Behav Ecol Sociobiol (2016) 70:1291–1304
DOI 10.1007/s00265-016-2137-8

ORIGINAL ARTICLE

The weather dictates the rhythms: Alpine chamois activity is well adapted to ecological conditions

Francesca Brivio[1] · **Cristiano Bertolucci**[2] · **Federico Tettamanti**[1] · **Flurin Filli**[3] · **Marco Apollonio**[1] · **Stefano Grignolio**[1]

Received: 29 August 2015 / Revised: 2 May 2016 / Accepted: 3 May 2016 / Published online: 23 May 2016

Abstract
Activity rhythms play an important role in the ecological relations of a species and form part of its evolutionary adaptation. Such rhythms are strongly synchronised with the annual cyclic changes by environmental stimuli, the so-called zeitgebers. Animals' reliance on environmental stimuli is highly species-specific and allows behavioural adjustments to be made in preparation for the conditions expected in each season. We investigated daily and annual activity rhythms of Alpine chamois (*Rupicapra rupicapra*) by analysing high-resolution data of animals monitored with GPS collars. This first detailed field study of chamois activity showed that this species exhibited clear daily and annual activity rhythms entrained to the light-dark cycle. Chamois were more active during spring-summer and less active during winter, likely in response to the variation in the availability of food resources: both sexes appeared to maximise energy intake during the season offering the highest amount of food resources to compensate for poor food supply during winter. Daily activity was influenced by the climatic factors considered. We showed a negative correlation between daily activity and adverse climatic conditions (i.e. precipitation and, during winter, snow depth). As activity was strongly influenced by the interplay between temperature and wind throughout the year and by radiation and wind in winter, we conjectured that it was critically dependent upon animals' thermal balance. In conclusion, our study highlighted that chamois is well adapted to the Alpine environment and seasonality but also raised questions about its ability to adapt to future climate change.

Significance statement
In this study, we investigated the effects of ecological factors on Alpine chamois activity. Thanks to radio collars with accelerometers, we obtained highly detailed information on activity levels of wild animals. We found that chamois were more active during spring-summer (i.e. the seasons with the highest quality and quantity of food) and less active during winter. Our results showed that chamois activity was strongly influenced by such climatic factors as temperature, precipitation and wind speed. In winter time, chamois activity increased during the days with high solar radiation and decreased with high snow depth. Given their wide distribution in the Alps, chamois can be considered as a sentinel species of Alpine habitats. Thus, our results on the current relationship between climate and chamois behaviour may shed light on the animals' ability to track and adapt to climate change.

Keywords Activity rhythms · Alpine environment · Climatic conditions · GPS collars · *Rupicapra rupicapra*

Introduction

Animals living in temperate habitats face pronounced changes in climatic conditions and food availability. This is

---

Communicated by K. E. Ruckstuhl

Electronic supplementary material The online version of this article (doi:10.1007/s00265-016-2137-8) contains supplementary material, which is available to authorized users.

✉ Francesca Brivio
fbrivio@uniss.it

[1] Department of Science for Nature and Environmental Resources, University of Sassari, via Muroni 25, 07100 Sassari, Italy

[2] Department of Life Sciences and Biotechnology, University of Ferrara, Via L. Borsari 46, 44121 Ferrara, Italy

[3] Parc Naziunal Svizzer, 7530, Zernez, Switzerland

particularly true for the species inhabiting Alpine regions where seasonal changes are marked. Alpine winter is generally characterised by a sharp decrease in temperature and the presence of snow which lead to an increase in energetic demands at a time when food resources are extremely scarce. Conversely, during spring and summer, the highly structured geomorphology of Alpine environments entails high spatial heterogeneity in climatic conditions as well as in the distribution of natural resources (i.e. high-quality forage, Pettorelli et al. 2005).

To cope with these annual cyclic changes, animals undergo several physiological, morphological and behavioural adjustments (Lovegrove 2005; Paul et al. 2008). Remarkable examples of these seasonal responses are the evolution of winter-specific physiological and behavioural patterns to conserve energy (i.e. a highly insulative pelage: Martinet et al. 1992; hibernation: Kondo et al. 2006; huddling: Gilbert et al. 2010), seasonal migrations (e.g. Kumar et al. 2010) and the periodic repetition of the rutting season: (e.g. Rutberg 1987; van Noordwijk et al. 1995).

The seasonal coordination of these phenotypic modifications is regulated by endogenous clocks which help animals to anticipate and prepare for environmental changes (Pittendrigh 1993; Paul et al. 2008). Circadian oscillators (i.e. endogenous clocks) are synchronised (*entrained*) with the time of the year by periodical changes in environmental stimuli, the so-called zeitgebers (from German, *zeit*: “time”; *geber*: “to give”; Pittendrigh 1993). Day length (i.e. photoperiod), the most accurate natural predictor of annual phase, is one of the main zeitgebers (Gorman et al. 2001; Gwinner 2003). However, other periodical factors in the animals’ environment can also act as time cues: in particular, food and water availability, ambient temperature and social signals have been shown to affect seasonal traits (reviewed in Paul et al. 2008). Besides the entrainment effect, environmental variables (geophysical and biological) usually have also a direct inhibitory or enhancing effect on the different physiological and behavioural patterns, resulting in a masking effect (i.e. the direct effect of the environment on the rhythmic output) on the circadian and circannual rhythms (Aschoff et al. 1982). Animals’ reliance on all these cues is highly species-specific and allows physiological adjustments to be made in preparation for the conditions expected in each season (Paul et al. 2008).

Behavioural adaptations to the change in environmental and social conditions have been shown to respond more rapidly than physiological or morphological ones (Van Buskirk 2012). Therefore, one of the first reactions to seasonal acclimatisation that vertebrates can implement is the modification of their behavioural rhythms. The activity rhythms of several species are highly entrained to the variation in environmental cues and strongly influenced by individual characteristics such as sex, age and body size (e.g. Prates and Bicca-Marques 2008; Owen-Smith and Goodall 2014). Activity rhythms are important in controlling the energy balance of a species (Aschoff 1979), thus resulting in a complex trade-off between optimal foraging time, social activities and environmental constraints (Aschoff 1963). These rhythms play a major role in the ecological relations of a species and form part of its evolutionary adaptation (Pittendrigh 1993).

Nowadays, the global climate change is altering seasonal patterns. For instance, global meta-analyses documented a significant mean shift towards earlier spring timing of 2.3 days/decade (Parmesan and Yohe 2003). Consequently, animal rhythms (e.g. reproduction phenology) may become out of phase with the periodic challenges posed by their environment (e.g. Pettorelli et al. 2007; Plard et al. 2014). Indeed, it has been demonstrated that earlier spring has already caused phenological modifications in most taxonomic groups (Parmesan and Yohe 2003; Root et al. 2003). The Alpine ecosystems are amongst the most vulnerable to rapid climate change (Ernakovich et al. 2014). Their climate is expected to be particularly affected by global warming through rising temperatures (about 0.25 °C/decade by the mid-twenty-first century), changes in the seasonal cycle of precipitation, global radiation, humidity, temperature and precipitation extremes, and closely related impacts such as floods, droughts, snow cover and natural hazards (Gobiet et al. 2014). Hence, it is likely that animals living in the Alps will have to face several drastic environmental modifications in the next decades but, in light of current knowledge, it is not clear which physiological or behavioural responses they will be able to adopt.

Studies on the current relationship between climate and animal behaviour should shed light on the species’ ability to track and adapt to climate change (Lehmann et al. 2008; Korstjens et al. 2010). Alpine chamois is a relatively eurythermic mountain ungulate, which has adapted to a wide range of temperatures and is distributed over a broad altitudinal range (500–3100 m; Shackleton 1997; Spitzenberger et al. 2001). Indeed, this species is the most widespread ungulate in the Alps (Apollonio et al. 2010) and is well adapted to their environment and seasonality. It is characterised by nearly monomorphic sexes, with only a weak and highly seasonal dimorphism in body mass (from approx. 40 % before the rut, to approx. 6 % in winter and 4 % in spring; Garel et al. 2009; Rughetti and Festa-Bianchet 2011). The seasonal changes in body mass, together with the very high survival rate of both sexes (Corlatti et al. 2012), are indicative of a conservative strategy. Indeed, as many capital breeders (Jönsson 1997), chamois accumulate fat resources during summer (Pérez-Barbería et al. 1998) to be used during the rut (i.e. November) in order to reduce over-winter mortality costs. Moreover, this species is characterised by seasonal dimorphism: the coat, which is light brown in summer, typically turns into black during the winter season (Couturier 1938). In other words, this ungulate is an ideal case study to investigate the plasticity in the response of a species to the variation in the environmental conditions of mountainous regions.

