



## Original investigation

## Is nocturnal activity compensatory in chamois? A study of activity in a cathemeral ungulate

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## ABSTRACT

Different species exhibit individual daily and annual activity patterns in response to a range of intrinsic and extrinsic drivers. Historically, research on the activity budgets of large wild animals focused on daylight hours due to the logistical difficulties of observing animals at night. Thanks to recent advances in animal-attached technology, however, this research can be extended to a 24-h timeframe. Taking advantage of GPS collars with activity sensors collecting a large amount of data per hour, we separately studied diurnal and nocturnal activity patterns of Alpine chamois (*Rupicapra rupicapra*), in order to identify the factors affecting them and the correlation between them. From March 2010 to November 2013, we collected data on 17 chamois in the Swiss National Park, a strict Alpine nature reserve where human management was forbidden and human harassment quite rare. Environmental factors were found to significantly influence both diurnal and nocturnal activity rhythms, with temperature and seasonality playing a pivotal role. Surprisingly, we detected a stable peak of activity in the first part of the night, which varied only slightly over the year. In summer, the nocturnal activity of males was inversely correlated to diurnal activity, arguably to compensate for scarce diurnal food intake. Conversely, winter nocturnal activity was positively related to the diurnal activity and served as a cumulative opportunity for energy intake. Chamois showed a weak lunarphilia, with a slight increase in activity levels during moonlit nights, especially during the mating season. In conclusion, our findings denote chamois as a cathemeral species able to adapt its behavioural patterns to match varying environmental conditions.

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## Introduction

Several animal species exhibit distinct activity rhythms in response to a plethora of intrinsic and extrinsic drivers. The majority of mammal species are nocturnal (Bennie et al., 2014): nocturnal activity is, in fact, considered the ancestral pattern of mammals (Crompton et al., 1978; Heesy and Hall, 2010) having evolved during the Mesozoic era, when eutherian mammals avoided diurnal activity to escape from the dominant taxon of dinosaurs (nocturnal bottleneck hypothesis – Menaker et al., 1997). Thus, one would expect that nocturnal activity would still play an important role, even in species that are not considered strictly nocturnal. As such, it is paramount to study activity budgets throughout the 24 h to

understand the relationship between diurnal and nocturnal activities, and how both respond to environmental factors.

Nowadays, human disturbance and the energy balance aimed at avoiding heat stress in an increasingly warm environment are key additional factors affecting activity rhythms: understanding their effects on the distribution of activity between day and night is a new challenge for researchers. Indeed, several wild species have been found to react strongly to human recreational activities, including hunting, by modifying their diurnal activity rhythms and shifting their activity to night hours (Brivio et al., 2017; Enggist-Düblin and Ingold, 2003; Oberosler et al., 2017; Raveh et al., 2012). Research into the effect of global warming on the distribution of activity has only recently been undertaken (Mason et al., 2017). The heat dissipation limit theory predicts that the trade-offs in energy allocation in endothermic organisms are driven more by the animals' ability to dissipate heat and avoid hyperthermia than by their ability to harvest energy (Speakman and Król, 2010). Since activity (i.e., locomotion and forage intake) entails energy expenditure and increases

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metabolic heat production (Long et al., 2014), its reduction during the hottest hours may be a strategy to avoid hyperthermia. Indeed, several studies showed that animals reduce activity levels in response to increasing air temperature, so as to buffer themselves from overheating (e.g. Orthoptera: Chappell, 1983; Parker, 1982 – Rodentia: Belovsky, 1984a; Kilpatrick, 2003 – Lefomorpha: Belovsky, 1984b – Cetartiodactyla: Brivio et al., 2017, 2016; Owen-Smith, 1998; Shi et al., 2006 – see Terrien et al., 2011 for a review on this topic). Moreover, animal behaviour and physiology are commonly characterised by seasonal variations, which have evolved as adaptation to match variations in resource availability, and thus maximise resource uptake and individual fitness (Prendergast et al., 2002). In this framework, it might be hypothesised that, during the warmer seasons, heat-sensitive species should modify their distribution of activity in favour of the nocturnal activity to compensate for the reduced energy intake during the warmest part of the day.

