Abstract

Alpine large herbivores have developed physiological and behavioral mechanisms to cope with fluctuations in climate and resource availability, but climate warming might induce behavioral maladaptation. We verified this hypothesis in female Alpine ibex (*Capra ibex*) by modelling seasonal and daily movement and activity patterns in function of temperature and vegetation productivity, based on bio-logging data and climate change projections. In late spring, ibex moved upslope, tracking the green-wave in plant phenology. Ibex sharply decreased diel activity above a threshold mean daily temperature of 13°C, indicating thermal stress, but compensating behaviorally by foraging earlier at dawn, and later at dusk, and by moving upslope higher than on cooler days. This temperature threshold will be exceeded more than three times as often under climate change projections. In such scenarios, the imperative requirement for thermal shelter may force Alpine ibex towards topographic edges, impacting individual performance and population distribution of this emblematic mountain ungulate.

Introduction

The effects of climate warming are accentuated across the marked environmental and climatic gradients of Alpine environments (Ernakovich *et al.* 2014). Higher temperatures, in particular, may alter plant altitudinal distribution (Parolo & Rossi 2008; Rammig *et al.* 2010), and constrain animal thermal balance, even in homeotherms (Arnold 1988; Signer *et al.* 2011). Moreover, earlier vegetation green up and senescence (Wipf *et al.* 2009; Ernakovich *et al.* 2014) may affect primary consumers demographic performance, as observed in mountain ungulates (Pettorelli *et al.* 2007; Lovari *et al.* 2020).

Mountain ungulates have developed physiological (e.g., Arnold *et al.* 2004, 2006; Heldmaier *et al.* 2004) and behavioral (Nicholson *et al.* 1997; Arnold *et al.* 2006; Rice 2008) mechanisms to cope with climatic constraints and seasonal heterogeneity in resource availability. Since behavioral adjustments are more rapid than physiological adaptation (Wong & Candolin 2015), behavioral plasticity can potentially buffer the impacts of climate change. For example, across the seasons, mountain ungulates adjust their daily feeding time (Green & Bear 1990) and ranging behavior, generally resulting in altitudinal shifts, to enhance acquisition of high-quality food in relation to vegetation green-up (see forage maturation hypothesis FMH, e.g. Hebblewhite & Merrill 2009, and green-wave hypothesis GWH, e.g. Merkle *et al.* 2016). Moreover, ungulates may use behavioral thermoregulation to remain within tolerated thermal limits, e.g. by either reducing activity or selecting specific habitats providing thermal shelter (van Beest *et al.* 2012) thus buffering the direct effect of temperature fluctuations on homeothermy. Mountain ungulates in particular are known to exploit the altitudinal thermal gradient to compensate for temperature fluctuations, so that, in summer, high altitude areas may be functionally equivalent to closed habitats at lower altitude with respect to protection from heat stress (in chamois *Rupicapra rupicapra*: Mason *et al.* 2014a; in Alpine ibex *Capra ibex*: Aublet *et al.* 2009).

These compensatory behavioral mechanisms may be challenged under severe climate change, when more acute heat stress may force animals to decrease foraging activity or to select sub-optimal forage habitats because seeking for thermal protection, generating a thermal shelter-food trade-off in habitat selection (moose *Alces alces*: van Beest & Milner, 2013; chamois: Mason *et al.* 2014b; ibex: Brivio *et al.* 2019). Alpine ibex, in particular, is a high altitude ungulate (typical range: 1600-3200 m a.s.l., Pedrotti *et al.* 2009) with a constrained thermal comfort range during summer (Signer *et al.* 2011). For example, male ibex foraged less during the hottest part of the day on the hottest days of summer (Aublet *et al.* 2009; Mason *et al.* 2017). Altitudinal shifts have been observed (Parrini *et al.* 2003; Grignolio *et al.* 2004), related to seasonal (Mason *et al.* 2017) and daily (Aublet *et al.* 2009) temperature fluctuations as a response to heat-stress, but they have been considered in apparent conflict with foraging needs, since plant productivity decreases with altitude (Aublet *et al.* 2009; Mason *et al.* 2017; Brivio *et al.* 2019). So far, we have little evidence of compensatory mechanisms for use of less productive habitats and reduced foraging activity during periods of heat-stress, suggesting a potential thermal shelter – food trade-off for Alpine ibex (Mason *et al.* 2017; Brivio *et al.* 2019).