Here, we compared daily mean activity levels of Alpine chamois of different sex and age throughout the years in order to investigate individual strategies of adaptation to seasonal and climatic variations. Based on studies on other ungulates, we recognised three main climatic stressors: thermal, wind-chill and precipitation. We formulated our alternative hypotheses and predictions (Table 1) to understand which of them played a remarkable effect on chamois activity regulation.

Since in mountainous regions the harshest conditions occur during the winter season, part of our analyses focused only on winter data to better understand how chamois managed to control their energy balance in response to different external factors under severe environmental conditions. With this aim, we defined specific alternative hypotheses to explain winter activity variations in chamois, by taking into account the climatic stressors which proved to be important in the full-year analysis and adding snow as a possible additional stressor (Table 2).

Material and methods

Study area and population

This study was carried out in the Swiss National Park (SNP; 46° 40 10.74″ N, 10° 9 15.15″ E), in south-eastern Switzerland. The SNP is an area of integral protection where hunting is not allowed. The area covers 170 km^2 and elevation ranges from 1500 to 3170 m above sea level (a.s.l.). The landscape consists of forests of Arolla pine (*Pinus cembra*), larch (*Larix decidua*) and mountain pine (*Pinus mugo*) below the tree line (approx. 2200 m a.s.l.) and alpine grasslands and rocky slopes above it. Annual precipitation amounts to 700–1200 mm.

The only predator of chamois is the Golden eagle (*Aquila chrysaetos*) that typically preys upon small kids. During the study period (2010–2013), population census showed that chamois density naturally fluctuated over the years from a maximum of 7.7 individuals/km^2 (in 2010) to a minimum of 6.2 individuals/km^2 (in 2013). Between 2010 and 2013, 11

Table 1 Set of alternative hypotheses predicting daily mean activity in Alpine chamois throughout the year in Swiss National Park

Model #	Model name	Hypothesis	Supporting examples
1	No weather effect	Chamois activity is expected to vary throughout the year, depending on animal age, with no influence of weather conditions	Stache et al. 2013
2	Thermal disturbance	Chamois activity is expected to vary throughout the year, depending on animal age, and is affected by daily mean temperature	Signer et al. 2011; Mason et al. 2014
3	Radiation disturbance	See the hypothesis of model #2, but chamois activity budget is more sensitive to solar radiation, rather than to air temperature	Porter et al. 2000
4	Wind-chill effect	See the hypothesis of model #2, but taking into account the wind-chill effect. Wind can cause better conditions during hotter days or it may be a disturbance for animals	Jingfors 1982
5	Opposite radiation and wind effects	Chamois activity is expected to vary throughout the year, depending on animal age, and is affected by the antithetical effects of radiation and wind	Beier and McCullough 1990; Ismail et al. 2011
6	Precipitation disturbance	Chamois activity is expected to vary throughout the year, depending on animal age, and is affected by daily precipitation	Loe et al. 2007
7	Thermal + precipitation disturbance	Chamois activity is expected to vary throughout the year, depending on animal age, and is affected by both thermal balance (influenced by daily mean temperature) and precipitation disturbance	Kamler et al. 2007
8	Radiation + precipitation disturbance	Chamois activity is expected to vary throughout the year, depending on animal age, and is affected by both thermal balance (influenced by solar radiation) and precipitation disturbance	Schütz et al. 2010
9	Wind-chill effect + precipitation disturbance	Chamois activity is expected to vary throughout the year, depending on animal age, and is affected by both thermal balance (influenced by wind-chill) and precipitation disturbance	Graunke et al. 2011
10	Opposite radiation and wind effects + precipitation disturbance	Chamois activity is expected to vary throughout the year, depending on animal age, and is affected by both thermal balance (influenced by the interplay of radiation and wind) and precipitation disturbance	Graunke et al. 2011
11	Null model	Intercept only	

Table 2 Set of alternative hypotheses predicting daily mean activity in Alpine chamois during winter months (1 December–29 February) in Swiss National Park

Model #	Model name	Hypothesis	Supporting examples
1 W	Best global model	Thermal balance (influenced by wind-chill factor) and precipitation affected chamois annual activity, as well as winter activity	See "Results" section
2 W	Global model, but with radiation	Since chamois have the black coat in winter, radiation, rather than air temperature, and the antithetical effect of wind affected activity rhythms during the cold season	Armitage 2009; Maia et al. 2015
3 W	Snow disturbance	Chamois activity is affected by snow fall and depth	Kufeld et al. 1988
4 W	Global model + snow disturbance	In addition to the hypothesis of the model #1w, chamois activity is also affected by snow depth	Signer et al. 2011
5 W	Radiation + snow disturbance	In addition to the hypothesis of the model #2w, chamois activity is also affected by snow depth	Beier and McCullough 1990
6 W	Null model	Intercept only	

females and 6 males were captured with box traps and equipped with GPS Plus Collar (Vectronic Aerospace GmbH, Berlin, Deutschland). The exact year of birth was determined by counting the number of annual incremental growth rings on the horns (Schröder and von Elsner-Schack 1985). The age at capture ranged between 3 and 15 years for females and between 6 and 13 years for males.

Data collection

It was not possible to record data blind because our study involved focal animals in the field. The locomotor activity was recorded continuously from the capture of the individuals (the first one in March 2010) until either the conclusion of data collection (November 2013) or when the collar stopped working (Supplementary material 1 Table A1). We collected an average of 514 days/chamois (minimum 190–maximum 780 days). The activity was recorded by means of an analogue accelerometer (i.e. activity sensor) installed on the GPS collars, which measured the activity based on the actual acceleration they experienced. The accelerometer had a dynamic range from $-2G$ to $+2G$ (G = gravitational constant) and measured activity as the change of static acceleration (gravity) and dynamic acceleration (collar) four times/s. The activity values were given within a relative range between 0 and 255. Value 255 was equal to $-2G/+2G$ and it indicated the maximum acceleration, whereas 0 indicated no acceleration at all. Measurements were averaged over sampling intervals of 5 min and stored with the date and time associated.

Such weather data as daily mean temperature (°C), daily mean solar radiation (W/m^2), daily mean wind speed (m/s) and daily precipitation (i.e. the amount of rain and snow expressed in millimetres of water) were provided by the Swiss Meteorological Institute (Begert et al. 2005) and collected at the weather station of Buffalora which is located at approx. 13 km from the study area, at an altitude of 1,968 m a.s.l. (46° 38 53″ N; 10° 16 02″ E). Daily snow depth (defined as the depth of snow cover in centimetres) was measured each day of the data collection period at the station of Val Trupchun (46° 35 44″ N; 10° 04 46″ E), inside the study area.

Data analysis

Data were presented graphically as actograms by using the Activity Pattern software (ver. 1.3.1, Vectronic Aerospace GmbH, Berlin, Deutschland). Visual inspection of the actograms was firstly used to establish: (i) the presence of synchronisation of locomotor activity with natural light-dark cycles; (ii) the distribution of activity over the day (i.e. unimodal: a single peak of activity per day, bimodal/trimodal: a double/triple peak of locomotor activity per day). The presence of periodicity in the locomotor activity rhythms was determined by means of the Lomb-Scargle periodogram (LSP) analysis and confirmed with the χ^2 periodogram analysis, by using the ActogramJ software for circadian analysis (Schmid et al. 2011). The significance was set to $P < 0.05$. Both procedures are widely used for the analysis of circadian rhythms (Refinetti et al. 2007). LSP procedure is based on a modification of Fourier analysis so as to accommodate unequally spaced time series (Lomb 1976). It is a method particularly suited to detect periodic components even in unequally sampled time series. For this reason, it was used to analyse time series obtained from free-living animals which are typically characterised by missing values (Ruf 1999). The other procedure, the χ^2 periodogram, is an implementation of the Enright periodogram (Enright 1965) and uses χ^2 instead of F distribution (Sokolove and Bushell 1978). It is widely employed to determine rhythmicity within a period different from 24 h. These procedures are almost equivalent in terms of accuracy, with LSP being slightly better (Ruf 1999). Furthermore, to exclude the detection of harmonics that do not really exist in the data (i.e. 8- and 12-h periods which were harmonics of 24-h periods, or vice versa), we compared the amplitude of the peaks (PN and Qp for LSP and χ^2 periodogram, respectively) and accepted the highest one (van Oort et al. 2005) as valid. As a consequence, an ultradian period (8- and 12-h length) that was harmonic of a daily (24 h) period, or vice versa, was rejected. For each chamois, analyses were performed monthly with intervals of 10 days. Intervals of 10 days enabled us to apply periodogram analysis on time series of sufficient length to have a reliable statistical significance. Longer intervals were not considered because they may have precluded us to show seasonal changes in the periodicity.