Mammals are usually classified as diurnal, nocturnal or crepuscular species based on anecdotal information. Research has only started taking into account the concept of cathemeral species in recent years (Hetem et al., 2012; Tattersall, 2006; Wu et al., 2018). The term “cathemerality” was defined for primates: it describes activity patterns distributed almost evenly throughout the 24 h of the daily cycle, or patterns with significant amounts of activity occurring within both the nocturnal and the diurnal periods (Tattersall, 2006, 1987). Curtis and Rasmussen (2006) expanded the concept of cathemerality to include the transfer of activity between diurnal and nocturnal periods, or viceversa, in response to chrono-ecological factors (temperature, moonlight, competition for resources, predation-risk). In this regard, analyses of the activity rhythms of the most widespread large herbivores suggested that they may potentially adopt cathemeral patterns, modifying the periodicity of their activity rhythms. For instance, wild boar (*Sus scrofa*), one of the most widespread ungulates in Europe, was reported by different studies to be, in turn, monophasic, biphasic and polyphasic (Brivio et al., 2017; Caley, 1997; Keuling et al., 2008; Russo et al., 1997), likely because this species may switch from predominantly diurnal to predominantly nocturnal activity in response to anthropogenic disturbance (Keuling et al., 2008; Ohashi et al., 2013; Podgórski et al., 2013). Similarly, chamois (*Rupicapra rupicapra*), the most ubiquitous ungulate in the Alps (Apollonio et al., 2010), has been defined as a diurnal species with unimodal (Šprem et al., 2015) or bimodal patterns (Darmon et al., 2014; Mason et al., 2014; Pachlatko and Nievergelt, 1985), even though others found it to be active also at night (Carnevali et al., 2016; Ingold et al., 1998). More recently, Brivio et al. (2016) showed that the daily activity of chamois was mainly diurnal and the pattern changed during the year from unimodal to bimodal and trimodal. Overall, these studies suggested that these species may modify their distribution of the activity across diurnal and nocturnal periods. Cathemerality may be a worthwhile strategy through which animals can respond to environmental drivers – i.e. thermal stressors, intense precipitation, moon cycle, and human harassment – by increasing nocturnal activity in order to compensate for the forced inactivity during the daylight period. If we exclude research on primates, however, studies on this topic are very rare. The Arabian oryx (*Oryx leucoryx*) has been shown to re-schedule its daily activity pattern in response to extreme environmental temperatures (Hetem et al., 2012). Similarly, Jetz et al. (2003) showed that nocturnal birds (nightjars: *Macrodipteryx longipennis* and *Caprimulgus climacurus*) increased twilight foraging activity during moonlit nights to compensate for the shorter nocturnal foraging window. In general for large mammals, the effect of moonlight on activity budgets has been mainly analysed in terms of predation risk and foraging efficiency, for prey and predator species, respectively. Additionally, moonlight could have opposing potential effects on activity. On the one hand, moonlight is expected to have a suppressive

effect on the activity levels of primary consumers feeding in open areas, since the risk of detection by predators is higher during the brightest moonlit nights (Prugh and Golden, 2014). On the other hand, moonlight is expected to increase foraging efficiency and detection of predators and thus to have a positive effect on prey activity (Prugh and Golden, 2014).

We analysed chamois activity records collected in a strict nature reserve in the Swiss Alps, where predation is negligible, hunting is forbidden and any human management and harassment are avoided. Most significantly, predation risk and human disturbance in the selected study area are likely the lowest across the whole of this species' range and we can therefore exclude a major role of predation on chamois activity rhythms. In this context, we tested whether chamois are a cathemeral species or not, and whether their activity patterns are affected by ecological factors, or driven mainly by their internal timing system. In this framework, we formulated the following predictions:

- 1 Since predation risk is low in our study area, we predicted that most of chamois activity would be carried out during the day and, consequently, only diurnal activity would be affected by extrinsic factors. Therefore, we separately analysed the effects of environmental factors on diurnal mean activity (DMA) and nocturnal mean activity (NMA). We expected significant effects only on DMA.
- 2 Conversely, we hypothesised that nocturnal activity played a compensatory role for the forced inactivity during the daylight period. Specifically, we predicted that:
  - a NMA would be affected by the amount of DMA more than by external factors;
  - b this effect would be more relevant during the more energy-demanding periods, i.e. summer, winter, and mating season;
  - c there would be no periodicity in the distribution of acrophase – i.e., the time when the rhythm peaks – of the nocturnal activity throughout the year.
- 3 Given our hypothesis of the compensatory role of nocturnal activity and taking into account the low levels of predation risk and human harassment in our study area, we predicted a positive effect of moonlight on NMA throughout the year, particularly during summer (when increasing forage intake allows chamois to prepare for winter), and during the mating season to increase the reproductive opportunities.

## Material and methods

### Study area

The data on Alpine chamois activity were collected in the Swiss National Park (SNP; 46°40'10.74"N, 10°9'15.15"E), a Strict Nature Reserve (IUCN Category 1a) where any human management activity is either forbidden (including hunting) or heavily regulated. The study area ranged from 1500 to 3170 m above sea level (a.s.l.) and covered 170 km<sup>2</sup> of conifer forests (mainly *Pinus cembra*, *Larix decidua*, *Pinus mugo*), Alpine meadows and rocky slopes. Its climate was largely continental: dry, with strong solar radiation, low air humidity and harsh winter conditions (Zoller, 1995). Annual precipitation ranged from 700 to 1200 mm. During the data collection period (from March 2010 to November 2013), censuses carried out by rangers of SNP recorded a natural fluctuation in the population, from a maximum of 7.7 individuals/km<sup>2</sup> to a minimum of 6.2 individuals/km<sup>2</sup>. During the study period the main predators of chamois, i.e. wolf (*Canis lupus*) and lynx (*Lynx lynx*), were not present, while golden eagle (*Aquila chrysaetos*) and red fox (*Vulpes vulpes*) only preyed upon kids and yearlings. Other ungulate species

inhabiting the SNP are Alpine ibex (*Capra ibex*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*).

