the rationale behind our findings, namely the escalation of intraspecific conflicts over limited food resources, is supported by evolutionary theory (Maynard Smith and Price, 1973; Sirot, 2000), as well as by empirical evidence spanning the animal kingdom (Peiman and Robinson, 2010; Andrade et al., 2021).

As to the geographic extent of this response, it will also vary according to the effects of climate change on primary productivity. Harsh weather triggered by ongoing climate change may reduce food resources for herbivores on a large-scale, with global analyses providing evidence that plant productivity is suppressed by cumulative effects of drought in ~75 % of the world's grasslands (Wei et al., 2022), and that droughts have reduced global vegetation productivity (Zhao and Running, 2010). Even if the current warming rate does not accelerate, climate change is predicted to intensify drought (Dai, 2013) and heat waves especially in summer (Christidis et al., 2015), which may increase in duration up to half a year (Wang et al., 2021). These considerations, combined with our findings, suggest that a boost in animal aggressiveness might be a widespread response under the anticipated warming scenarios, at least amongst terrestrial primary consumers highly reliant on vegetation growth. At the same time, however, contrasting effects of accumulated warming and drought on primary productivity may also occur in some regions (Yuan et al., 2022), potentially leading to an increase in vegetation productivity with global warming. Therefore the geographic spread of this response would depend on the combination of the site-specific magnitude and direction of both temperature- and precipitation-effects in driving vegetation productivity. We should also consider that, although the increase in aggression may emerge primarily on herbivorous species as being dependent directly on autotrophic productivity, we cannot rule out their emergence at higher trophic levels, such as in predator species due to climate change-induced alterations in prey availability (cf. Amstrup et al., 2006). Finally, the effect of climate change on aggressive contests might also operate at the interspecific level through competition for coveted abiotic resources, as preliminary data suggest (Berger et al., 2022).

#### 4.4. Caveats and conclusions

Our study, inevitably, is not exempt from limitations relevant to any field data collection involving bounded across-year variability in climatic conditions. Nonetheless, we should note that the within-year variability of accumulated temperature and rainfall observed in our study years ( $T_{30}$  range: 12.1–17.7 °C;  $P_{30}$  range: 20–134.6 kg m<sup>-2</sup>) captured 100 % of the average across-year variability of these factors occurring over the last 30 years in our study area ( $T_{30}$  range: 12.7–16.7 °C;  $P_{30}$  range: 19.5–95.1 kg m<sup>-2</sup>), thus being representative of the variability in the accumulated summer climatic conditions over the long-term. Moreover we predicted future responses by limiting our projection to the next 60 years (ratio ‘years of observed data:years of predicted data’ = 1:30), hence we have been conservative compared to previous forecasts developed to predict ecological responses of wild herbivores and based on a similar timespan in data collection (e.g. Mason et al., 2014a, ratio ~ 1:80; Espunyes et al., 2019, ratio ~ 1:100). In any case, despite the above precautions, future studies based on long-term behavioural data collection from different species would be required to improve our models and to evaluate the broad, between-species applicability of our findings.

Additionally, we used a remote-sensing indicator of vegetation productivity to support the cumulative effects of hot-dry weather in reducing pasture availability for chamois. Despite the large use of such indicators as surrogates of habitat productivity and vegetation growth, they might not capture entirely the impact of weather on both pasture availability and quality, as well as how this impact might vary between different plant communities occurring in the same area. To this end, measuring the availability and nutritional quality of plants through field surveys conducted at fine spatial and temporal grains could have better quantified the cumulative effects of weather on the resource value for chamois. At same time, however, vegetation surveys conducted in our study area in the past confirmed strong sensitivity of the plant community selected by chamois to warming (Lovari et al., 2020), supporting our findings.

So far, climate change research has revealed manifold ecological responses by animal populations (Walther et al., 2002; Root et al., 2003; Parmesan, 2006; Cohen et al., 2018), yet effects on animal conflicts have been ignored. Although correlative in nature, our study opens the doors for a better understanding of the multifactorial origin of intraspecific aggression in group-living foragers, emphasising its close connection with climate change and the escalation of agonistic contests as a potential response animal societies could manifest under ongoing global warming.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.161789>.