For each chamois, we calculated the daily mean activity (DMA) as the average of the raw values recorded by the accelerometer within the collar during each day of the data collection period. We focused on the DMA of each individual to assess the effect of intrinsic and extrinsic factors on chamois daily activity patterns. To allow for the likelihood of a non-linear response to the covariates, we chose to fit a non-parametric model to the data in which the exact functional form was determined from the data themselves and not specified a priori. Generalised additive models (GAMs) are an ideal tool for such analysis, as they are flexible in modelling the shape of non-linear relationships. Non-parametric smoothing functions are used on sections of the data and the response curves are connected at their end-points to generate an overall smooth curve (Wood 2006). In addition to the non-parametric smoothing functions, parametric fixed and random predictor terms may also be included (Wood 2013). The DMA was modelled as the response variable by fitting alternative GAMs (Supplementary material 2 Table A2, 3) implemented within the mgcv package (version 1.8-10) in R (version 3.0.2; R Core Team 2014). The predictor variables considered were the weather parameters measured at the station of Buffalora (temperature, radiation, wind speed, precipitation) and the snow depth measured in the study area (only for the winter period). Moreover, in order to identify the pattern of variation of DMA fluctuating throughout the year, we included the Julian date as a continuous variable in the models. To investigate whether females and males reacted differently to the environmental variables considered, for each variable included in the models, we added the interaction with sex. We controlled for the effect of age on chamois activity levels by including it as a covariate (continuous variable) in all the models tested. Chamois identity was used as a random factor to control for repeated measurements of the same individual, fitting it in the GAMs by using "re" terms, and smoother linkage (Wood 2013). Possible correlations between the predictor variables were checked by means of a correlation matrix (Pearson correlation coefficient, r_p) to avoid collinearity (Sokal and Rohlf 1995). Highly correlated variables ($r_p > 0.7$) were used separately in the alternative models (Supplementary material 3 Fig. A1, 2). Precipitation and wind speed were log-transformed in order to improve the homogeneity of residual distribution. Effects of all continuous predictor variables, except the Julian date, were modelled as natural cubic spline functions. The effect of the Julian date was modelled as a cyclic cubic regression spline in order to take into account the circularity of this variable: in doing so, we ensured that the value of the smoother at the far left point (1 January) was the same as the one at the far right point (31 December). The optimal roughness of the smoothing terms was determined by minimising the generalised cross-validation value.

Analyses were performed by using the information-theoretic approach (Dochtermann and Jenkins 2011). In the light of biological relevance and previous research on related species, we defined a set of alternative hypotheses, which were used to construct 11 a priori GAMs (Table 1). In formulating alternative hypotheses, we made allowances for three main climatic stressors: thermal (measured alternatively by means of temperature or radiation data), wind-chill and precipitation. In all models, we included the Julian date and age as fixed factors: their effect on the activity rhythms of vertebrates is well documented in literature (e.g. Prates and Bicca-Marques 2008; Stache et al. 2013). The analysis of literature brought to light that the thermal stressor affects the activity of several animal species (e.g. Belovsky and Slade 1986; Owen-Smith 1998; Signer et al. 2011). To measure its effects, we used two alternative measures: temperature and radiation. The latter may be particularly important as chamois uses open areas at high altitude, i.e. an environment with high radiation (models # 2–4). It is well known that precipitation can be a disturbance for vertebrates (e.g. Loe et al. 2007). Thus, we evaluated the role of this stressor alone (model # 6) as well as in combination with other meteorological events (models # 7–10). Lastly, wind increases evaporation and therefore may cause an improvement of the thermal stressor during the hottest days as well as exacerbate the difficulties during winter days (e.g. Jingfors 1982; Beier and McCullough 1990; Ismail et al. 2011). Hence, we analysed the wind-chill effect in models # 4, 5, 9 and 10.

The alternative models were ranked and weighted with the minimum second-order Akaike Information Criterion (AICc) criterion (Symonds and Moussalli 2011). AICc of each model was calculated by using the AICcmodavg package in R, with the number of independent clusters (i.e. 17 individuals) employed for the correction of the equation. We confirmed the global goodness-of-fit (i.e. homoscedasticity, normality of errors and independence) of the best model by visual inspection of residuals (Zuur et al. 2009).

Finally, in order to investigate how chamois managed to control their energy balance under the severe environmental conditions of the winter season, we analysed data from 1 December to 29 February separately. Even for this part of the analyses, we formulated alternative hypotheses (Table 2). We constructed the model #1w by using the same variables of the model selected in the global model analysis (model #5). We chose to test the thermal stressor by using alternatively temperature (model #1w) and radiation (model #2w). Even though the global model analysis does not select radiation, we hypothesised that its effect may be important during winter because in this season, the chamois coat turns almost completely black. Indeed, coat colour was seen to affect reflectance and absorption of radiation (Armitage 2009), with light colours increasing the former and dark colours increasing the latter. For instance, Maia et al. (2015) showed that, under intense solar radiation, the absorption in black goats is twice that in white goats. Finally, we conjectured that the snow stressor (measured as precipitation and snow depth) may strongly influence chamois activity (e.g. Kufeld et al. 1988; Beier and McCullough 1990; Signer et al. 2011). We hypothesised that this stressor was so strong that it managed to mask the effect of other stressors (model #3w). Alternatively, we supposed that activity variations were better explained by the interplay between the snow stressor and the other ones (models #4w, #5w). In all these models, the effect of the Julian date was evaluated by using a continuous variable, namely the winter date, scored from 1 (1 December, year x) to 91 (29 February, year $x+1$), in order to account for both the discontinuity between 29 February and 1 December of the same year and the continuity between 31 December and 1 January of the following year. The hypotheses were used to construct six a priori GAMs (Table 2). Then, we followed the same approach described earlier in order to identify the best model amongst the alternative ones.

Results

A total of 5884 days/chamois for females and a total of 2869 days/chamois for males were obtained during data collection. In all the chamois investigated, the visual inspection of the actograms showed a diurnal pattern of locomotor activity affected by the changes in photoperiod naturally occurring across the year (Fig. 1, Supplementary material 4 Fig. A3–17). Bouts of nocturnal activity were also present during most of the year (Figs. 1, 2, Supplementary material 4 Fig. A3–17). Interestingly, the pattern of locomotor activity showed a marked seasonal variation in both females and males; it gradually changed from unimodal (with a single peak of activity from December to May/June) to bimodal/trimodal during summer and autumn (Fig. 2). During summer, the periodogram analysis showed a significant rhythm with a period of 12 h ($P < 0.05$, LSP; Fig. 2b, f) for both females and males. During autumn, the period shortened to 8 h ($P < 0.05$, LSP; Fig. 2c, g) and the pattern of activity became trimodal, with a marked increase of nocturnal activity peaking at midnight (Fig. 1, Supplementary material 4 Fig. A3–17).

Global models The hypothesis best supported by data showed that the DMA of chamois varied according to individual age throughout the year and was affected by wind-chill and precipitation. Indeed, the best model selected (model #9, AICc = 60708.6, ΔAICc of the second-ranked model: 63.9—Supplementary material 2 Table A2) included the predictor variables: age, day of the year, the interaction term temperature × wind speed and precipitation (R-sq.(adj) = 0.81). Older females were more active than younger ones, whereas age had an opposite effect in males (Supplementary material 5 Fig. A18a). Results showed that, throughout the year, the DMA of both sexes followed a bell-shaped pattern, with maximum activity at the beginning of summer (females' peak on the 178th day of the year—27 June; males' peak on the 181th day of the year—30 June) and minimum values in January (Fig. 3a). In males, a second peak of activity was reported from mid-October to late November. Just prior to this period, males showed an abrupt increase in activity whereas female activity plateaued. After that, males had reached the peak of activity early in the rut, both male and female activity decreased at the same pace. The wind-chill factor, expressed as the interaction between temperature and wind speed, affected chamois DMA with slight differences between the two sexes (Fig. 4). DMA of both sexes reached maximum levels during days with mean temperatures around 3–7 °C characterised by weak or no wind. Chamois activity decreased with both warmer and colder temperatures and, more importantly, with the increase in wind, until reaching minimum DMA during windier and colder days. The effect of this interaction between wind and temperature appeared to be more important in females than in males. Female and male DMA was also weakly influenced by precipitation, with DMA decreasing with increasing daily precipitation (Fig. 3b).