#### Data collection

The staff of the SNP captured 11 female and 6 male chamois with box traps and equipped them with GPS Plus Collars (Vectronic Aerospace GmbH, Berlin, Deutschland). We determined their age by counting the annual incremental growth rings on their horns (Schröder and von Elsner-Schack, 1985). The age of the monitored chamois, estimated by annuli count at the moment of their capture, ranged between 2 and 15 years for females, and between 6 and 13 years for males.

The collars recorded the animals' activity by means of an analogue accelerometer (i.e., activity sensor), which measured the actual acceleration experienced by the collar along two orthogonal axes (x-values recording forward/backward motions, y-values recording left/right motions) four times per second. The accelerometer recorded the accelerations on a dynamic range from  $-2G$  to  $+2G$  ( $G$  = gravitational constant) and measured activity as the change of static acceleration (gravity) and dynamic acceleration (collar). Activity values were given within a relative range between 0 and 255. Value 255 was equal to  $-2G$  /  $+2G$  and indicated maximum acceleration, whereas 0 indicated no acceleration at all. The collars provided mean values averaged over sampling intervals of 5 min.

Activity data were then associated with weather information (mean temperature, mean solar radiation, mean wind speed, precipitation) provided by a weather station in Buffalora, which is located at a distance of approx. 13 km from the study area ( $46^{\circ}38'53''N$ ;  $10^{\circ}16'02''E$  - Swiss Meteorological Institute). We obtained the cloud cover estimates (i.e., percentage of sky covered by clouds over the entire atmosphere, estimated in eighths) recorded every 10 min from a weather station in Robbia, which is located at a distance of approx. 40 km from the study area (Poschivo, Swiss Meteorological Institute). The Astronomical Applications Department of the U.S. Naval Observatory website (<http://aa.usno.navy.mil>) provided sunrise and sunset time (civil twilight) and moon phase data, expressed as the proportion of moon disk illuminated at 00.00 AM. A value of 0 corresponded to new moon conditions and a value of 1 to full moon conditions.

#### Data analysis

The raw activity data recorded by the collars were divided by the maximum value recorded by the accelerometer (255) in order to obtain values ranging from 0 (i.e., no activity) to 1 (i.e. maximum activity). We split the whole dataset into two subsets: diurnal and nocturnal. To do this, activity values recorded between sunrise of day<sub>*i*</sub> and sunset of day<sub>*i*</sub> were assigned to the subset of diurnal activity of day<sub>*i*</sub>, while those recorded after sunset of day<sub>*i*</sub> and prior to sunrise of day<sub>*i+1*</sub> were assigned to the subset of nocturnal activity of day<sub>*i*</sub>. Then, we calculated the average of the activity values recorded during each diurnal subset and each nocturnal subset, and we defined them as DMA and NMA, respectively. These indexes were aimed at analysing the overall activity of each chamois in relation to environmental conditions during light and dark hours, separately. Likewise, we calculated the diurnal and nocturnal average for each meteorological parameter (i.e., minimum, mean and maximum temperature; maximum and mean solar radiation for daylight hours only). For each date of the data collection period, diurnal and nocturnal precipitation values were calculated by summing the values recorded throughout the corresponding day and night. Wind speed was provided by the weather station administration as a daily mean. To estimate moonlight illuminance (hereafter,

moonlight), we implemented the index proposed by Brivio et al. (2017):

$$\text{Moonlight} = \text{moon phase of day}_i - (\text{moon phase of day}_i * \text{cloud cover of day}_i)$$

Firstly, we looked for possible correlations between the predictor variables by means of a correlation matrix (Pearson correlation coefficient,  $r_p$ ) to avoid collinearity (Sokal and Rohlf, 1995). As some predictor variables were found to be collinear, they were screened with a machine-learning method in order to select the best candidate predictors for the final models (Supplementary materials 1, Table S1.1 for DMA; Supplementary materials 2, Table S2.1 for NMA). Predictors were thus scrutinized through a Random Forest calculation (by means of randomForest package for R), which ranks the importance of the parameters based on a certain number ( $n = 500$ ) of randomly generated decision trees (Breiman, 2001). For DMA the following predictor variables were selected, based on the percent increase in mean square error: sex, age, Julian date, maximum air temperature, solar radiation, wind speed, and amount of precipitation (Supplementary materials 1, Fig. S1.1). The same predictors were selected for the NMA, with the exception of solar radiation and the addition of moonlight and of the DMA value recorded in the previous daylight hours (Supplementary materials 2, Fig. S2.1).

The effect of the selected intrinsic and extrinsic factors on activity patterns was assessed by modelling DMA and NMA separately by means of Generalised Additive Models (GAMs) with Gaussian distribution. GAMs allow for non-linear effects, using non-parametric smoothing functions; we estimated such effects for each predictor variable to obtain the best possible prediction for each variable. GAMs were implemented within the mgcv package in R (version 3.3.3; R Core Team, 2016). NMA was arcsinroot transformed in order to improve the homogeneity of residual distribution. To check for repeated measurements of the same individual, chamois identity was included in GAMs as a random intercept factor by using "re" terms and smoother linkages (Wood, 2013). The visual inspection of data distribution (Cleveland plots) highlighted that precipitation and wind speed were not homogeneously distributed. As homogeneity is a crucial assumption of the statistical approach used, we log-transformed these variables, thus improving their homogeneity (Zuur et al., 2007).