We addressed this knowledge gap by investigating the maintenance of behavioral compensation mechanisms to cope with heat stress and to respond to fluctuating energy needs in this temperature-sensitive mountain ungulate, using a multi-scale movement ecology framework (Fig. 1; Nathan *et al.* 2008). First, at the annual scale, we evaluated whether female ibex adjusted their activity and movement to variations in temperature and resource availability (‘external state’, via hidden internal state processes; Fig. 1A; H1). We predicted that ibex would increase the total daily active time mainly in response to the seasonal increase in temperature, in accordance with physiological cycles (Signer *et al.* 2011; P1a), and that they would shift altitude in summer, influenced both by temperature, and vegetation green-up, to exploit thermal refuges and maximize access to high quality food (Aublet *et al.* 2009; Bischof *et al.* 2012; P1b). Therefore, we also predicted that these summer movements would provide individuals with access to areas with better resource quality compared to their respective winter ranges (GWH, Bischof *et al.* 2012; P1c).

Second, at the daily scale, we assessed whether female ibex could compensate for heat stress by adjusting their diel patterns of activity and altitudinal movements (Fig. 1B; H2.1). We predicted that ibex would decrease their activity during the hottest hours of the day, especially on the hottest days (Aublet *et al.* 2009), to maintain homoeothermic conditions (Signer *et al.* 2011) (P2.1a), resulting in an increase in activity at dawn and dusk in order to maintain a constant overall daily activity budget (Bourgoin *et al.* 2011) (P2.1b). We also predicted that female ibex would use high altitude areas as thermal refuges (Aublet *et al.* 2009), depending on hourly temperature (P2.1c). Assuming that these behaviors are compensatory mechanisms to meet resource needs while minimizing thermal stress, we also hypothesized that selection of forage habitat types would vary across the day in relation to activity rhythms (H2.2), with the most pronounced selection for forage habitats during activity peaks (P2.2). Finally, in order to explore how these behavioral adjustments could be influenced by climate change, we generated predictions of altitudinal shifts and activity rhythms under future scenarios of predicted climate warming in the Alps (Bucchignani *et al.* 2015).

Our results indicate that female ibex adopted compensatory behavioral mechanisms to cope with heat stress during summer while responding to foraging needs at both annual and daily scales. However, we suggest that the efficiency of these mechanisms will likely be impaired under the predicted warming scenarios, resulting in behavioral maladaptation and potentially detrimental effects on the population dynamics of this emblematic Alpine ungulate.

Materials and Methods

Study area

The study area (65 km^2 *ca*) is situated in the intermediate-to-high elevations of the Marmolada massif (1,700 to 2,900 m a.s.l.), in the Eastern Italian Alps (Dolomites - 46°26' 13" N, 11°51' 54" E). Narrow valleys with steep slopes and rocky ridges are dominated by abrupt vegetation shifts along the elevation gradient, from dense and sparse forest (*Picea abies*, *Larix decidua*), to shrubs (*Pinus mugus, Rhododendrum hirsutum, Salix sp.i*, and *Alnus viridis*), and Alpine grassland. Steep screes and rocky cliffs dominate the landscape above 2,100 m a.s.l, where pioneer organisms include lichens and high-altitude cushion plants (e.g., *Androsace* sp.). The climate is typically Alpine (snowy and humid climate with cool summers/polar tundra; Köppen-Geiger climate classification, Rubel *et al.* 2017). Total yearly precipitation is approximately 1,400±7.4 mm (snow cover: late October to early June) and mean annual temperature is 2.0±0.1°C (winter: -4.0±0.3°C; summer: 8.2±0.2°C; Regional Agency for Environment Protection of Veneto, ARPAV).

The local Alpine ibex colony had comprised a minimum of about 200 individuals during the study period (block census from the Province Police Corp of Belluno, http://www.provincia.belluno.it/nqcontent.cfm?a_id=3165).