Winter models The hypothesis best supported by data showed that chamois DMA fluctuated during the winter season according to individual age and was affected by radiation, wind speed, precipitation and snow depth (model #w5, AICc = 8672.9, ΔAICc of the second-ranked model: 17.2—R-sq.(adj) = 0.68; Supplementary material 2 Table A3). Age affected male activity, though with no clear relationship, and had a slightly positive effect on female activity (Supplementary material 5 Fig. A18b). Results showed that during this period (1 December–29 February) the variation in chamois DMA was better explained by radiation than by temperature, with a positive effect on both females and males (Fig. 5a). Chamois DMA considerably decreased with increasing snow depth (Fig. 5b), while the relationship between DMA and precipitation was weakly negative only for females and did not affect male activity (Fig. 5c). Finally, wind speed seemed to have a negative effect only on female DMA and, in particular, female chamois had higher activity levels during days with weak or no wind and lower ones during windier days (Fig. 5d).

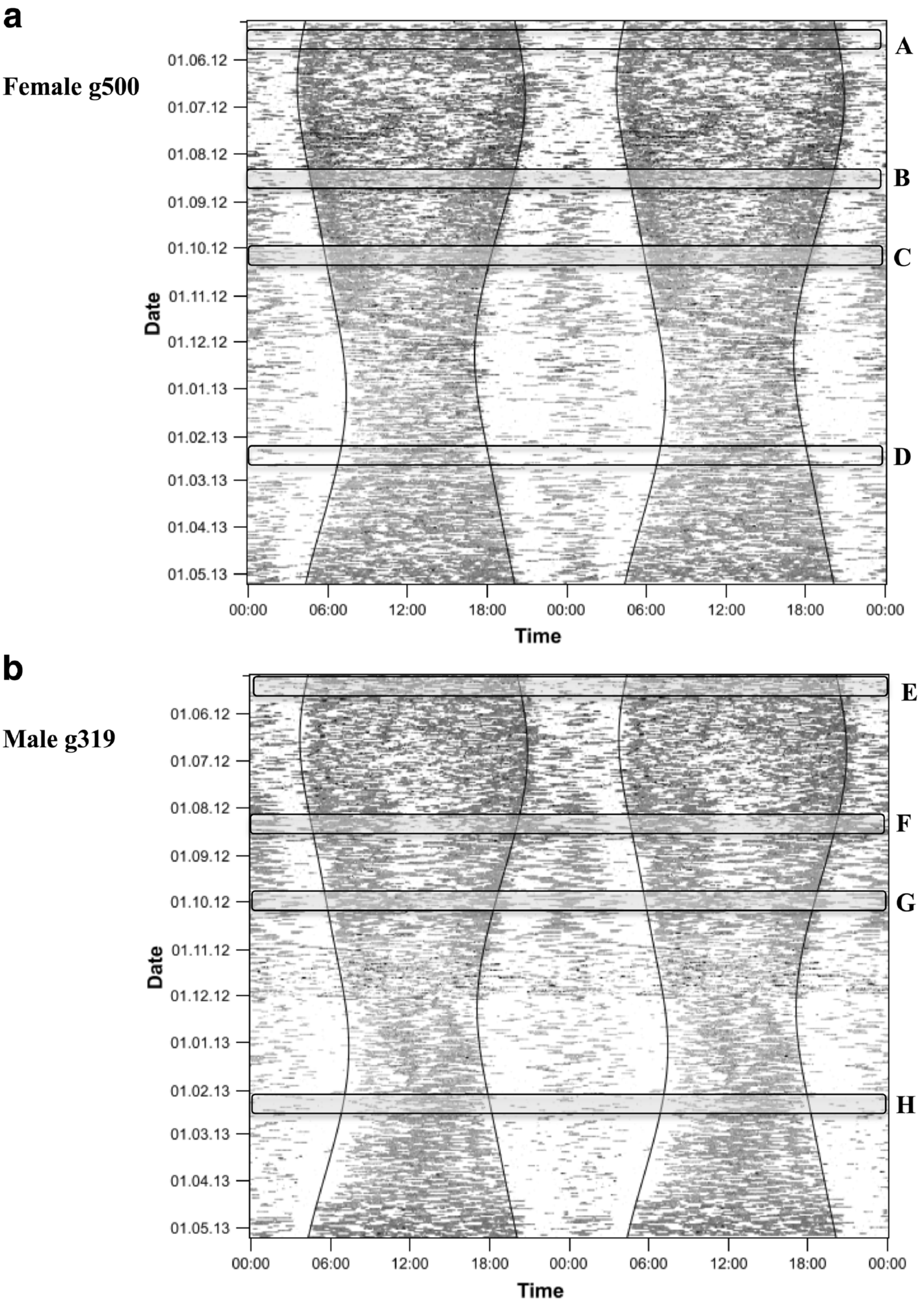
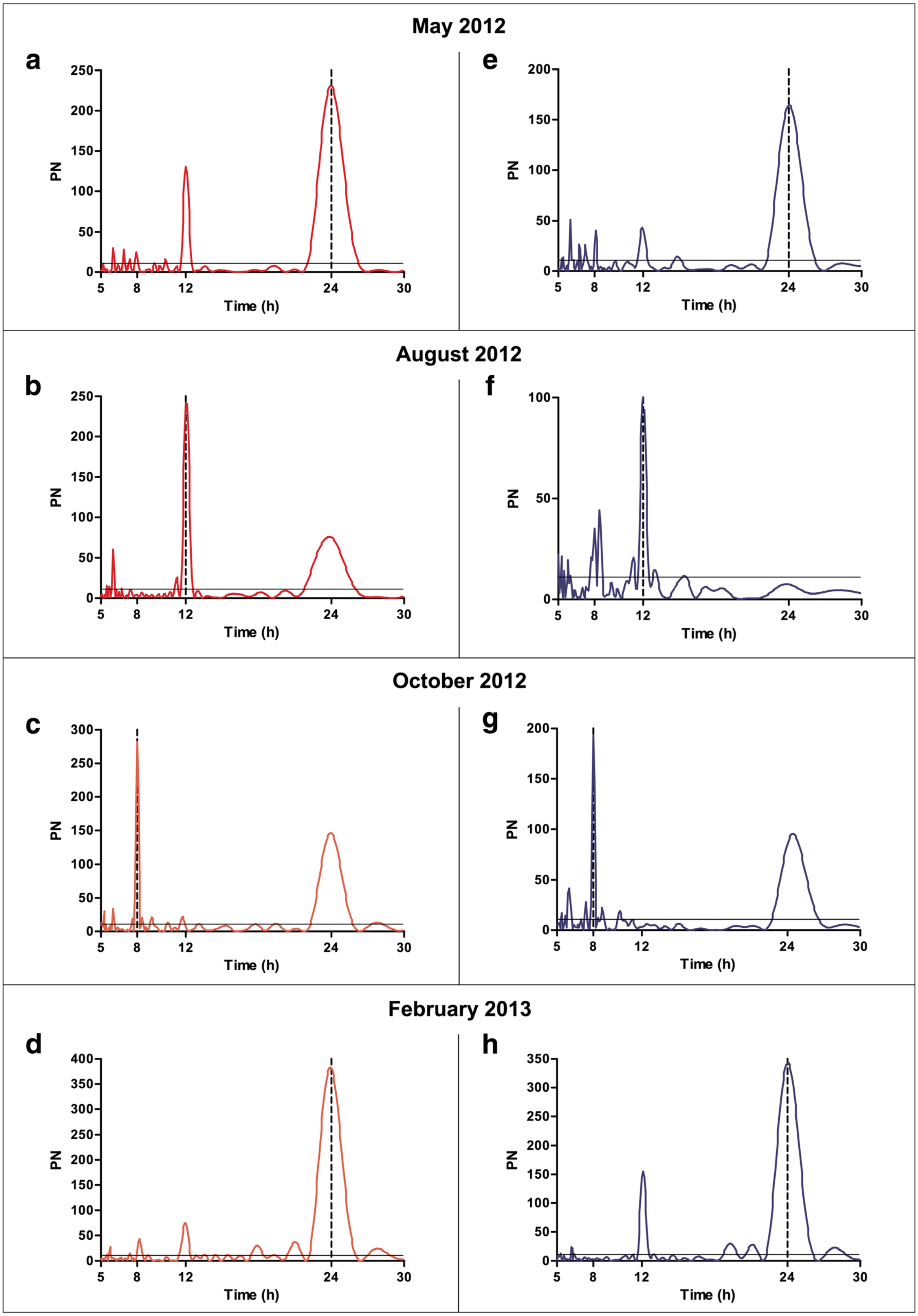


Fig. 1 Representative actograms of daily activity of **a** one radio-collared female Alpine chamois and **b** one radio-collared male Alpine chamois in the Swiss National Park. *Vertical bars* represent their activity levels (over intervals of 5 min), the *colour of the bar* being a function of activity level: from *white* (=0) to *black* for maximum values (i.e. 255). *Black vertical lines* indicate dawn and dusk according to civil twilight. Records are double plotted on a 48-h time scale to help the interpretation. Squares *A–H* delimit the 10-day intervals in four different periods of the year analysed with periodogram analysis, as showed in Fig. 2

Discussion

This first detailed field study on Alpine chamois activity showed that this species exhibited an evident diurnal pattern of locomotor activity. DMA was significantly influenced by climatic factors, with females and males showing similar reactions to the environmental factors analysed.