In order to validate our predictions 1, 2a, and 3, we built a full model for DMA and another for NMA, in which we considered the effects of all continuous variables, except for Julian date, as natural cubic spline functions. The effect of Julian date was modelled as a cyclic cubic regression spline in order to take into account the circularity of this variable; this ensured the value of the smoother at the far-left point (1st of January) was the same as the one at the far-right point (31st of December). To investigate differences in the behavioural patterns of females and males, we added interactions with sex for each variable included in the models. We fitted a set of models considering all the possible combinations of the predictors included in the full model by using the dredge function of R package MuMIn (Barton, 2013). We assessed model parsimony using Akaike's Information Criterion (AIC, Richards et al., 2011). We checked the goodness of fit of the best models performed (homoscedasticity, normality of errors and independence) by visual inspection of residuals (Zuur et al., 2009). Finally, in order to test whether chamois modified their nocturnal activity as a compensation for the reduction in daylight activity in summer, winter, and mating season (prediction 2b and 3), we considered the NMA values recorded from the 21st of June to the 23rd of September, (i.e., from the first to the last day of astronomical summer), and from the 21st of December to the 21st of March (i.e., from the first to the last day of astronomical winter). We defined the 1st and 30th of November as beginning and end of the mating season (Von Hardenberg et al., 2000). We re-fitted the best model selected for the full-year anal-

yses using only the data collected in summer, winter, and mating season, to carry out separate analyses.

In order to study the nocturnal periodicity of chamois activity (prediction 2c), the acrophase of each chamois' nocturnal activity was calculated with ActogramJ (Schmid et al., 2011). To calculate the nocturnal acrophase, we took into account the raw data used to estimate the NMA. For each night, we obtained a record including individual identity, Julian date, sex and acrophase. The hypothesis that periodicity was absent during the night was tested by means of a GAM. For this analysis, we used a dataset including, for each night of data collection: chamois identity, sex, Julian date and acrophase. The effect of Julian date on acrophase was assessed by expressing the latter as minutes before or after midnight, in order to account for continuity between 23:59 and 00:00 of the following day. The effect of Julian date was modelled as a cyclic cubic regression spline. The interaction with sex was included in the model to test for differences in the periodicity patterns between sexes. Chamois identity was included as a random factor using the same statistical procedure described above.

## Results

The best model for DMA, according to AIC, included sex, Julian date, age, radiation, precipitation, maximum temperature and wind as predictor variables ( $R\text{-sq.}=0.678$ , Supplementary materials 1, Tables S1.2–S1.3). Likewise, the model including the same variables with the exception of radiation and the addition of moonlight and the DMA recorded on the previous day best described NMA ( $R\text{-sq.}=0.595$ , Supplementary materials 2, Table S2.2–S2.3).

Throughout the year, the highest peak of male DMA was recorded around the 23th of June and a second peak was recorded during the mating season (the 21st of November – Fig. 1a), while females showed a higher peak around the 8th of June, which dropped off later than that of males. In summer, the amount of the DMA of both males and females is about double than during winter. The best model for NMA predicted different seasonal trends depending on sex. Females were similarly active in spring and summer, with a reduction in activity levels from the second part of autumn to the end of winter. In males, the trend of NMA was similar to that of DMA, with two peaks – on the 30th of July and 10th of November – and a sharp decrease in winter (Fig. 1b). Males are generally less active than females, with the exception of the NMA during the last part of spring and the beginning of summer. The analysis showed that, for males, DMA peaked at intermediate temperatures ( $\sim 8^\circ$ ) and declined further from these. For females, the effect had a similar form, but generally much weaker (Fig. 1c). In contrast, temperature affected the NMAs of either sex linearly and to a similar extent: male and female chamois alike increased their nocturnal activity with higher ambient temperatures and the NMA values doubled from the lowest temperatures to the highest ones (Fig. 1d). The contrasting forms of NMA and DMA temperature effects suggested that there seems to be a threshold temperature up to which activity is maximised. Precipitation negatively affected male and female DMA (Fig. 1e) and male NMA only (Fig. 1f). Only female chamois' activity levels were slightly lower on windy days, both during daylight and night hours (Fig. 1g–h). A weak influence of solar radiation was observed, though only female chamois were found to be slightly less active on days with either lower or higher than average radiation (Supplementary materials 1, Fig. S1.2); this could possibly explain the weaker effect of temperature on this sex.