#### CRedit authorship contribution statement

**Niccolò Fattorini:** Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Supervision, Writing - original draft, Writing - review & editing. **Sandro Lovari:** Methodology, Funding acquisition, Project administration, Supervision, Conceptualization, Writing - review & editing. **Sara Franceschi:** Methodology, Formal analysis, Writing - review & editing. **Gianpasquale Chiatante:** Investigation, Writing - review & editing. **Claudia Brunetti:** Investigation, Writing - review & editing. **Carolina Baruzzi:** Investigation, Writing - review & editing. **Francesco Ferretti:** Methodology, Formal analysis, Project administration, Supervision, Conceptualization, Writing - review & editing.

#### Data availability

Behavioural data are available from the authors upon reasonable request. Weather data are available from Centro Funzionale e Ufficio Idrografico Regione Abruzzo (Italy) upon request. Vegetation productivity data can be accessed at <https://earthexplorer.usgs.gov>.



## Declaration of competing interest

The authors declare no competing interests.

## Acknowledgements

We thank D. Febbo, G. Rossi, A. Carrara and the ALMNP staff for logistic support; Centro Funzionale e Ufficio Idrografico Regione Abruzzo for access to meteorological data; N. Pallari, V. Pietrocini and D. Scornavacca for help in data collection; M.C. Pagliarella for help in statistical modelling; L. Fattorini for advice on simulations; M. Festa-Bianchet for comments on early drafts and English editing. Two anonymous reviewers improved our manuscript with valuable comments.

## Funding

Financial support was provided by the Abruzzo, Lazio and Molise National Park Agency, the Italian Ministry of University and Research (PRIN project no. 2010P7LFW4) and by the University of Siena (PhD scholarship to N. Fattorini in 2014–2016).