The pattern of locomotor activity varied from a unimodal pattern during winter to a bimodal one during summer and autumn. It is no coincidence that, according to the findings on DMA, chamois were more active during spring and summer and less active during winter. Previous studies indicated that chamois typically spend about 67–70 % of their active time foraging (Rüttimann et al. 2008). Thus, in accordance with other studies on ungulate behaviour (Collins et al. 1978; Risenhoover 1986; Beier and McCullough 1990), we can assume that changes in chamois activity mainly reflected changes in the time spent feeding. Hence, we can argue that the variation in the activity patterns was accounted for by the response of chamois to seasonal variations in the availability



of food resources. In mountainous areas, the rapid growth of fresh plant forage typically begins immediately after snowmelt (generally in April–June and earlier at lower altitudes), thus providing an abundant and protein-rich source of

◀ **Fig. 2** Lomb-Scargle Periodogram (LSP) analysis of locomotor activity rhythms of one radio-collared female Alpine chamois (g500: **a**–**d**) and one radio-collared male Alpine chamois (g319: **e**–**h**) in the Swiss National Park (Switzerland) showed in Fig. 1. The analyses were performed over intervals of 10 days in four different periods of the year. LSP analysis showed the presence and periodicity of rhythms of locomotor activity. Amplitudes of the peaks are used to indicate the main period (*dotted lines*). Periodicity confirmed the presence of unimodal (24-h period; **a**, **d**, **e**, **h**), bimodal (12-h period; **b**, **f**) and trimodal (8-h period; **c**, **g**) patterns in both females and males in the same month of the year. The periodogram indicates the normalised power (PN) of the rhythm explained by each period analysed within a range of 5–30 h. The *straight horizontal lines* represent the threshold of significance set at $P = 0.05$

food for a relatively brief period. The shift from unimodal to bimodal pattern during spring and summer may be a physiological consequence related to rumination rhythms. Whenever ruminants eat more abundant forage, they typically fill their rumen more rapidly and therefore have to lie down to ruminate and digest plant material earlier in the day (VanSoest 1994). In addition, when the forage is protein-rich, the digestion is faster, so that animals are able to engage in a second bout of foraging activity later in the day (VanSoest 1994). Moreover, even the summer peak of activity levels pointed out by our analyses can be interpreted as a strategy of adaptation to the availability of food resources. The peak of activity during the spring-summer months may enable chamois to use the most favourable forage conditions in order to storage fat tissue to survive during long, cold and snowy winters, as reported for other Northern-temperate mammals (Tyler and Blix 1990; Adamczewski et al. 1997; Parker et al. 2009). Accordingly, the reduction of activity during winter and the use of the unimodal pattern showed by our analyses may be seen as an adaptation strategy to conserve energy in response to unfavourable conditions (i.e. harsh weather, cold temperature with wind-chill, decrease in forage quality and food availability due to snow). For both female and male chamois, the decrease in forage quality and quantity may be offset by a decrease in metabolic rate and the use of the stored energy reserves. The reduction of food intake and, in general, of metabolic rate during winter is widespread amongst northern ungulates as a strategy to cope with cold conditions and low availability of food resources (reviewed in Arnold et al. 2004).

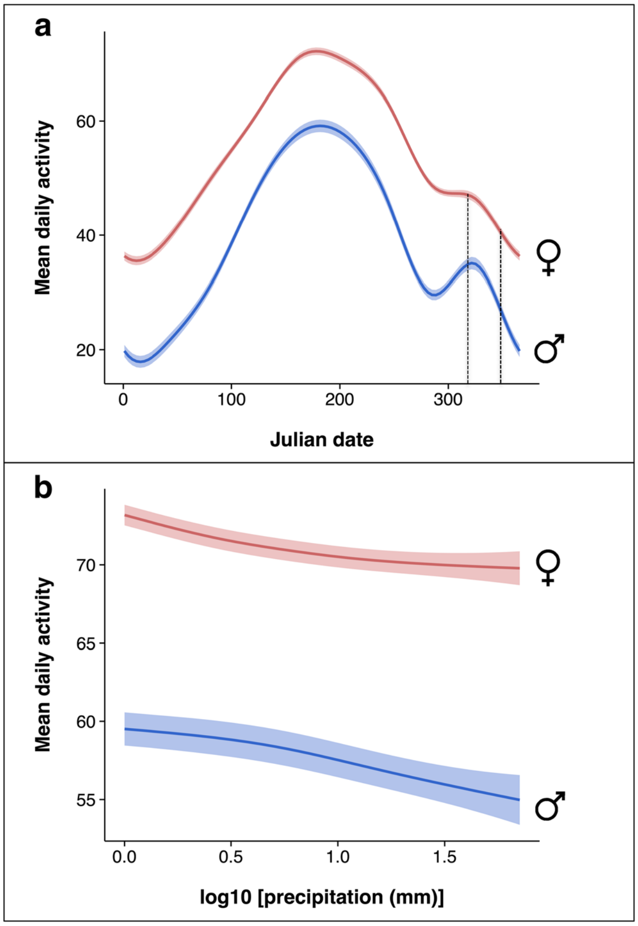


Fig. 3 Values predicted by the best generalised additive model (see the text for more details) of daily mean activity of Alpine chamois in the Swiss National Park. The figure shows the effects of Julian date (**a**) and daily precipitation (**b**). The predictions are given according to the mean of all other covariates in the model, for the collar ID g26 and the collar ID g375, for females and males, respectively. In the graphs, females are represented by the *red line*, males by the *blue line*, while the *coloured shaded areas* are the estimated standard errors. The *vertical broken lines* (**a**) represent the starting (1 November) and the ending day of the rut period (30 November)

At first glance, activity followed a bell-shaped pattern with maximum values at the end of June, when day length is highest, and minimum values in winter. Throughout the year, activity rhythms can deviate from this pattern, thus suggesting that other biological and environmental factors may act as time cues for chamois activity regulation. In November, for example, a peak of activity in males disrupted the decreasing pattern characterising the period from mid-summer to winter. This coincided with chamois mating season, which peaks between 16 and 25 November (Corlatti et al. 2013b). This peak of activity cannot be ascribed to foraging behaviour as males typically reduce forage intake during the rut (Willisch and Ingold 2007). Therefore, according to Corlatti et al. (2013b), the high activity levels found in this study were likely due to social activities aimed at gaining mating opportunities. Our results showed that chamois nocturnal activity increased during autumn, with a third peak of daily activity reported at midnight. Thus, our results match with previous knowledge on this species and contribute to explain why males lose weight faster than females during the rutting period (Garel et al. 2009; Mason et al. 2011; Rughetti and Festa-Bianchet 2011). In fact, during the rut, males spent noticeably less time foraging (i.e. reduction of food intake; Willisch and Ingold 2007; Corlatti et al. 2013a) and were more active (i.e. increase in energy expenditure).

