

1 **Is the chamois's nocturnal activity compensatory?**

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3 Grignolio S.<sup>1\*</sup>, Brivio F.<sup>1</sup>, Apollonio M<sup>1</sup>, Frigato E.<sup>2</sup>, Tettamanti F. <sup>1</sup>, Filli F. <sup>3</sup>, Bertolucci C.<sup>2</sup>

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5 <sup>1</sup> Department of Veterinary Medicine, University of Sassari, Via Vienna 2, I-07100 Sassari, Italy

6 <sup>2</sup> Department of Life Sciences and Biotechnology, University of Ferrara, Via L. Borsari 46, I-44121  
7 Ferrara, Italy

8 <sup>3</sup> Parc Naziunal Svizzer, 7530, Zernez, Switzerland

9

10 \* Corresponding author: University of Sassari, Department of Veterinary Medicine, University of  
11 Sassari, Via Vienna 2, I-07100 Sassari, Italy. Email: sgrigno@uniss.it

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13

14 **ABSTRACT**

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

34  
35 **KEYWORDS:** acrophase, activity rhythms, cathemerality, moonlight, *Rupicapra rupicapra*, ambient  
36 temperature

## 37 INTRODUCTION

38 Circadian rhythms are the outward manifestation of an internal timing system. This is  
39 composed of an intricate molecular mechanism regulated by a master clock located in the  
40 hypothalamus, which is synchronised with light inputs received from the environment (Reppert and  
41 Weaver, 2002). Different species exhibit distinct activity rhythms in response to a plethora of  
42 intrinsic and extrinsic drivers. The majority of mammal species are nocturnal (Bennie et al., 2014):  
43 nocturnal activity is, in fact, considered the ancestral pattern of mammals (Crompton et al., 1978;  
44 Heesy and Hall, 2010) having evolved during the Mesozoic era, when eutherian mammals avoided  
45 diurnal activity to escape from the dominant taxon of dinosaurs (nocturnal bottleneck hypothesis –  
46 Menaker et al., 1997). Thus, one would expect that nocturnal activity would still play a pivotal role,  
47 even in species that are not considered strictly nocturnal. It is then paramount to study activity  
48 budgets throughout the 24 hours to understand the relationship between diurnal and nocturnal  
49 activities, and how both respond to environmental factors.

50 Nowadays, human disturbance and the energy balance aimed at avoiding heat stress in an  
51 increasingly warm environment are key additional factors affecting activity rhythms: understanding  
52 their effects on the distribution of activity between day and night is a new challenge for  
53 researchers. Indeed, several wild species were found to react strongly to human recreational  
54 activities, including hunting, by modifying their diurnal activity rhythms and shifting their activity to  
55 night hours (Brivio et al., 2017; Enggist-Düblin and Ingold, 2003; Oberosler et al., 2017; Raveh et  
56 al., 2012). Research on the effect of global warming on the distribution of activity has only recently  
57 been undertaken (Mason et al., 2017). The heat dissipation limit theory predicts that the trade-offs  
58 in energy allocation in endothermic organisms are driven more by the animals' ability to dissipate  
59 heat and avoid hyperthermia than by their ability to harvest energy (Speakman and Król, 2010).  
60 Since activity (i.e., locomotion and forage intake) entails energy expenditure and increases  
61 metabolic heat production (Long et al., 2014), its reduction during the hottest hours may be a  
62 strategy to avoid hyperthermia. Indeed, several studies showed that animals reduce activity levels  
63 in response to increasing air temperature, so as to buffer themselves from overheating (e.g.  
64 Orthoptera: Chappell, 1983; Parker, 1982 – Rodentia: Belovsky, 1984a; Kilpatrick, 2003 –  
65 Lafomorpha: Belovsky, 1984b – Cetartiodactyla: Brivio et al., 2017, 2016; Owen-Smith, 1998; Shi  
66 et al., 2006 – see Terrien et al., 2011 for a review on this topic). Moreover, animal behaviour and  
67 physiology are commonly characterised by seasonal variations, which evolved as an adaptation to  
68 match the variations of resource availability in the environment and, thus, to maximise the animals'  
69 ability to use them and increase individual fitness (Prendergast et al., 2002). In this framework, one  
70 may hypothesize that, during the warmer seasons, heat-sensitive species should modify their  
71 distribution of activity in favour of the nocturnal activity to compensate for the reduced energy  
72 intake during the warmest part of the day.