The analysis detected a weak influence of moonlight on NMA, with female and male chamois being slightly more active when the available moonlight was more intense (Fig. 2a). Finally, results showed that chamois NMA did not correlate with diurnal activity of the previous day (Fig. 2b). In order to ascertain whether

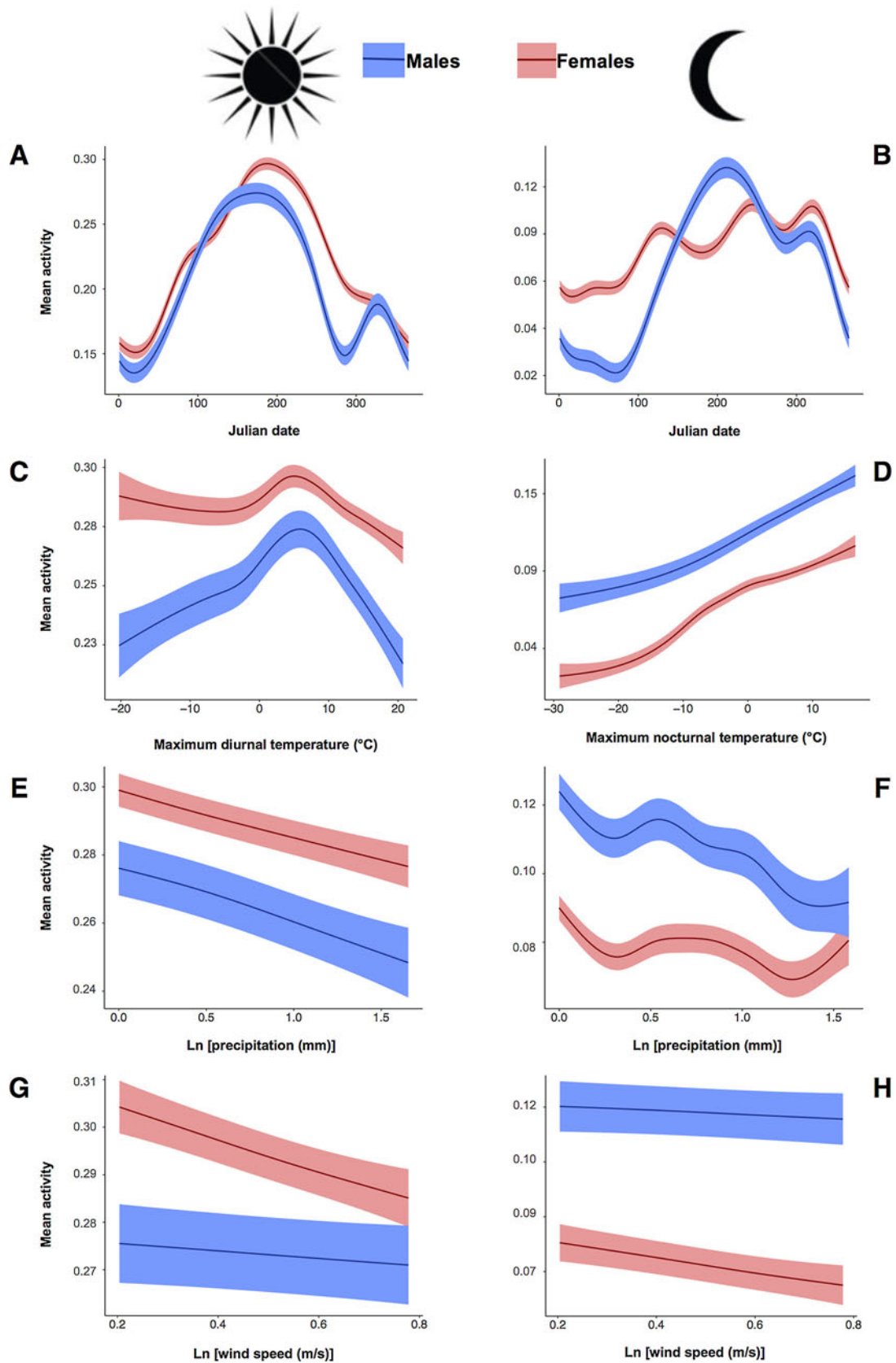
NMA was related to the activity during the previous daylight hours when environmental conditions were more demanding in terms of energy expenditure (i.e., in summer, winter, and mating season – Supplementary materials 3), we refitted the best model for NMA considering the respective subsets only. Surprisingly, the males' NMA was negatively affected by their diurnal activity only in summer: when DMA exceeded the threshold of 0.43, NMA decreased. NMA of females was not influenced by their DMA (Fig. 3a). In winter, conversely, the NMA of both sexes was positively related to their DMA (Fig. 3b). We did not find any relationship between DMA and NMA during the mating season (Supplementary materials 3, Fig. S3.1); though, we detected a significant increase in male activity during bright moonlit nights (Supplementary materials 3, Fig. S3.2).

The analysis also detected a significant relationship between nocturnal acrophase, i.e. the peak of activity during the night, and Julian date for both males and females. However, this slight difference in the timing of nocturnal acrophase did not produce any detectable effect on activity patterns (Fig. 4). Indeed, for females, the range of the acrophase throughout the year covered only 24 min, being comprised between 74–50 min before midnight (i.e., 22:46–23:10). Whereas the males' range was larger (50 min): the acrophase occurred between 87–37 min before midnight (i.e., hours 22:33–23:23).