Climate is another time cue for chamois activity: they adjusted their activity responding to variations of the wind-chill

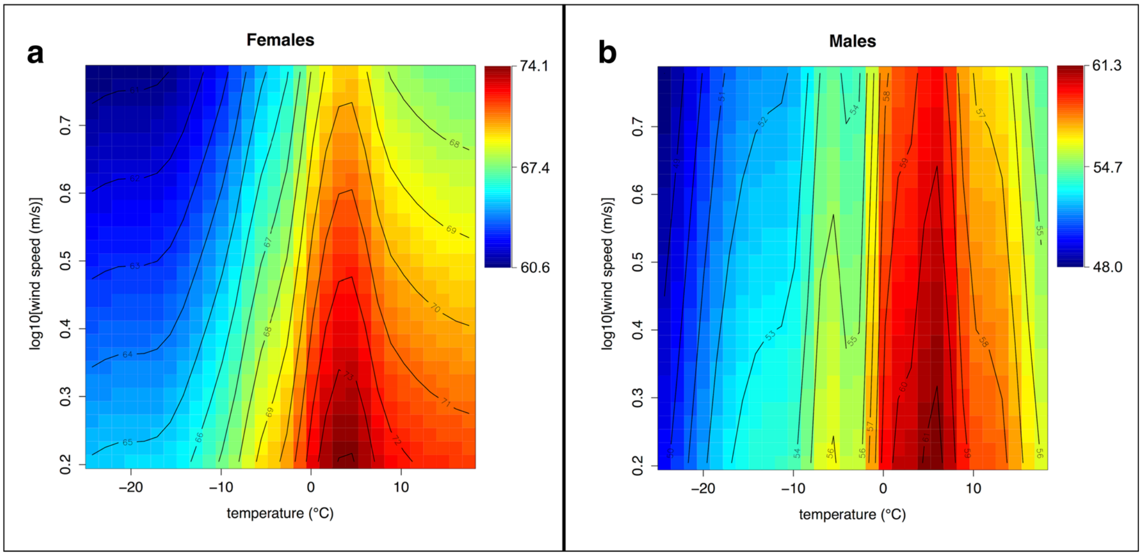


Fig. 4 Predicted variation of daily mean activity in female (**a**) and male chamois (**b**) in the Swiss National Park under the effect of the interaction term between temperature and wind speed. The figures show the contour plots with the values predicted by the best generalised additive model (see the text for more details). The predictions are given according to the mean of all other covariates in the model, for the collar ID g26 and the collar ID g375, for females and males, respectively. *Red colour* indicates the higher values and *blue colour* the lower ones

factor, as well as to changes in precipitation levels and, during winter, snow abundance and solar radiation. The interaction between air temperature and wind speed (wind-chill factor) appeared to influence chamois activity rhythms, either by reducing or by stirring daily activity levels. The response of chamois activity to temperature was parabolic for both sexes: in July for instance, the highest activity levels occurred during days with mean temperatures around 3–7 °C characterised by weak wind speed, while a decline in activity levels was observed at higher and lower temperatures (Fig. 4). Such effect of temperature was exacerbated by wind speed and DMA reached minimum levels during windier and colder days.

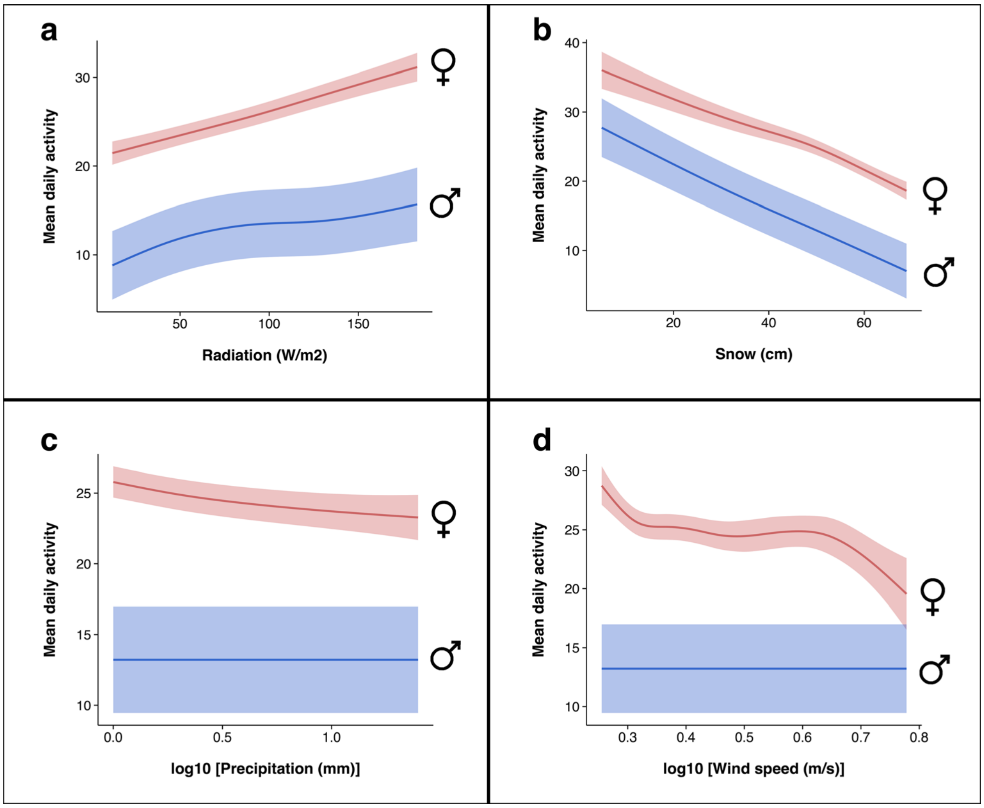


Fig. 5 Values predicted by the best generalised additive model (see the text for more details) of Alpine chamois daily activity during winter months (1 December–29 February) in the Swiss National Park. The figure shows the effect of radiation (**a**), snow depth (**b**), precipitation (**c**) and wind speed (**d**). The predictions are given according to the mean of all other covariates in the model, for the collar ID g26 and the collar ID g375, for females and males, respectively. In the graphs, females are represented by the *red line*, males by the *blue line*, while the *coloured shaded areas* are the estimated standard error

Therefore, activity appeared to be strictly dependent upon animal thermal balance. On the one hand, when air temperatures are below the animals' thermoneutral zone and wind intensifies, the decrease in activity can be seen as a strategy to lower the costs of thermoregulation by seeking shelter (in time budget terms, by resting) in order to prevent heat loss, which may be exacerbated by the higher evapotranspiration caused by the wind. Likewise, Moen (1976) and Gates and Hudson (1979) showed that lying position and inactivity significantly reduce the metabolic costs of thermoregulation in cold weather. On the other hand, when air temperatures rise above the species' thermoneutral zone, the reduction of activity may be an attempt to avoid thermal overload by reducing such heat-generating activities as feeding, moving and possibly even social interaction. This result is consistent with a previous observational study on Alpine chamois, which were reported to allocate less time to foraging with increasing temperatures during summer (Mason et al. 2014). In this respect, chamois appeared not to take advantage of wind as an agent reducing thermal overload and, according to our results, wind speed was likely perceived just as a disturbance during both cold and warm days.

Several authors showed that thermal stress places an upper limit on the time animals devote to daily activity (e.g. Orthoptera: Parker 1982; Chappell 1983; American crow [*Corvus brachyrhynchos*], grey squirrel [*Sciurus carolinensis*]: Kilpatrick 2003; North American beaver [*Castor canadensis*]: Belovsky 1984b; snowshoe hare [*Lepus americanus*]: Belovsky 1984a; moose [*Alces alces*]: Belovsky 1978; greater kudu [*Tragelaphus strepsiceros*]: Owen-Smith 1998). Each species has developed a tolerance to heat depending on the habitat in which it lives. Therefore, ungulates living in temperate regions appear to have their activity levels reduced by lower temperatures in comparison with species living in the African savannah (e.g. Belovsky and Slade 1986; Owen-Smith 1998). Our results showed that in July, chamois started to decrease their activity already at 7–10 °C. Given the rapid alteration in the seasonal cycle of climatic variables characterising the last few decades, the annual activity rhythms of chamois, which have evolved over thousands of years and are well synchronised with the time of the year, may become out of phase with the future periodic challenges posed by their environment. As a consequence of the rising temperatures predicted for the Alpine regions (approx. 0.25 °C/decade, Gobiet et al. 2014), chamois daily activity is expected to decrease, particularly during summer, thus compromising their ability to accumulate body reserves if the availability and/or quality of food resources do not increase. This may affect the animals' ability to cope with the food shortages of the Alpine winter season, with important effects on individual life history. This scenario is supposed to worsen according to the forecasts on global radiation along the Alpine ridge, which indicate an increase in radiation during summer and a decrease during winter (Gobiet et al. 2014). On the one hand, increasing radiation during summer may exacerbate the reduction of chamois activity in order to avoid thermal overload. On the other hand, the decrease of radiation during winter may increase thermoregulation costs. Indeed, we found that chamois activity was positively related to radiation during winter months; thus, we conjectured that during winter, chamois were able to benefit from the absorption of solar radiation. By using sunny areas and taking advantage of exogenous heat for thermoregulation, they might have managed to reduce the amount of endogenous heat produced to maintain constant body temperature. Consistently, Signer et al. (2011) showed that radiant heat-assisted rewarming is a key strategy for Alpine ibex (*Capra ibex*) to endure harsh over-wintering conditions. In this framework, it is useful to note the role of chamois black coat during the winter season. Our findings suggest that this specific evolutionary characteristic favoured a greater absorption of solar radiation (exogenous heat) and thus an increase in daily activity.