Marked animal data

From September 2010 to October 2015, we caught 21 female ibex (2 or more year old at capture) by dart-gunning with sedation, and equipped them with GPS-GSM collars (GPS PRO Light collar, Vectronic Aerospace GmbH). Animals were caught with veterinary assistance in compliance with current Italian laws, with the approval of the National Agency for Environmental Protection and Research (ISPRA; ref. n. 9097-9501/2012). GPS collars were programmed to attempt a location every hour, and to drop-off after 54 weeks. Our final database included 148,365 locations for 21 individuals (fix success rate: 95%; outliers excluded as described in Bjørneraas *et al.* 2010; Urbano & Cagnacci 2014; median location error < 10 m, Párraga Aguado *et al.* 2017). We obtained activity data from those collars that could be retrieved after drop-off (15 out of 21, n=5,221 monitoring days in total; 6 dropped off on unreachable cliffs). Specifically, the collar units included a two-axis activity sensor scheduled to record average acceleration readings over 5-minute intervals. We classified these intervals as 'active' or 'inactive' based on a threshold value (Gervasi *et al.* 2006), and we validated them with observational data (see Appendix S1 in Supporting Information). Females were active for 39.5% of overall monitoring time. When active, they spent about 82.3% of this time foraging, and the remaining 17.7% in locomotion, so we considered time spent active as an informative proxy for foraging behavior. From these activity data, we computed the 'total active time per day' (in minutes per day; final sample size n=5,133 after excluding days with incomplete sampling, i.e. less than 24 hours) and the 'total active time per hour' (in minutes per hour; final sample size n=62,696).

Environmental data

We defined two six-months seasonal periods based on Alpine climatic conditions: 'summer', between mid-April and mid-October (17th – 42nd weeks), and 'winter' (43rd – 16th weeks), with the order of the weeks starting from the first day of winter solstice (21st December).

To assess the effect of biotic and abiotic factors on ibex behavioral responses (Fig. 1), we derived and processed raw environmental data from different sources, i.e. weather stations, geographic raster layers and land cover maps. Specifically, we obtained records of both hourly and mean daily temperature from the closest available weather station ('Monti Alti di Ornella', 2,227 m a.s.l., see Appendix S2 in Supporting Information) and modelled the smoothed yearly trend of mean daily temperature (see Appendix S3, Fig. S3.1A in Supporting Information). For the purpose of the analysis of summer diel patterns of activity, we classified the mean daily summer temperature in three levels based on percentiles, obtaining the categorical variable 'daily summer temperature class' ("low", 0-25%: mean daily temperature ≤ 3.80°C; "intermediate", 25-75%: > 3.80°C and < 10.2°C; and "high", 75-100%: ≥ 10.2°C). To evaluate the effect of climate change on the observed behavioral responses, we used climatic projections from low – medium emission and high emission rate scenarios (RCP 4.5 and RCP 8.5 respectively; Riahi *et al.* 2011; Thomson *et al.* 2011) to predict the distribution of the mean daily summer temperature between 2006 and 2070 at the same weather station. We then derived the three levels of the 'daily summer temperature class' variable according to the percentiles of these distributions between 2051-2070 (Bucchignani *et al.* 2015; Appendix S2).

We derived weekly measures of *vegetation productivity* based on the smoothed and corrected Normalized Difference Vegetation Index (NDVI) (MODIS, NASA, USA, spatial resolution: 250m x 250m; temporal resolution: 8 days, processed as in Klisch & Atzberger 2016; see also Pettorelli *et al.* 2006; Hebblewhite *et al.* 2008), and we modelled its annual trend both across the study area (5,000 random points; Appendix S3, Fig. S3.1B) and, for comparison, at all ibex locations (Fig. S3.1D). We then assessed the *vegetation phenology* of the study area by computing the weekly ΔNDVI, i.e. the difference in NDVI values between subsequent weeks, across the same 5,000 random points, and we modelled its yearly trend (Fig. S3.1C). Lastly, to evaluate the use of phenological gradients by ibex, we compared the summer ΔNDVI experienced by ibex at locations used in summer, with the summer ΔNDVI computed at the female late winter locations (13^{th}-16^{th} weeks). We then built a binomial variable 'summer_loc', that links ΔNDVI values to the summer (summer_loc = 1) or late winter (summer_loc = 0) locations used by female ibex.

We extracted the altitude of female ibex locations from a regional digital elevation model (resolution: 5 m; https://www.regione.veneto.it/web/ambiente-e-territorio/ctr; http://www.territorio.provincia.tn.it). We derived habitat use from a land-cover map (resolution: 50 m) with five habitat types: "forest" (coniferous and mixed forest, and shrubs), "grassland" (Alpine pastures and natural grasslands), "scree", "mixed grass and rocks" (grassland interspersed with rocks and scree), and "rocks" (bare rocks) (Scillitani *et al.* 2013).