73 Mammals are usually classified as diurnal, nocturnal or crepuscular species based on  
74 anecdotal information. Researches started taking into account the concept of cathemeral species  
75 only in recent years (Hetem et al., 2012; Tattersall, 2006; Wu et al., 2018). The term  
76 “cathemerality” was defined for primates: it describes activity patterns distributed almost evenly  
77 throughout the 24h of the daily cycle, or patterns with significant amounts of activity occurring  
78 within both the nocturnal and the diurnal periods (Tattersall, 2006, 1987). Curtis and Rasmussen  
79 (2006) expanded the concept of cathemerality to include the transfer of activity from diurnal to  
80 nocturnal period, or viceversa, in response to chrono-ecological factors (temperature, moonlight,  
81 competition for resources, predation-risk). In this regard, analyses of the activity rhythms of the  
82 most widespread large herbivores suggested that they may potentially adopt cathemeral patterns,  
83 modifying the periodicity of their activity rhythms. For instance, wild boar (*Sus scrofa*), one of the  
84 most widespread ungulates in Europe, was reported by different studies to be, in turn,  
85 monophasic, biphasic and polyphasic (Brivio et al., 2017; Caley, 1997; Keuling et al., 2008; Russo  
86 et al., 1997), likely because this species may switch from predominantly diurnal to predominantly  
87 nocturnal activity in response to anthropic disturbance (Keuling et al., 2008; Ohashi et al., 2013;  
88 Podgórski et al., 2013). Similarly, chamois (*Rupicapra rupicapra*), the most ubiquitous ungulate on  
89 the Alps (Apollonio et al., 2010), has been defined as a diurnal species with unimodal (Šprem et  
90 al., 2015) or bimodal patterns (Darmon et al., 2014; Mason et al., 2014; Pachlatko and Nievergelt,  
91 1985), even though others found it to be active also at night (Carnevali et al., 2016; Ingold et al.,  
92 1998). More recently, Brivio et al. (2016) showed that chamois’s daily activity was mainly diurnal  
93 and the pattern changed during the year from unimodal to bimodal and trimodal. Overall, these  
94 studies suggested that these species may modify the distribution of the activity on diurnal and  
95 nocturnal periods. Cathemerality may be a worthwhile strategy to respond to environmental drivers  
96 – i.e. thermal stressors, intense precipitation, moon cycle, and human harassment – by increasing  
97 nocturnal activity in order to compensate for the forced inactivity during the daylight period. If we  
98 exclude research on primates, however, studies on this topic are very rare in literature. As regards  
99 large herbivores, *Oryx leucoryx* has to date been reported to re-schedule its daily activity pattern  
100 according to environmental temperature (Hetem et al., 2012). Similarly, Jetz and colleagues (2003)  
101 showed that nocturnal birds (nightjars: *Macrodipteryx longipennis* and *Caprimulgus climacurus*)  
102 increased twilight foraging activity during moonlight nights to compensate for the shorter nocturnal  
103 foraging window. In large mammals, the effect of moonlight on activity budgets has been mainly  
104 analysed in terms of predation risk and foraging efficiency, for prey and predator species,  
105 respectively. On the one hand, moonlight is expected to have a suppressive effect on the activity  
106 levels of primary consumers feeding in open areas, since the risk of detection by predators is  
107 higher during the brightest moonlit nights (Prugh and Golden, 2014). On the other hand, moonlight  
108 is expected to increase foraging efficiency and detection of predators and thus to have a positive  
109 effect on prey activity (Prugh and Golden, 2014).