Conversely, chamois winter activity may benefit from the substantial decrease in Alpine snow duration and quantity resulting from the global climate change (Gobiet et al. 2014). Our analyses on winter data highlighted a strong negative correlation between daily activity and snow abundance (both in terms of precipitation and snow depth). Several studies analysed the effect of snow depth on spatial behaviour (Tyler and Blix 1990), activity rhythms (Cederlund 1981; Beier and McCullough 1990), life history and population dynamics (Jacobson et al. 2004; Apollonio et al. 2013; Willisch et al. 2013). It is well known that deep snow causes higher energy expenditure for large mammals, arguably a consequence of both lower food availability and higher energy expenditure related to locomotion. Our study showed that chamois reduced their activity when snow depth increased: indeed, when snow depth was higher, chamois adopted a safe strategy by reducing their total activity, likely because of the reduced food availability as well as to avoid mobility problems and reduce accident risks (i.e. avalanches). As chamois have an interdigital membrane to increase the distribution of weight and favour mobility on snow surfaces (Couturier 1938), we may expect a reduced effect of snow depth on their behaviour. Nonetheless, this anatomic adaptation to snow surfaces does not seem sufficient to maintain regular activity rhythms in case of deep snow. Further research should be conducted to assess the effect of such activity reduction on individual life history and population dynamics and estimate the real effect of interdigital membrane by comparing chamois activity budget with information about sympatric ungulate species without this membrane (e.g. Alpine ibex).

In conclusion, our study pointed out that well-detailed information on activity may be used to analyse how behavioural strategies evolved in animals to adapt to their environment, take advantage of available resources and respond to environmental changes (e.g. global climate change). In our case, we showed that Alpine chamois is well adapted to high mountain environment and seasonality, even though it can be susceptible to climate change. In this respect, our work showed the complexity of potential behavioural responses to the variation in multiple environmental factors such as climatic variables and food resources.

It is important to note that our findings were obtained by using the daily mean activity. In doing so, we did not take into account the distribution of the activity over the day. The analysis of detailed activity data, rather than a study on the daily mean activity, will likely highlight the effects of individual and environmental factors on the distribution of chamois activity during the day and will consequently improve our understanding of this species' behavioural plasticity in the use of energy resources.

Acknowledgments We wish to thank all the park rangers of the Swiss National Park who captured, marked and monitored the chamois. We are grateful to S. Ciuti for his constructive and helpful comments on the first draft of this manuscript. Finally, we wish to thank two anonymous reviewers for constructive comments on a previous draft of this manuscript. This project was supported by the Italian Ministry of Education, University and Research (PRIN 2010–2011, 20108 TZKHC, J81J12000790001). SG had the support of the fund "P.O.R. F.S.E. 2007–2013—Obiettivo competitività regionale e occupazione. Asse IV Capitale umano—Linea di attività 1.3.1". The English version was edited by C. Polli.

Author contributions SG, FB and MA originally formulated the idea. FF and FT conducted fieldwork. SG, CB, FB and MA collaborated in imaging analysis. FB, CB and SG performed statistical analyses. FB wrote the manuscript and other authors provided editorial advice.

Compliance with ethical standards

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

Ethical standards Female and male Alpine chamois were tagged by rangers of the Swiss National Park under the legal authorization of the Swiss Veterinary Office. All applicable institutional and/or national guidelines for the care and use of animals were followed.

References

Adamczewski JZ, Flood PF, Gunn A (1997) Seasonal patterns in body composition and reproduction of female muskoxen (*Ovibos moschatus*). J Zool 241:245–269

Apollonio M, Andersen R, Putman R (2010) European ungulates and their management in the 21st century. Cambridge University Press, Cambridge, UK

Apollonio M, Brivio F, Rossi I, Bassano B, Grignolio S (2013) Consequences of snowy winters on male mating strategies and reproduction in a mountain ungulate. Behav Process 98:44–50

Armitage KB (2009) Fur color diversity in marmots. Ethol Ecol Evol 21: 183–194

Arnold W, Ruf T, Reimoser S, Tataruch F, Onderscheka K, Schober F (2004) Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). Am J Physiol-Reg I 286:R174–R181

Aschoff J (1963) Comparative physiology: diurnal rhythms. Annu Rev Physiol 25:581–600

Aschoff J (1979) Circadian rhythms: influences of internal and external factors on the period measured in constant conditions. Z Tierpsychol 49:225–249

Aschoff J, Daan S, Honma KI (1982) Zeitgebers, entrainment, and masking: some unsettled questions. In: Aschoff J, Daan S, Groos G (eds) Vertebrate circadian systems. Springer, Berlin, pp 13–24

Begert M, Schlegel T, Kirchhofer W (2005) Homogeneous temperature and precipitation series of Switzerland from 1864 to 2000. Int J Climatol 25:65–80

Beier P, McCullough DR (1990) Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monogr 109:3–51

Belovsky GE (1978) Diet optimization in a generalist herbivore: the moose. Theor Popul Biol 14:105–134

Belovsky GE (1984a) Moose and snowshoe hare competition and a mechanistic explanation from foraging theory. Oecologia 61: 150–159

Belovsky GE (1984b) Summer diet optimization by beaver. Am Midl Nat 111:209–222

Belovsky GE, Slade JB (1986) Time budgets of grassland herbivores: body size similarities. Oecologia 70:53–62

Cederlund G (1981) Daily and seasonal activity pattern of roe deer in a boreal habitat. Swed Wildlife Res 11:315–348

Chappell MA (1983) Thermal limitations to escape responses in desert grasshoppers. Anim Behav 31:1088–1093

Collins WB, Urness PJ, Austin DD (1978) Elk diets and activities on different lodgepole pine habitat segments. J Wildlife Manage 42: 799–810

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Corlatti L, Lebl K, Filli F, Ruf T (2012) Unbiased sex-specific survival in Alpine chamois. Z Saugetierkd 77:135–139

Corlatti L, Bassano B, Valencak TG, Lovari S (2013a) Foraging strategies associated with alternative reproductive tactics in a large mammal. J Zool 291:111–118

Corlatti L, Caroli M, Pietrocini V, Lovari S (2013b) Rutting behaviour of territorial and nonterritorial male chamois: is there a home advantage? Behav Process 92:118–124

Couturier M (1938) Le chamois. B. Arthaud Editeur, Grenoble, France

Dochtermann NA, Jenkins SH (2011) Developing multiple hypotheses in behavioral ecology. Behav Ecol Sociobiol 65:37–85

Enright JT (1965) The search for rhythmicity in biological time-series. J Theor Biol 8:426–468

Ernakovich JG, Hopping KA, Berdanier AB, Simpson RT, Kachergis EJ, Steltzer H, Wallenstein MD (2014) Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. Global Change Biol 20:3256–3269

Garel M, Loison A, Jullien J-M, Dubray D, Maillard D, Gaillard J-M (2009) Sex-specific growth in Alpine chamois. J Mammal 90: 954–960

Gates CC, Hudson RJ (1979) Effects of posture and activity on metabolic responses of Wapiti to cold. J Wildlife Manage 43:564–567

Gilbert C, McCafferty D, Le Maho Y, Martrette JM, Giroud S, Blanc S, Ancel A (2010) One for all and all for one: the energetic benefits of huddling in endotherms. Biol Rev 85:545–569

Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J, Stoffel M (2014) 21st century climate change in the European alps—a review. Sci Total Environ 493:1138–1151

Gorman MR, Goldman BD, Zucker I (2001) Mammalian photoperiodism. In: Takahashi JS, Turek FW, Moore RY (eds) Handbook of behavioral neurobiology: circadian clocks. Kluwer Academic/Plenum Publishers, New York, pp 481–508

Graunke KL, Schuster T, Lidfors LM (2011) Influence of weather on the behaviour of outdoor-wintered beef cattle in Scandinavia. Livest Sci 136:247–255