Statistical analysis

We analyzed data in R (R Core Team 2016) using the package mgcv (Wood 2016) to fit generalized additive mixed models (GAMM) to our empirical dataset. In all models, we included the individual identity as a random factor on the intercept to control for repeated observations. We used Akaike Information Criterion (AIC; Burnham *et al.* 2002) and AIC weights to select the model with the most support.

Seasonal behavioral responses to temperature and vegetation productivity and phenology (H1)

To evaluate whether activity and altitudinal movement of female ibex varied seasonally to obtain thermal shelter and access to vegetation green-up (H1, Fig. 1A), we modeled the 'total active time per day' (P1a) and the 'mean altitude used per day' (P1b) by fitting GAMM models with and without linear or non-linear effects of the week (see Table S5.1a) including *a priori* the year as a random effect on the intercept. Then, we used the ANODEV procedure (Grosbois *et al.* 2008; see Appendix S4 in Supporting Information) to quantify the proportion of the weekly variation accounted for by NDVI and temperature. Lastly, we compared vegetation phenology (i.e., growing vegetation areas, Hamel *et al.* 2009) of winter and summer ranges (P1c), by fitting a GAMM to ΔNDVI with the cyclic cubic regression spline smooth of the week and the binomial variable summer_loc as a fixed factor (Tab. S5.2a).

Diel behavioral responses to heat stress during summer in current conditions and in relation to climate change scenarios (H2)

To evaluate whether female ibex compensated for thermal stress during summer by adjusting the daily pattern of activity and altitudinal movements (H2.1), while maintaining access to feeding habitat (H2.2) (Fig. 1B) we computed the 'total active time per hour' (in minutes per hours; P2.1a) and 'mean altitude used per hour' (P2.1c). We then modelled these two response variables by fitting GAMM models with and without linear or non-linear effects of the hour of the day, and with 'hourly mean temperature' or 'daily summer temperature class' as fixed effects (see Table S5.3a and S5.7a for the set of models). We included daylength in all models to account for seasonality (Krop-Benesch *et al.* 2013; Ensing *et al.* 2014; Bonnot *et al.* 2016). We also computed the mean total daily activity budget for days with different 'daily summer temperature class' values (P2.1b).

To predict daily activity patterns of female ibex in relation to climate change scenarios, we replicated the analysis for P2.1 using the variable 'daily summer temperature class' computed from the projected mean daily temperatures for 2051-2070 (Appendix S2; Tab. S5.5a), and estimated the mean daily activity budget for these predicted temperature classes.

To predict altitudinal shifts due to climate warming, we modelled the linear rate of maximum daily altitude gain in relation to mean daily temperature, and multiplied this rate by the expected temperature increase under ICPP warming scenarios (Appendix S2).

Finally, we assessed the selection of habitats for each hour with respect to the rest of the day by means of hourly matched-case Resource Selection Functions (RSF, Boyce & McDonald 1999; P2.2). Specifically, for each day having at least 20 locations, we extracted 10 points per used location at a distance randomly extracted from the empirical distribution of the hourly step lengths across all locations and all individuals (Fig. S5.1), and at a random absolute angle drawn from a uniform distribution, thus obtaining a set between 200 and 240 available locations/individual/day. We matched each hourly location with its correspondent daily set of available points, to fit two-step conditional logistic regression models for each hour of the day, obtaining the relative probability of selecting a given habitat in relation to the observed daily trajectories of each female ibex, with individual as a random effect on the intercept (R package TwoStepCLogit, Craiu *et al.* 2011, 2016).

Results

Seasonal behavioral responses to temperature and vegetation productivity and phenology (H1)

At the seasonal scale, the total time that female ibex were active per day varied over the year ('total active time per day', Table S5.1b), with very low activity levels in winter, a sharp increase as mean daily temperature started to rise in early spring (mid-March, week 12), to peak in the beginning of May (week 20), followed by a gradual decrease until early October (week 42), when activity fell to winter levels (Fig. 2A). Similarly, female ibex showed a seasonal shift towards higher altitudes ('mean altitude used per day', Table S5.1b) that began at approximately the seasonal peak of activity (week 20), increased at a rate that was notably synchronized with the increase in vegetation productivity (NDVI) over the study area, peaked in mid-July (week 30), before subsequently declining, decreasing more sharply after early October (week 42; Fig. 2B). Variation in activity of female ibex over the year was mainly related to the mean daily temperature, and, secondarily, to NDVI (82% and 66% of the temporal variation accounted for, respectively; Table S4.2), while variation in the mean altitude used over the year was mainly related to NDVI and, secondarily, temperature (89% and 76% of the overall temporal variation accounted for, respectively; Table S4.2).