110 We analysed chamois activity records collected in a strict nature reserve on the Swiss Alps,  
111 where predation is negligible, hunting is forbidden and any human management and harassment  
112 are avoided. Most significantly, predation risk and human disturbance in the selected study area  
113 are likely the lowest of the whole chamois distribution range and we can therefore exclude that  
114 they are the main factors affecting chamois activity rhythms. In this context, we tested whether  
115 chamois is a cathemeral species or not and whether its activity patterns are affected by ecological  
116 factors, or driven mainly by their internal timing system. In this framework, we formulated the  
117 following hypotheses:

- 118 1. Since predation risk is low in our study area, we predicted that most of chamois  
119 activity would be carried out during the day and, consequently, only diurnal activity  
120 would be affected by extrinsic factors. Therefore, we separately analysed the effects  
121 of environmental factors on diurnal mean activity (DMA) and nocturnal mean activity  
122 (NMA) and we expected significant effects only on DMA.
- 123 2. Conversely, we hypothesised that nocturnal activity played a compensatory role,  
124 i.e., it compensated for the forced inactivity during the daylight period. Specifically,  
125 we predicted that:
  - 126 a. NMA would be affected by the amount of DMA more than by external  
127 factors;
  - 128 b. this effect would be more relevant during the more energy-demanding  
129 periods, i.e. summer, winter, and mating season;
  - 130 c. there would be no periodicity in the distribution of acrophase – i.e., the time  
131 at which the peak of a rhythm occurs – of the nocturnal activity throughout  
132 the year.
- 133 3. Given our assumption on the compensatory role of nocturnal activity and taking into  
134 account the low levels of predation risk and human harassment in our study area,  
135 we hypothesised a positive effect of moonlight on NMA throughout the year,  
136 particularly during summer (when increasing forage intake is paramount for chamois  
137 in order to prepare for winter) and during the mating season to increase the  
138 reproductive opportunities.

## 141 MATERIAL AND METHODS

### 142 STUDY AREA

143 The data on Alpine chamois activity were collected in the Swiss National Park (SNP;  
144 46°40'10.74" N, 10°9'15.15" E), a Strict Nature Reserve (IUCN Category 1a) where any human

145 management activity is either forbidden (including hunting), or heavily regulated. The study area  
146 ranged from 1500 to 3170 m above sea level (a.s.l.) and covered 170 Km<sup>2</sup> of conifer forests  
147 (mainly *Pinus cembra*, *Larix decidua*, *Pinus mugo*), Alpine meadows and rocky slopes. Its climate  
148 was largely continental: dry, with strong solar radiation, low humidity in the air and harsh winter  
149 conditions (Zoller, 1995). Annual precipitation ranged from 700 to 1,200 mm. During the data  
150 collection period (from March 2010 to November 2013), censuses carried out by rangers of SNP  
151 recorded a natural fluctuation of the population, from a maximum of 7.7 individuals/Km<sup>2</sup> to a  
152 minimum of 6.2 individuals/Km<sup>2</sup>. During the study period the main predators of chamois, i.e. wolf  
153 (*Canis lupus*) and lynx (*Lynx lynx*), were not present, whereas golden eagle (*Aquila chrysaetos*)  
154 and red fox (*Vulpes vulpes*) only preyed upon kids and yearlings. Other ungulate species  
155 inhabiting the SNP are Alpine ibex (*Capra ibex*), red deer (*Cervus elaphus*) and roe deer  
156 (*Capreolus capreolus*).  
157

## 158 DATA COLLECTION

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

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

174 Activity data were then associated with weather information (mean temperature, mean solar  
175 radiation, mean wind speed, precipitation) provided by a weather station in Buffalora, which is  
176 located at a distance of approx. 13 km from the study area (46°38'53" N; 10°16'02" E - Swiss  
177 Meteorological Institute). We obtained the cloud cover estimates (i.e., percentage of sky covered  
178 by clouds over the entire atmosphere, estimated in eighths) recorded every 10 minutes from a  
179 weather station in Robbia, which is located at a distance of approx. 40 km from the study area  
180 (Poschiavo, Swiss Meteorological Institute). The Astronomical Applications Department of the U.S.