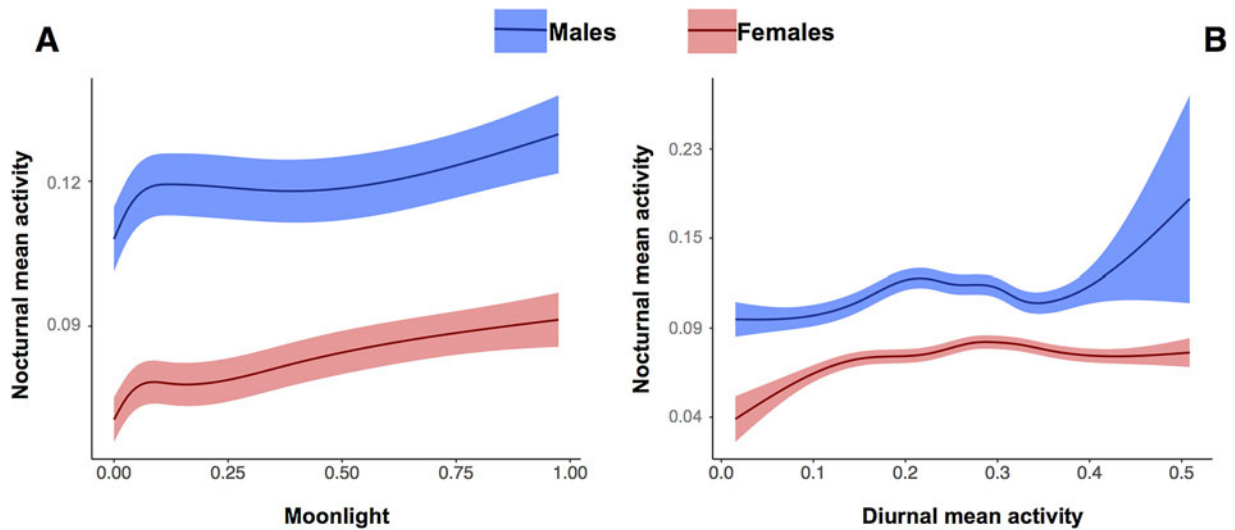
## Discussion

To date, the role of nocturnal activity in the daily activity budget of mammals has been seldom investigated (Hetem et al., 2012). Our study reveals that species that can be active both during day and night – i.e. cathemeral – can have a high level of plasticity in their activity budgets, thus being able to cope with demanding environmental conditions by modifying their distribution of activity across daylight and darkness hours. While Alpine chamois have generally been considered a diurnal species, the present study shows that nocturnal activity plays an important role in their activity budget, especially when diurnal activity decreases due to unfavourable environmental conditions. Additionally, we showed that, over the whole year, nocturnal activity reached the acrophase – i.e., the peak of activity – during the first half of the night, consistently and without significant sexual differences (prediction 2c). Previous investigations on Alpine chamois reported that nocturnal activity peaked around midnight (Ingold et al., 1998), or during the second half of the night (Carnevali et al., 2016). The differences in the timing of acrophase between these studies could depend either on the methodology of activity recording or on such external factors as date of sampling, geographical location and environmental conditions. Overall, our findings strongly indicate a stable entrainment of nocturnal activity. Which environmental cue contributed to maintaining such stable entrainment is not clear. However, changes in light intensity and spectrum occurring at sunset could be suitable entraining signals, as they are present all year round (Walmsley et al., 2015). Consistently with these findings and those of Brivio et al. (2016), showing seasonal variations of daily activity periodicity, Alpine chamois should be considered a cathemeral species.