## References

- Adams, C., Ide, T., Barnett, J., Detges, A., 2018. Sampling bias in climate–conflict research. *Nat. Clim. Chang.* 8 (3), 200–203.
- Aho, K., Derryberry, D., Peterson, T., 2014. Model selection for ecologists: the worldviews of AIC and BIC. *Ecology* 95, 631–636.
- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–267.
- Amstrup, S.C., Stirling, I., Smith, T.S., Perham, C., Thiemann, G.W., 2006. Recent observations of intraspecific predation and cannibalism among polar bears in the southern Beaufort Sea. *Polar Biol.* 29, 997–1002.
- Anderwald, P., Campell Andri, S., Palme, R., 2021. Reflections of ecological differences? Stress responses of sympatric alpine chamois and red deer to weather, forage quality, and human disturbance. *Ecol. Evol.* 11, 15740–15753.
- Andrade, M.A., Oliveira, D., Mazzochini, G.G., Amado, T.F., Gouveia, S.F., Martinez, P.A., 2021. Drivers of intraspecific lethal aggression in mammals. *J. Biogeogr.* 48, 2445–2454.
- Bartoń, K., 2020. MuMin: Multi-model Inference. R Package Version 1.43.17. <https://cran.r-project.org/web/packages/MuMin>.
- Baruzzi, C., Lovari, S., Fattorini, N., 2017. Catch me if you can: antipredatory behaviour of chamois to the wolf. *Ethol.Ecol.Evol.* 29, 589–598.
- Berger, J., Biel, M., Hayes, F.P., 2022. Species conflict at Earth's edges – Contests, climate, and coveted resources. *Front. Ecol. Evol.* 10 10:991714.
- Billman, P.D., Beever, E.A., McWethy, D.B., Thurman, L.L., Wilson, K.C., 2021. Factors influencing distributional shifts and abundance at the range core of a climate-sensitive mammal. *Glob. Chang. Biol.* 27, 4498–4515.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400.
- Bruno, E., Lovari, S., 1989. Foraging behaviour of adult female apennine chamois in relation to seasonal variation in food supply. *Acta Theriol.* 34, 513–523.
- Burke, M.B., Miguel, E., Satyanath, S., Dykema, J.A., Lobell, D.B., 2009. Warming increases the risk of civil war in Africa. *Proc. Natl. Acad. Sci.* 106, 20670–20674.
- Christidis, N., Jones, G.S., Stott, P.A., 2015. Dramatically increasing chance of extremely hot summers since the 2003 European heatwave. *Nat. Clim. Chang.* 5, 46–50.
- Ciucci, P., Tosoni, E., Di Domenico, G., Quattrocchi, F., Boitani, L., 2014. Seasonal and annual variation in the food habits of Apennine brown bears, central Italy. *J. Mammal.* 95, 572–586.
- Ciucci, P., Mancinelli, S., Boitani, L., Gallo, O., Grottolli, L., 2020. Anthropogenic food subsidies hinder the ecological role of wolves: insights for conservation of apex predators in human-modified landscapes. *Glob. Ecol. Conserv.* 21, e00841.
- Clutton-Brock, T.H., Albon, S.D., 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69, 145–170.
- Clutton-Brock, T.H., Parker, G.A., 1995. Punishment in animal societies. *Nature* 373, 209–216.
- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M., Guinness, F.E., 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* 27, 211–225.
- Cohen, J.M., Lajeunesse, M.J., Rohr, J.R., 2018. A global synthesis of animal phenological responses to climate change. *Nat. Clim. Chang.* 8, 224–228.
- Craine, J.M., Towne, E.G., Joern, A., Hamilton, R.G., 2009. Consequences of climate variability for the performance of bison in tallgrass prairie. *Glob. Chang. Biol.* 15, 772–779.