181 Naval Observatory web site (<http://aa.usno.navy.mil>) provided sunrise and sunset time (civil  
182 twilight) and moon phase data, expressed as the proportion of moon disk illuminated at 00.00 AM.  
183 The value 0 corresponded to new moon conditions and the value 1 to full moon conditions.

184

## 185 DATA ANALYSIS

186 The raw activity data recorded by the collars were divided by the maximum value recorded  
187 by the accelerometer (255) in order to obtain values ranging from 0 (i.e., no activity) to 1 (i.e.  
188 maximum activity). We split the whole dataset into two subsets: diurnal and nocturnal. To do this,  
189 activity values recorded between sunrise of day<sub>*i*</sub> and sunset of day<sub>*i*</sub> were assigned to the subset of  
190 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  
191 assigned to the subset of nocturnal activity of day<sub>*i*</sub>. Then, we calculated the average of the activity  
192 values recorded during each diurnal subset and each nocturnal subset, and we defined them as  
193 DMA and NMA, respectively. These indexes were aimed at analysing the overall activity of each  
194 chamois in relation to environmental conditions, during light and dark hours separately. Likewise,  
195 we calculated the diurnal and nocturnal average for each meteorological parameter (i.e., minimum,  
196 mean and maximum temperature; maximum and mean solar radiation for daylight hours only). For  
197 each date of the data collection period, diurnal and nocturnal precipitation values were calculated  
198 by summing the values recorded throughout the corresponding day and night. Wind speed was  
199 provided by the weather station administration as a daily mean. To estimate moonlight illuminance  
200 (hereafter, moonlight), we implemented the index proposed by Brivio et al. (2017) and calculated  
201 as:

202

$$203 \text{ Moonlight} = \text{moon phase of day}_i - (\text{moon phase of day}_i * \text{cloud cover of day}_i)$$

204

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

217 The effect of the selected intrinsic and extrinsic factors on activity patterns was assessed  
218 by modelling DMA and NMA separately by means of Generalised Additive Models (GAMs) with  
219 Gaussian distribution, as these allow for the likelihood of a non-linear response to the predictor  
220 variables. By means of GAMs, non-parametric smoothing functions were estimated for each  
221 predictor, to obtain the best prediction of the dependent variable values. GAMs were implemented  
222 within the mgcv package (version 1.8-22) in R (version 3.3.3; R Core Team, 2016). NMA was  
223 arcsinroot transformed in order to improve the homogeneity of residual distribution. To check for  
224 repeated measurements of the same individual, chamois identity was included in GAMs as a  
225 random intercept factor by using "re" terms and smoother linkage (Wood, 2013). Precipitation and  
226 wind speed were log-transformed in order to improve the homogeneity of the data distribution.

227 In order to validate our hypotheses 1, 2a, and 3, we built a full model for DMA and another  
228 for NMA, in which we considered the effects of all continuous variables, except for Julian date, as  
229 natural cubic spline functions. The effect of Julian date was modelled as a cyclic cubic regression  
230 spline in order to take into account the circularity of this variable: thus, we ensured that the value of  
231 the smoother at the far-left point (1<sup>st</sup> of January) was the same as the one at the far-right point (31<sup>st</sup>  
232 of December). To investigate differences in the behavioural patterns of females and males, we  
233 added the interaction with sex for each variable included in the models. We fitted a set of models  
234 considering all the possible combinations of the predictors included in the full model by using the  
235 dredge function of R package MuMIn (Barton, 2013). We assessed model parsimony using  
236 Akaike's Information Criterion (AIC, Richards et al., 2011). We checked the goodness of fit of the  
237 best models performed (homoscedasticity, normality of errors and independence) by visual  
238 inspection of residuals (Zuur et al., 2009). Finally, in order to test whether chamois modified their  
239 nocturnal activity as a compensation for the reduction in daylight activity in summer, winter, and  
240 mating season (hypotheses 2b and 3), we considered the NMA values recorded from the 21<sup>st</sup> of  
241 June to the 23<sup>rd</sup> of September, (i.e., from the first to the last day of astronomical summer), and from  
242 the 21<sup>st</sup> of December to the 21<sup>st</sup> of March (i.e., from the first to the last day of astronomical winter).  
243 We defined the 1<sup>st</sup> and 30<sup>th</sup> of November as beginning and end of the mating season (Von  
244 Hardenberg et al., 2000). We re-fitted the best model selected for the full-year analyses  
245 (Supplementary materials 2, Table S2.3) using only the data collected in summer, winter, and  
246 mating season, to carry out separate analyses.