The index of vegetation phenology, or 'green-up' (weekly difference in vegetation productivity ΔNDVI) varied seasonally, as well as between the winter and summer ranges of female ibex (Table S5.2b; Fig. 3). The pattern of vegetation phenology of used summer locations largely mirrored the altitudinal shifts of the ibex, but slightly anticipated (Fig. 3, Fig. 2B). The rate of green-up was positive and higher for locations that were actually used by ibex between weeks 17 and 32, i.e. between mid-April and late July, when female ibex moved at higher altitudes (up to a maximum of 10% higher at week 24, early June), compared to their winter ranges. After week 32, the rate of green-up became negative (indicating vegetation senescence), but sharply dropped only around week 42 (early October) when ibex moved to lower altitudes.

Diel behavioral responses to heat stress during summer in current conditions and in relation to climate change scenarios (H2)

During summer, female ibex followed a very strong bimodal pattern of diel activity ('total active time per hour') that varied in intensity in relation to the mean daily temperature (expressed in three classes: Table S5.3b). Activity peaked in the early morning and in late afternoon or evening, and was lowest at mid-morning (Fig. 4A). During hot days, the daily low in activity per hour was more pronounced compared to cooler days, while the early morning activity peak occurred slightly earlier, and the evening peak was slightly later and lasted longer. These behavioral adjustments maintained the total activity budget per day almost constant (cool days: 12h 1' (SD = 12'); hot days: 12h 20' (SD = 9'); Table S5.4).

The analysis replicated with the forecasted temperature classes for the two climate warming scenarios produced similar patterns (Tables S5.5b), but with more pronounced peaks and lows (see Fig. 4B for the RCP 8.5 scenario). Under these forecasts, the daily activity budget of ibex is predicted to remain almost identical relative to current conditions (Table S5.4), but peak activity is predicted to occur up to 42 minutes earlier in the mornings and up to 28 minutes later in the evenings (comparison between the current and RCP 8.5's high temperature class). For visualization purposes, we also plotted the model of active time per hour predicted by hourly temperature as a continuous variable (Table S5.6): the activity level of female ibex steadily increased with temperature up to a maximum at 13°C, then dropped sharply beyond this threshold (Fig. 4C). During the study period (2010-2015), female ibex actually experienced a median of 16 days with mean daily temperature >13°C (25% = 13; 75% = 16.5). Under climate forecasts, the number of days with mean daily temperature >13°C would represent 25% of the summer days in both climate warming scenarios (i.e., up to 55.5 days in median for RCP 8.5; Appendix S2, Fig. S2.2).

Altitude used by female ibex ('mean altitude used per hour') increased almost linearly as a function of hourly temperature (Fig. 4D, Table S5.7b), which resulted in daily movements over an altitudinal gradient of about 100 m, with the night time spent at the lowest altitudes, a rapid upslope shift after dawn to reach the highest altitude around mid-morning, and a more gradual return to lower altitudes during the day (Fig. 4E; Table S5.8). The maximum altitude used by ibex increased by 28.4 m for each °C increase in mean daily temperature (Fig. 4F; Table S5.9), which would result in a projected upward shift of around 86 m under RCP 8.5 scenarios (60 m under RCP4.5; Fig. S5.2), for the period 2051-2070. The spatial projection of these forecasts onto our study area (Fig. 5) revealed that these shifts would mean that summer ranges included extensive areas of vertical rock cliffs or mountain tops.

During summer, the relative probability of use of land-cover types by female ibex varied over the day alongside variations in activity and altitude (Fig. 6; see also Fig. 4 and Fig. 5). Rock and scree were selected more than forest during daylight. Grassland was positively selected during the two activity peaks (early morning and late evening-early night). Grassland mixed with rock was selected more than forest-shrubs during daylight. With the exception of grassland mixed with rock, all land cover types were negatively selected with respect to forest-shrubs at night.