- Dai, A., 2013. Increasing drought under global warming in observations and models. *Nat. Clim. Chang.* 3, 52–58.
- Ding, Y., Li, Z., Peng, S., 2020. Global analysis of time-lag and-accumulation effects of climate on vegetation growth. *Int. J. Appl. Earth Obs. Geoinf.* 92, 102179.
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob. Chang. Biol.* 17, 1022–1035.
- Doering, G.N., Scharf, I., Moeller, H.V., Pruitt, J.N., 2018. Social tipping points in animal societies in response to heat stress. *Nat.Ecol.Evol.* 2, 1298–1305.
- Elsen, P.R., Tingley, M.W., 2015. Global mountain topography and the fate of montane species under climate change. *Nat. Clim. Chang.* 5, 772–776.
- Espunyes, J., Lurgi, M., Büntgen, U., Bartolomé, J., Calleja, J.A., Gálvez-Cerón, A., et al., 2019. Different effects of alpine woody plant expansion on domestic and wild ungulates. *Glob. Chang. Biol.* 25, 1808–1819.
- Fattorini, N., Brunetti, C., Baruzzi, C., Macchi, E., Pagliarella, M.C., Pallari, N., et al., 2018a. Being “hangry”: food depletion and its cascading effects on social behaviour. *Biol. J. Linn. Soc.* 125, 640–656.
- Fattorini, N., Lovari, S., Brunetti, C., Baruzzi, C., Cotza, A., Macchi, E., et al., 2018b. Age, seasonality, and correlates of aggression in female apennine chamois. *Behav. Ecol. Sociobiol.* 72, 1–17.
- Fattorini, N., Brunetti, C., Baruzzi, C., Chiatante, G., Lovari, S., Ferretti, F., 2019. Temporal variation in foraging activity and grouping patterns in a mountain-dwelling herbivore: environmental and endogenous drivers. *Behav. Process.* 167, 103909.
- Ferretti, F., Costa, A., Corazza, M., Pietrocini, V., Cesaretti, G., Lovari, S., 2014. Males are faster foragers than females: intersexual differences of foraging behaviour in the Apennine chamois. *Behav. Ecol. Sociobiol.* 68, 1335–1344.
- Ferretti, F., Corazza, M., Campana, I., Pietrocini, V., Brunetti, C., Scornavacca, D., Lovari, S., 2015. Competition between wild herbivores: reintroduced red deer and Apennine chamois. *Behav. Ecol.* 26, 550–559.
- Ferretti, F., Lovari, S., Stephens, P.A., 2019. Joint effects of weather and interspecific competition on foraging behavior and survival of a mountain herbivore. *Curr.Zool.* 65, 165–175.
- Festa-Bianchet, M., Jorgenson, J.T., 1998. Selfish mothers: reproductive expenditure and resource availability in high ewes. *Behav. Ecol.* 9, 144–150.
- Fisher, D.N., Kilgour, R.J., Siracusa, E.R., Foote, J.R., Hobson, E.A., Montiglio, P.O., et al., 2021. Anticipated effects of abiotic environmental change on intraspecific social interactions. *Biol. Rev.* 96, 2661–2693.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toigo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* 31, 367–393.
- Gherardi, F., Coignet, A., Souty-Grosset, C., Spigoli, D., Aquiloni, L., 2013. Climate warming and the agonistic behaviour of invasive crayfishes in Europe. *Freshw. Biol.* 58, 1958–1967.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J.L.B., et al., 2012. Continent-wide response of mountain vegetation to climate change. *Nat. Clim. Chang.* 2, 111–115.
- Grunst, A.S., Grunst, M.L., Thys, B., Raap, T., Daem, N., Pinxten, R., Eens, M., 2018. Variation in personality traits across a metal pollution gradient in a free-living songbird. *Sci. Total Environ.* 630, 668–678.