Gwinner E (2003) Circannual rhythms in birds. Curr Opin Neurobiol 13:770–778

Ismail K, Kamal K, Plath M, Wronski T (2011) Effects of an exceptional drought on daily activity patterns, reproductive behaviour, and reproductive success of reintroduced Arabian oryx (*Oryx leucoryx*). J Arid Environ 75:125–131

Jacobson AR, Provenzale A, von Hardenberg A, Bassano B, Festa-Bianchet M (2004) Climate forcing and density dependence in a mountain ungulate population. Ecology 85:1598–1610

Jingfors KT (1982) Seasonal activity budgets and movements of a reintroduced Alaskan muskox herd. J Wildlife Manage 46:344–350

Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66

Kamler JF, Jxdrzejewska B, Jxdrzejewski W (2007) Activity patterns of red deer in Bialowieza National Park, Poland. J Mammal 88:508–514

Kilpatrick AM (2003) The impact of thermoregulatory costs on foraging behaviour: a test with American Crows (*Corvus brachyrhynchos*) and eastern grey squirrels (*Sciurus carolinensis*). Evol Ecol Res 5:781–786

Kondo N, Sekijima T, Kondo J, Takamatsu N, Tohya K, Ohtsu T (2006) Circannual control of hibernation by HP complex in the brain. Cell 125:161–172

Korstjens AH, Lehmann J, Dunbar RIM (2010) Resting time as an ecological constraint on primate biogeography. Anim Behav 79:361–374

Kufeld RC, Bowden DC, Schrupp DL (1988) Habitat selection and activity patterns of female mule deer in the Front Range, Colorado. J Range Manage 41:515–522

Kumar V, Wingfield JC, Dawson A, Ramenofsky M, Rani S, Bartell P (2010) Biological clocks and regulation of seasonal reproduction and migration in birds. Physiol Biochem Zool 83:827–835

Lehmann J, Korstjens AH, Dunbar RIM (2008) Time and distribution: a model of ape biogeography. Ethol Ecol Evol 20:337–359

Loe LE, Mysterud A, Stien A, Steen H, Evans DM, Austrheim G (2007) Positive short-term effects of sheep grazing on the alpine avifauna. Biol Lett 3:110–112

Lomb N (1976) Least-squares frequency analysis of unequally spaced data. Astrophys Space Sci 39:447–462

Lovegrove B (2005) Seasonal thermoregulatory responses in mammals. J Comp Physiol B 175:231–247

Maia ASC, da Silva RG, Nascimento ST, Nascimento CCN, Pedroza HP, Domingos HGT (2015) Thermoregulatory responses of goats in hot environments. Int J Biometeorol 59:1025–1033

Martinet L, Mondain-Monval M, Monnerie R (1992) Endogenous circannual rhythms and photorefractoriness of testis activity, moult and prolactin concentrations in mink (*Mustela vison*). J Reprod Fertil 95:325–338

Mason THE, Chirichella R, Richards SA, Stephens PA, Wills SG, Apollonio M (2011) Contrasting life histories in neighbouring populations of a large mammals. PLoS One 6:e28002

Mason THE, Stephens PA, Apollonio M, Willis SG (2014) Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. Global Change Biol 20:3872–3882

Moen AN (1976) Energy conservation by white-tailed deer in the winter. Ecology 57:192–198

Owen-Smith N (1998) How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). J Zool 246:183–192

Owen-Smith N, Goodall V (2014) Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. J Zool 293:181–191

Parker MA (1982) Thermoregulation by diurnal movement in the barberpole grasshopper (*Dactylotum bicolor*). Am Midl Nat 107:228–237

Parker KL, Barboza PS, Gillingham MP (2009) Nutrition integrates environmental responses of ungulates. Funct Ecol 23:57–69

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Paul MJ, Zucker I, Schwartz WJ (2008) Tracking the seasons: the internal calendars of vertebrates. Philos T Roy Soc B 363:341–361

Pérez-Barbería F, Mutuberría G, Nores C (1998) Reproductive parameters, kidney fat index, and grazing activity relationships between the sexes in Cantabrian chamois *Rupicapra pyrenaica parva*. Acta Theriol 43:311–324

Pettorelli N, Mysterud A, Yoccoz NG, Langvatn R, Stenseth NC (2005) Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proc R Soc Lond B 272:2357–2364

Pettorelli N, Pelletier F, Av H, Festa-Bianchet M, Côté SD (2007) Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390

Pittendrigh CS (1993) Temporal organization: reflections of a Darwinian clock-watcher. Annu Rev Physiol 55:16–54

Plard F, Gaillard J-M, Coulson T, Hewison AJM, Delorme D, Warnant C, Bonenfant C (2014) Mismatch between birth date and vegetation phenology slows the demography of roe deer. PLoS Biol 12:e1001828

Porter WP, Budaraju S, Stewart WE, Ramankutty N (2000) Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. Am Zool 40:597–630

Prates H, Bicca-Marques J (2008) Age-sex analysis of activity budget, diet, and positional behavior in Alouatta caraya in an orchard forest. Int J Primatol 29:703–715

Refinetti R, Lissen GC, Halberg F (2007) Procedures for numerical analysis of circadian rhythms. Biol Rhythm Res 38:275–325

Risenhoover KL (1986) Winter activity patterns of moose in interior Alaska. J Wildlife Manage 50:727–734

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Ruf T (1999) The Lomb-Scargle periodogram in biological rhythm research: analysis of in-complete and unequally spaced time-series. Biol Rhythm Res 30:178–201

Rughetti M, Festa-Bianchet M (2011) Seasonal changes in sexual size dimorphism in northern chamois. J Zool 284:257–264

Rutberg AT (1987) Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. Am Nat 130:692–710

Rüttimann S, Giacometti M, McElligott A (2008) Effect of domestic sheep on chamois activity, distribution and abundance on subalpine pastures. Eur J Wildlife Res 54:110–116

Schmid B, Helfrich-Forster C, Yoshii T (2011) A new ImageJ plug-in "ActogramJ" for chronobiological analyses. J Biol Rhythm 26:464–467

Schröder W, von Elsner-Schack I (1985) Correct age determination in chamois. In: Lovari S (ed) The biology and management of mountain ungulates. Croom Helm, London, pp 67–70

Schütz KE, Clark KV, Cox NR, Matthews LR, Tucker CB (2010) Responses to short-term exposure to simulated rain and wind by dairy cattle: time budgets, shelter use, body temperature and feed intake. Anim Welfare 19:375–383

Shackleton DM (1997) Wild sheep and goats and their relatives: status survey and conservation action plan for Caprinae. World Conservation Union - IUCN, Gland, Switzerland

Signer C, Ruf T, Arnold W (2011) Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. Funct Ecol 25:537–547

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn. Freeman, New York

Sokolove PG, Bushell WN (1978) The chi square periodogram: its utility for analysis of circadian rhythms. J Theor Biol 72:131–160

Spitzenberger F, Bauer K, Mayer A, Weiß E, Preleuthner M, Sackl P, Sieber J (2001) Die Säugetierfauna Österreichs, Grüne Reihe des Bundesministeriums für Land-und Forstwirtschaft, Umwelt und Wasserwirtschaft. Austria medien service, Graz

Stache A, Heller E, Hothorn T, Heurich M (2013) Activity patterns of European roe deer (*Capreolus capreolus*) are strongly influenced by individual behaviour. Folia Zool 62:67–75

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21

Tyler NJC, Blix AS (1990) Survival strategies in arctic ungulates. Rangifer, Special Issue 3:211–230

Van Buskirk J (2012) Behavioural plasticity and environmental change. In: Candolin U, Wong BBM (eds) Behavioural responses to a changing world. Oxford University Press, Oxford, pp 145–158

van Noordwijk AJ, McCleery RH, Perrins CM (1995) Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. J Anim Ecol 64:451–458

van Oort BEH, Tyler NJC, Gerkema MP, Folkow L, Blix AS, Stokkan K-A (2005) Circadian organization in reindeer. Nature 438:1095–1096

VanSoest PJ (1994) Nutritional ecology of the ruminant, 2nd edn. Cornell University Press, Ithaca, New York

Willisch CS, Ingold P (2007) Feeding or resting? The strategy of rutting male Alpine chamois. Ethology 113:97–104

Willisch CS, Bieri K, Struch M, Franceschina R, Schnidrig-Petrig R, Ingold P (2013) Climate effects on demographic parameters in an unhunted population of Alpine chamois (*Rupicapra rupicapra*). J Mammal 94:173–182

Wood S (2006) Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, FL

Wood S (2013) A simple test for random effects in regression models. Biometrika 100:1005–1010

Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) Mixed effects models and extensions in ecology with R. Springer, New York, USA