Discussion

In this work, we found empirical support for the hypothesis that behavioral plasticity may promote resilience to current climate change (Boyles *et al.* 2011). We showed that female ibex used compensatory behavioral mechanisms to cope with heat-stress during summer, while satisfying foraging needs, at both seasonal (H1; Fig. 1A) and daily scales. Adjustments to diel activity rhythms, altitudinal movement patterns and resource selection can mitigate thermal stress (van Beest & Milner 2013) by balancing the energetic constraints of thermal exposure and forage acquisition. However, our results indicate that these mechanisms will likely be insufficient to shield Alpine ibex from thermal stress under future climate scenarios, with potentially detrimental effects on individual performance and population dynamics of this heat-sensitive ungulate.

Species that are exposed to an increase in temperature beyond the thermal limits in which they evolved are expected to experience decreased fitness. In chamois, the increase of temperature under climate change reduced forage activity (Mason *et al.* 2014b), with negative consequences on body condition (Mason *et al.* 2014a). Here, we showed that female ibex were able to compensate for increased heat stress by modifying their daily patterns of activity, thus maintaining a constant total activity budget per day. In summer, females drastically reduced activity above the threshold value of 13.0°C, which is within the temperature range previously reported to lead to thermal stress for Alpine ibex (Aublet *et al.* 2009; Signer *et al.* 2011). Female ibex also responded by moving to higher altitudes during daylight and by increasing nocturnal foraging activity (H2) (P2.1a), so that total daily foraging time was constant across a wide range of temperatures (P2.1b; study area: from -6.9°C to +17.7 °C), a behavior so far not investigated (Aublet *et al.* 2009; Mason *et al.* 2017; Brivio *et al.* 2019). These mechanisms to compensate for heat stress were associated with selection for forage habitats (grassland and grassland mixed with rocks) during peak activity, and refuge habitats (rocks, screes, forest) during resting periods (P2.2). Therefore, by moving through food-rich habitats when shifting between low altitude bed-sites and high altitude cooler areas, female ibex were able to maximize both thermal cover and resource acquisition (see Mitchell & Lima 2002; van Beest *et al.* 2013). Under climate warming forecasts, our models indicated a marked increase in the number of summer days on which ibex would need to avoid thermal stress (see Appendix 2, Fig. S2.2: number of summer days with mean daily temperature > 13° more than tripling by 2050), decreasing the time available for foraging during *daylight* (Fig. 4B: one hour less in total/day). Increased nocturnal feeding may negatively impact survival directly, for example, due to prolonged exposure to predators, or an increased probability of cliff falls. Similarly, high summer temperatures could force ibex to prolong the use of sub-optimal habitats, or simply reach the limit of the available altitudinal niche. The spatial projections of our models under climate change forecasts showed that further shifts to higher elevations by Alpine ibex would be either not possible, or involve extensive use of vertical rock cliffs (Fig. 5).