- Gudka, M., Santos, C.D., Dolman, P.M., Abad-Gómez, J.M., Silva, J.P., 2019. Feeling the heat: elevated temperature affects male display activity of a lekking grassland bird. *Plos One* 14, e0221999.
- Hamel, S., Gaillard, J.-M., Festa-Bianchet, M., Côté, S.D., 2009. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* 90, 1981–1995.
- Hardy, I., Briffa, M. (Eds.), 2013. *Animal Contests*. Cambridge University Press, Cambridge.
- Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E., et al., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6, e4794.
- Hegerl, G.C., Brönnimann, S., Schurer, A., Cowan, T., 2018. The early 20th century warming: anomalies, causes, and consequences. *WIREs Clim.Chang.* 9, e522.
- Herfindal, I., Anderwald, P., Filli, F., Campell, Andri S., Rempfler, T., 2019. Climate, competition and weather conditions drive vertical displacement and habitat use of an alpine ungulate in a highly topographic landscape. *Landsc. Ecol.* 34, 2523–2539.
- Hidalgo Aranzamendi, N., Hall, M.L., Kingma, S.A., van de Pol, M., Peters, A., 2019. Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. *J. Anim. Ecol.* 88, 1799–1811.
- Holway, D.A., Suarez, A.V., Case, T.J., 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* 282, 949–952.
- Hsiang, S.M., Meng, K.C., Cane, M.A., 2011. Civil conflicts are associated with the global climate. *Nature* 476, 438–441.
- Hsiang, S.M., Burke, M., Miguel, E., 2013. Quantifying the influence of climate on human conflict. *Science* 341, 1235367.
- Jonasson, S., Bryant, J.P., Chapin III, F.S., Andersson, M., 1986. Plant phenols and nutrients in relation to variations in climate and rodent grazing. *Am. Nat.* 128, 394–408.
- Kua, Z.X., Hamilton, I.M., McLaughlin, A.L., Brodrik, R.M., Keitzer, S.C., Gilliland, J., et al., 2020. Water warming increases aggression in a tropical fish. *Sci. Rep.* 10, 1–13.
- Latini, R., Asprea, A., Pagliaroli, D., Gentile, L., Argenio, A., Di Pirro, V., 2013. Life + Coornata. Development of coordinated protection measures for Apennine chamois (*Rupicapra pyrenaica ornata*). Stato dell'arte delle azioni C2 e C6. Marzo 2013. Available at: [http://www.parcoabruzzo.it/pdf/Relazione\\_conteggio\\_camoscio\\_finale\\_2012.pdf](http://www.parcoabruzzo.it/pdf/Relazione_conteggio_camoscio_finale_2012.pdf).
- Little, A.G., Fisher, D.N., Schoener, T.W., Pruitt, J.N., 2019. Population differences in aggression are shaped by tropical cyclone-induced selection. *Nat. Ecol. Evol.* 3, 1294–1297.
- Locati, M., Lovari, S., 1990. Sexual differences in aggressive behaviour of the Apennine chamois. *Ethology* 84, 295–306.
- Locati, M., Lovari, S., 1991. Clues for dominance in female chamois: age, weight, or horn size? *Aggress. Behav.* 17, 11–15.
- Loison, A., Jullien, J.M., Menaut, P., 1999. Subpopulation structure and dispersal in two populations of chamois. *J. Mammal.* 80, 620–632.
- Loison, A., Darmon, G., Cassar, S., Jullien, J.M., Maillard, D., 2008. Age- and sex-specific settlement patterns of chamois (*Rupicapra rupicapra*) offspring. *Can. J. Zool.* 86, 588–593.
- Lovari, S., 1985. Behavioural repertoire of the Abruzzo chamois, *Rupicapra pyrenaica ornata* Neumann, 1899 (Artiodactyla: Bovidae). *Säugetierkundliche Mitteilungen* 32, 113–116.
- Lovari, S., Cosentino, R., 1986. Seasonal habitat selection and group size of the Abruzzo chamois (*Rupicapra pyrenaica ornata*). *Ital.J.Zool.* 53, 73–78.