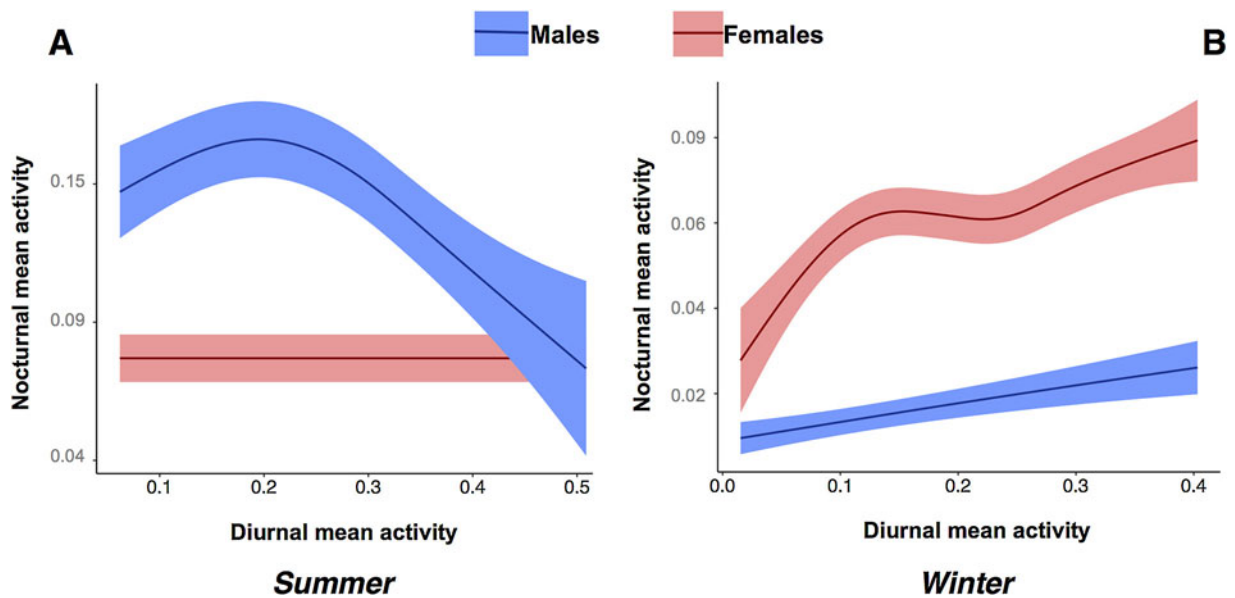
As regards our specific predictions, findings pointed out that nocturnal activity plays an important role in the activity budgets of chamois. We had predicted nocturnal activity in chamois to be limited, or to play an exclusively compensatory role when diurnal activity was limited (prediction 2a), and we expected it not to be affected by external factors (prediction 1). Instead, our findings showed that the amount of nocturnal activity was not negligible since it amounted to about one-third of the diurnal activity. Moreover, the same factors similarly affected nocturnal and diurnal patterns, with the only exception of ambient temperature. During daylight hours, when temperature typically reached



**Fig. 1.** Values predicted by the best generalised additive model of mean activity of Alpine chamois in the Swiss National Park. The figure shows the effects of Julian date (A–B), maximum daily temperature (C–D), daily precipitation (E–F), and wind speed (G–H) on diurnal (left side of the figure) and nocturnal (right side of the figure) mean activity. The predictions are given according to the mean of all other covariates in the model. 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 values on the y axes for nocturnal activity have been back transformed from the arcsin square root values used to calculate the best models (see the text for more details). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



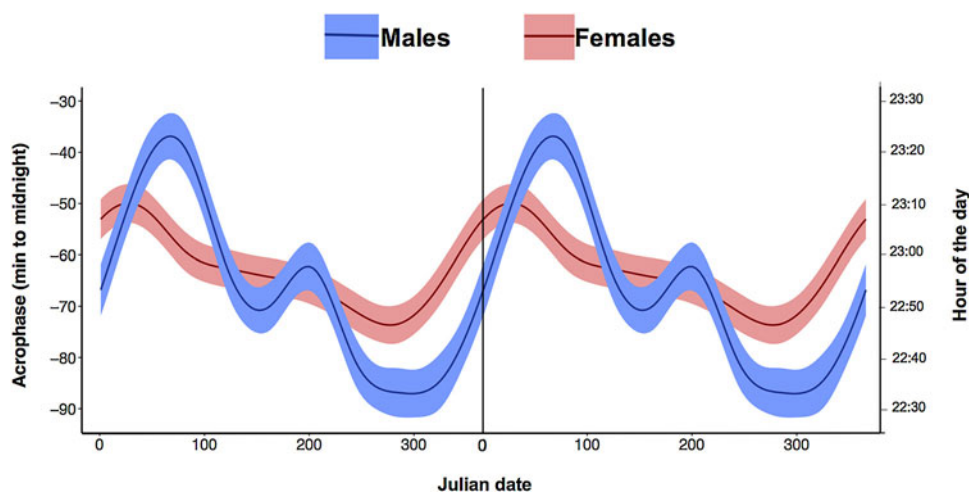
**Fig. 2.** Values predicted by the best generalised additive model of nocturnal mean activity of Alpine chamois in the Swiss National Park. The figure shows the effects of moonlight (A) and diurnal mean activity (B). The predictions are given according to the mean of all other covariates in the model. 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 values on the y axes have been back transformed from the arcsin square root values used to calculate the best models (see the text for more details). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



**Fig. 3.** Values predicted by the best generalised additive model of nocturnal mean activity of Alpine chamois in the Swiss National Park during summer (A) and winter (B). The predictions are given according to the mean of all other covariates in the model. 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 values on the y axes have been back transformed from the arcsin square root values used to calculate the best models (see the text for more details). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

the highest values, chamois increased their activity levels when temperature increased up to the threshold of 8 °C ca. When temperature exceeded this threshold value, however, DMA decreased, more sharply in males than in females. The reduction in activity levels in response to increasing air temperature as a strategy against overheating has previously been detected in ungulates (e.g., Belovsky and Slade, 1986; Brivio et al., 2017; Shi et al., 2003), including chamois (Brivio et al., 2016). Our separate analyses for diurnal and nocturnal hours, on the other hand, showed that NMA was positively and linearly affected by ambient temperature and it increased also well past the diurnal threshold of around 8°, when DMA started to decrease. We can conjecture that the absence of the additional effect of solar radiation, which would increase the temperature that animals experience at the same ambient tem-

perature during the day, allowed chamois to be active at higher temperatures without the risk of overheating during the night. In the Alps, instead, they typically face the risk of hypothermia, which they cope with by reducing their activity levels (Brivio et al., 2016). Thus, we may hypothesise that chamois take advantage of milder nights to increase their activity and, as a consequence, their energy intake. More in general, we may argue that chamois have evolved to take advantage of favourable periods: chamois may increase their activity – and consequently their food intake – when vegetation is at a more profitable phenological stage, when precipitation is low, and when winds are calmer. Such plasticity in chamois behavioural patterns, already suggested by Brivio et al. (2016), was also supported by our analyses concerning the most demanding periods of the year (prediction 2b). Chamois adapted their nocturnal activity