Climate warming can affect mountain ungulates even indirectly, via spatio-temporal variation of resource availability, including alteration of plant phenology (Lovari et al. 2020). In a capital breeder, like Alpine ibex (Toïgo *et al.* 2002), the spring vegetation flush is critical to regain body mass after the limiting winter season and, in females, to offset the high energetic costs of parturition and lactation. Climate change is predicted to generate an increase of the altitudinal threshold for snow cover accumulation, and higher late winter-spring temperatures. This will generate a rapid snowmelt, with earlier and more prolonged vegetation growth seasons (Ernakovich *et al.* 2014). Nevertheless, in Alpine regions, photoperiod limits plant productivity, constraining the extent to which the growing season can lengthen (Keller & Körner 2003; Ernakovich *et al.* 2014). Moreover, early snowmelt may also alter water availability (Marty *et al.* 2017) on which Alpine plants depend for growth (Jonas *et al.* 2008), so that earlier senescence could be expected (Ernakovich *et al.* 2014). These changes might lead to an earlier, but also shorter period of availability of high-quality forage for mountain ungulates, causing a mismatch between the peak of resource availability and their energetic demand (e.g., late gestation and lactation in Alpine ibex in May-June), with direct consequences on growth, body mass and survival of kids (Pettorelli *et al.* 2007; Rughetti & Festa-Bianchet 2012; Mason *et al.* 2014a). In our work, we demonstrated that Alpine ibex track the seasonal variation of resource availability, i.e. phenology, therefore being exposed to such mismatch. Indeed, after a very low activity in mid-winter (as predicted: P1a), female ibex first sharply increased their activity levels alongside temperature, while remaining in their winter range; then they initiated an altitudinal migration which was synchronized with the temporal trend in vegetation productivity (P1b). Hence, our results suggest that this Alpine ungulate initially fed on new-born vegetation in the winter range at the snowmelt, to then exploit the altitudinal gradient in plant phenology, while migrating upslope. During this period, ibex were able to access areas experiencing a more rapid increase in vegetation productivity compared to their winter ranges, despite lower absolute vegetation productivity (P1c). When the average vegetation productivity reached a plateau and then started to decrease, female ibex ceased their altitudinal migration and used habitats with a later peak in plant productivity and senescence (i.e. grasslands mixed with rocks and scree, see Fig. S3.1). Our results are in agreement with research on other ungulates (mainly deer, e.g., Albon & Langvatn, 1992, and African antelopes, e.g., Fryxell & Sinclair, 1988), predicting that animals migrate along a phenological gradient of plant development in order to maximize energy intake (H1; Green Wave Hypothesis: Bischof *et al.* 2012; Merkle *et al.* 2016; Aikens *et al.* 2020). Although this hypothesis is commonly supported in grazers (e.g. Geremia *et al.* 2019) and intermediate feeders (e.g., Peters *et al.* 2019), here we report evidence for a Caprinae species living at high altitude in rocky habitats, mostly feeding on sparse vegetation. High altitude areas have previously been identified as low productivity habitats which are selected by both Alpine ibex (Brivio *et al.* 2019), and chamois (Mason *et al.* 2017) for thermal comfort. Schweiger et al., (2015) observed that Alpine ibex foraged in areas where plant biomass was lower, but of higher nutritional value, compared to red deer or chamois. In agreement with this, Aublet *et al.* (2009) found that the nitrogen content of Alpine grasslands increased, while biomass and fiber content decreased, along an altitudinal gradient and over the summer. Further research on the biomass, diversity and quality of plant species consumed in these extreme environments could clarify how climate change driven alteration in phenology may impact the behavioral adaptations for maximizing feeding in relation to green-up, and the consequences for individual fitness (Mason *et al.* 2014a).

In this work, we have explored the multi-scale behavioral responses of a heat-sensitive species to abiotic variation of the external environment (*sensu* Nathan *et al.* 2008; Fig. 1), and the adaptive value of these responses under climate change, taking Alpine ibex as a model species. Most forecasts evaluating animal species distribution and persistence under climate change are indeed based on projections of current observed adaptations in different abiotic scenarios. However, little is known regarding behavioral responses at the limit of the fundamental abiotic niche of species (*sensu* Hutchinson 1957), and how this would interact with the concurrent changes in the biotic component of the ecosystem. For example, the expected upward shift of plant communities (Walther *et al.* 2005; Dirnböck *et al.* 2011), might reduce the available area of suitable habitat for Alpine ibex. Conversely, habitats might also become richer in nutrients at high elevation, notwithstanding the topographic limit of mountain tops. Hence, further research in other Alpine ibex populations and mountain ungulates should be undertaken in order to improve our ability to forecast mountain ungulate species resilience to long-term changes in temperature and forage variability. Current knowledge suggests that the exposure to thermal stress under future climate change scenarios that we have shown for Alpine ibex could be a concern for other wild ruminants in mountain areas (e.g., Maloney *et al.* 2005; Bourgoin *et al.* 2008, 2011; Marchand *et al.* 2015), and northern latitudes (e.g., van Beest *et al.* 2012; van Beest & Milner 2013; Melin *et al.* 2014; Street *et al.* 2015), particularly in those areas with marked daily temperature fluctuations (e.g., Aublet *et al.* 2009; Mason *et al.* 2014b). Under the current observed temperature increase in summer at extreme latitudes and altitudes (Begert *et al.* 2005; Beniston *et al.* 2018), urgent further research is required across ungulate species adapted to these environments to evaluate if physiological traits are becoming maladaptive, and in what measure behavioral responses may provide compensation mechanisms and resilience, as we have shown here for the Alpine ibex.

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