- Lovari, S., Locati, M., 1993. Intrasexual social behaviour of female Apennine chamois *Rupicapra pyrenaica ornata* (Neumann 1899). *Ethol. Ecol. Evol.* 5, 347–356.
- Lovari, S., Ferretti, F., Corazza, M., Minder, I., Troiani, N., Ferrari, C., Saggi, A., 2014. Unexpected consequences of reintroductions: competition between reintroduced red deer and Apennine chamois. *Anim. Conserv.* 17, 359–370.
- Lovari, S., Franceschi, S., Chiatante, G., Fattorini, L., Fattorini, N., Ferretti, F., 2020. Climatic changes and the fate of mountain herbivores. *Clim. Chang.* 162, 2319–2337.
- Mason, T.H., Apollonio, M., Chirichella, R., Willis, S.G., Stephens, P.A., 2014b. Environmental change and long-term body mass declines in an alpine mammal. *Front. Zool.* 11, 69.
- Mason, T.H., Stephens, P.A., Apollonio, M., Willis, S.G., 2014a. Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. *Glob. Chang. Biol.* 20, 3872–3882.
- Maynard Smith, J.P., Price, G.R., 1973. The logic of animal conflict. *Nature* 246, 15–18.
- McClelland, S.C., Ribeiro, R.D., Mielke, H.W., Finkelstein, M.E., Gonzales, C.R., Jones, J.A., et al., 2019. Sub-lethal exposure to lead is associated with heightened aggression in an urban songbird. *Sci. Total Environ.* 654, 593–603.
- McLoughlin, P.D., Gaillard, J.-M., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., et al., 2007. Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology* 88, 3192–3201.
- Melin, M., Matala, J., Mehtätalo, L., Tiilikainen, R., Tikkanen, O.P., Maltamo, M., et al., 2014. Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests—an analysis based on airborne laser scanning of the canopy structure at moose locations. *Glob. Chang. Biol.* 20, 1115–1125.
- Meroni, M., Fasbender, D., Rembold, F., Atzberger, C., Klisch, A., 2019. Near real-time vegetation anomaly detection with MODIS NVDI: timeliness vs. accuracy and effect of anomaly computation options. *Remote Sens. Environ.* 221, 508–521.
- Miles-Novelo, A., Anderson, C.A., 2019. Climate change and psychology: effects of rapid global warming on violence and aggression. *Curr. Clim. Chang. Rep.* 5, 36–46.
- Milner-Gulland, E.J., Bukreeva, O.M., Coulson, T., Lushchekina, A.A., Kholodova, M.V., Bekenov, A.B., Grachev, I.A., 2003. Reproductive collapse in saiga antelope harems. *Nature* 422, 135.
- Morelli, T.L., Daly, C., Dobrowski, S.Z., Dulen, D.M., Ebersole, J.L., Jackson, S.T., et al., 2016. Managing climate change refugia for climate adaptation. *PLoS One* 11, e0159909.
- Moss, J.B., While, G.M., 2021. The thermal environment as a moderator of social evolution. *Biol. Rev.* 96, 2890–2910.
- Nabinger, D.D., Altenhofen, S., Bitencourt, P.E.R., Nery, L.R., Leite, C.E., et al., 2018. Nickel exposure alters behavioral parameters in larval and adult zebrafish. *Sci. Total Environ.* 624, 1623–1633.
- Nguyen, K., Stahlschmidt, Z.R., 2019. When to fight? Disentangling temperature and circadian effects on aggression and agonistic contests. *Anim. Behav.* 148, 1–8.
- Nomoto, H.A., Alexander, J.M., 2021. Drivers of local extinction risk in alpine plants under warming climate. *Ecol. Lett.* 24, 1157–1166.
- Packer, C., Collins, D.A., Sindimwo, A., Goodall, J., 1995. Reproductive constraints on aggressive competition in female baboons. *Nature* 373, 60–63.
- Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* 37, 637–669.
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J.L.B., et al., 2012. Recent plant diversity changes on Europe's mountain summits. *Science* 336, 353–355.
- Peiman, K., Robinson, B., 2010. Ecology and evolution of resource-related heterospecific aggression. *Q. Rev. Biol.* 85, 133–158.
- Pepin, N., Bradley, R.S., Diaz, H.F., Baraër, M., Caceres, E.B., Forsythe, N., et al., 2015. Elevation-dependent warming in mountain regions of the world. *Nat. Clim. Chang.* 5, 424–430.
- Pesaresi, S., Galdenzi, D., Biondi, E., Casavecchia, S., 2014. Bioclimate of Italy: application of the worldwide bioclimatic classification system. *J. Maps* 10, 538–553.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* 20, 503–510.
- Pettorelli, N., Pelletier, F., Hardenberg, A.V., Festa-Bianchet, M., Côté, S.D., 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. *Ecology* 88, 381–390.
- Potter, D.A., Wrensch, D.L., Johnston, D.E., 1976. Aggression and mating success in male spider mites. *Science* 193, 160–161.
- Querejeta, J.I., Ren, W., Prieto, I., 2021. Vertical decoupling of soil nutrients and water under climate warming reduces plant cumulative nutrient uptake, water-use efficiency and productivity. *New Phytol.* 230, 1378–1393.
- Rachlow, J.L., 2008. Wildlife ecology. In: Jørgensen, S.E., Fath, B.D. (Eds.), *Encyclopedia of Ecology*. Elsevier, pp. 3790–3794.