**Fig. 4.** Values predicted by the best Generalised Additive Model (see the text for more details) of Alpine chamois nocturnal acrophase in Swiss National Park. 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

to respond to the seasonality of the environmental pressures typical of the Alps. During winter, nocturnal activity was positively related to the diurnal activity and, therefore, served as a cumulative opportunity for energy intake when food availability and quality were scarce. Conversely, during summer nocturnal activity was compensatory: male chamois were less active in the warmest days and they had higher nocturnal activity in days of low diurnal activity, likely to maximise energy intake. Surprisingly, this compensatory role was observed in males only, possibly because they are more sensitive to high temperatures and, thus, less active during the warmest days. Further analyses are needed to understand these different activity patterns between the sexes which are partially unexpected since sexual dimorphism is not accentuated in chamois.

In a more general perspective, our findings support the theory proposed by Bennie et al. (2014), who stated that light and temperature combine to define available temporal niches. From a biogeographical perspective, diurnal activity patterns are expected to be most common in high altitude areas, where nocturnal temperatures are very low; whereas crepuscular and cathemeral activity patterns should be prevalent in the Arctic regions, which are characterized by long hours of twilight and high seasonal variation in the hours of daylight (Bennie et al., 2014). Our results stressed that seasonality – rather than altitude – seems to be the key factor affecting activity rhythms in the Alpine region and that behavioural plasticity, which is intrinsic to cathemerality, may contribute to increase energy intake. In fact, heat-sensitive species may largely rely on responding to overheating by means of behavioural strategies (du Plessis et al., 2012; Stelzner and Hausfater, 1986), such as decreasing their activity level when ambient temperature increases over a critical threshold during the day (Terrien et al., 2011). Cathemeral species could be particularly adaptable in the face of environmental change, such as climate change. A recent study revealed that alpine ungulates could experience reductions in resource availability at high altitudes due to climate change, but are unlikely to be able to compensate by increasing foraging activity during daylight hours (Mason et al., 2017). However, our study suggests that cathemeral species such as chamois may be able to compensate by switching to increased nocturnal activity.

For our third prediction, our findings on the effect of moonlight on activity patterns seem to support the idea that chamois increase their activity in favourable nocturnal conditions (prediction 3). Even though the increase in activity during moonlit nights was weak, this result supports the visual acuity hypothesis formu-

lated by Prugh and Golden (2014), who maintained that moonlight increases the foraging efficiency and favours the detection of predators, so that prey species relying on vision to locate food and predators are more active in the moonlight than on darker nights. Our study area was free from predators and human harassment, including hunting and poaching. Accordingly, moonlight could only favour foraging efficiency and not predator detection. This may contribute to explaining the weak effect of moonlight on activity patterns. Conversely, our results did not support the “habitat-mediated predation risk” hypothesis, which predicts that, in open habitats, predators detect prey more easily during moonlit nights (Prugh and Golden, 2014). According to the latter hypothesis, in prey species lunar phobia and its negative effect on activity should decrease as habitat cover increases. Interestingly, moonlight positively affected male NMA during the mating season, even though the rut occurs in late autumn when climatic conditions are severe and, possibly, the ground can be snow-covered. We may conjecture that the reproductive efforts stimulate males to be active whenever the environmental conditions are favourable. Male chamois commonly adopt visual displays in inter- and intra-sexual interactions during the mating season. Accordingly, males increase their activity in order to increase their reproductive opportunities. Our findings on the moonlight effect on NMA are in accordance with other recent findings (Carnevali et al., 2016), even though the magnitude of these patterns was found to be weaker, maybe due either to the use of a different equipment in collecting data (VHF signal vs. accelerometer data), or to different environmental conditions.

In answer to the question in the title of this paper, current data do not allow us to state that chamois nocturnal activity serves an exclusively compensatory function. What the present study shows, however, is that nocturnal activity seems a flexible behavioural response meant to exploit any favourable set of environmental conditions and that chamois may accordingly be considered a cathemeral species. Further studies on this and other cathemeral species may investigate how and to what extent behavioural and physiological adaptations act on the periodicity of activity rhythms in order to match varying extrinsic factors. Ultimately, gaining a better understanding of how cathemeral and heat-sensitive species cope with thermal stressors is currently paramount: in fact, it is not possible to exclude that chamois may switch part of their activity from day to night in response to environmental changes such as increasing temperatures.

## Author contributions

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

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.mambio.2018.06.003>.

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