- Reiner, R., Zedrosser, A., Zeiler, H., Hackländer, K., Corlatti, L., 2021. Forests buffer the climate-induced decline of body mass in a mountain herbivore. *Glob. Chang. Biol.* 27, 3741–3752.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60.
- Rughetti, M., Festa-Bianchet, M., 2012. Effects of spring-summer temperature on body mass of chamois. *J. Mammal.* 93, 1301–1307.
- Schaller, G.B., 1977. *Mountain Monarchs*. The University of Chicago Press, Chicago (US).
- Schmeller, D.S., Urbach, D., Bates, K., Catalan, J., Cogălniceanu, D., Fisher, M.C., et al., 2022. Scientists' warning of threats to mountains. *Sci. Total Environ.* 158611.
- Scornavacca, D., Brunetti, C., 2016. Cooperative defence of female chamois successfully deters an eagle attack. *Mammalia* 80, 453–456.
- Scornavacca, D., Lovari, S., Cotza, A., Bernardini, S., Brunetti, C., Pietrocini, V., Ferretti, F., 2016. Pasture quality affects juvenile survival through reduced maternal care in a mountain-dwelling ungulate. *Ethology* 122, 807–817.
- Semenzato, P., Cagnacci, F., Ossi, F., Eccel, E., Morellet, N., Hewison, A.M., et al., 2021. Behavioural heat-stress compensation in a cold-adapted ungulate: forage-mediated responses to warming alpine summers. *Ecol. Lett.* 24, 1556–1568.
- Siroi, E., 2000. An evolutionarily stable strategy for aggressiveness in feeding groups. *Behav. Ecol.* 11, 351–356.
- Sorvari, J., Eeva, T., 2010. Pollution diminishes intra-specific aggressiveness between wood ant colonies. *Sci. Total Environ.* 408, 3189–3192.
- Stamps, J., 2008. *Habitat*. In: Jørgensen, S.E., Fath, B.D. (Eds.), *Encyclopedia of Ecology*. Elsevier, pp. 1807–1810.
- Therrien, J.F., Côté, S.D., Festa-Bianchet, M., Ouellet, J.P., 2007. Conservative maternal care in an iteroparous mammal: a resource allocation experiment. *Behav. Ecol. Sociobiol.* 62, 193–199.
- Tuomainen, U., Candolin, U., 2011. Behavioural responses to human-induced environmental change. *Biol. Rev.* 86, 640–657.
- Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., López-Moreno, J.J., et al., 2013. Response of vegetation to drought time-scales across global land biomes. *Proc. Natl. Acad. Sci.* 110, 52–57.
- Villamuelas, M., Fernández, N., Albaladejo, E., Gálvez-Cerón, A., Bartolomé, J., Mentaberre, G., et al., 2016. The enhanced vegetation index (EVI) as a proxy for diet quality and composition in a mountain ungulate. *Ecol. Indic.* 61, 658–666.
- Walther, F., 1974. Some reflections on expressive behavior in combat and courtship of certain horned ungulates. In: Geist, V., Walther, F. (Eds.), *Behavior of Ungulates and its Relation to Management*. IUCN, Morges (CH), pp. 56–106.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebe, T.J., et al., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Wang, J., Guan, Y., Wu, L., Guan, X., Cai, W., Huang, J., et al., 2021. Changing lengths of the four seasons by global warming. *Geophys. Res. Lett.* 48, e2020GL091753.
- Wei, X., He, W., Zhou, Y., Ju, W., Xiao, J., Li, X., et al., 2022. Global assessment of lagged and cumulative effects of drought on grassland gross primary production. *Ecol. Indic.* 136, 108646.
- Wen, Y., Liu, X., Xin, Q., Wu, J., Xu, X., Pei, F., et al., 2019. Cumulative effects of climatic factors on terrestrial vegetation growth. *J. Geophys. Res. Biogeosci.* 124, 789–806.
- White, K.S., Gregovich, D.P., Levi, T., 2019. Projecting the future of an alpine ungulate under climate change scenarios. *Glob. Chang. Biol.* 24, 1136–1149.
- Wilson, A.J., Gelin, U., Perron, M.C., Réale, D., 2009. Indirect genetic effects and the evolution of aggression in a vertebrate system. *Proc. R. Soc. B Biol. Sci.* 276, 533–541.
- Wong, B., Candolin, U., 2015. Behavioral responses to changing environments. *Behav. Ecol.* 26, 665–673.
- Xu, A., Liu, C., Wan, Y., Bai, Y., Li, Z., 2021. Monkeys fight more in polluted air. *Sci. Rep.* 11, 1–7.
- Yuan, Y., Bao, A., Jiapaer, G., Jiang, L., De Maeyer, P., 2022. Phenology-based seasonal terrestrial vegetation growth response to climate variability with consideration of cumulative effect and biological carryover. *Sci. Total Environ.* 817, 152805.
- Zhang, Z., Ju, W., Zhou, Y., Li, X., 2022. Revisiting the cumulative effects of drought on global gross primary productivity based on new long-term series data (1982–2018). *Glob. Chang. Biol.* 28, 3620–3635.
- Zhao, M., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329, 940–943.
- Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., et al., 2021. Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *Sci. Total Environ.* 783, 146896.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology*. With R. Springer, New York (US).