247 In order to study the nocturnal periodicity of chamois activity (hypothesis 2c), the acrophase  
248 of each chamois' nocturnal activity was calculated with ActogramJ (Schmid et al., 2011). To  
249 calculate the nocturnal acrophase, we took into account the raw data used to estimate the NMA.  
250 For each night, we obtained a record including individual identity, Julian date, sex and acrophase.  
251 The hypothesis that periodicity was absent during the night was tested by means of a GAM. For  
252 this analysis, we used a dataset including, for each night of data collection: chamois identity, sex,  
253 Julian date and acrophase. The effect of Julian date on acrophase was assessed by expressing



254 the latter as minutes before or after midnight, in order to account for a continuity between 23:59  
255 and 00:00 of the following day. The effect of Julian date was modelled as a cyclic cubic regression  
256 spline. The interaction with sex was included in the model to test for differences in the periodicity  
257 patterns between sexes. Chamois identity was included as a random factor using the same  
258 statistical procedure described above.

259

## 260 **RESULTS**

261 According to the minimum AIC criterion, the best model for DMA included sex, Julian date,  
262 age, radiation, precipitation, maximum temperature and wind as predictor variables (R-sq. = 0.678,  
263 Supplementary materials 1, Tables S1.2 - S1.3). Likewise, the model including the same variables  
264 with the exception of radiation and the addition of moonlight and the DMA recorded on the  
265 previous day, best described NMA (R-sq. = 0.595, Supplementary materials 2, Table S2.2 - S2.3).

266 Throughout the year, the highest peak of male DMA was recorded around the 23<sup>th</sup> of June  
267 and a second peak during the mating season (the 21<sup>st</sup> of November – Figure 1a), while females  
268 showed a higher peak around the 8<sup>th</sup> of June, which dropped off later with respect to that of males.  
269 The best model for NMA predicted different seasonal trends depending on sex. Females were  
270 similarly active in spring and summer, with a reduction in activity levels from the second part of  
271 autumn to the end of winter. In males, the trend of NMA was similar to that of DMA, with two peaks  
272 - on the 30<sup>th</sup> of July and 10<sup>th</sup> of November - and a sharp decrease in winter (Figure 1b). The  
273 analysis showed that, for males, DMA peaked at intermediate temperatures (~ 8 degrees) and  
274 declined further from these. For females, the effect had a similar form, but generally much weaker  
275 (Figure 1c). Instead, temperature affected the NMAs of either sex linearly and to a similar extent:  
276 male and female chamois alike increased their nocturnal activity with higher ambient temperatures  
277 (Figure 1d). The contrasting forms of the NMA and DMA temperature effects suggested that there  
278 seems to be a temperature sweet spot where activity is maximised. Precipitation negatively  
279 affected male and female chamois DMA (Figure 1e) and male NMA only (Figure 1f). On the  
280 contrary, only female chamois' activity levels were slightly lower on windy days, both during  
281 daylight and night hours (Figure 1g-h). A weak influence of solar radiation was observed, though  
282 only female chamois were found to be slightly less active on days with either lower or higher than  
283 average radiation (Supplementary materials 1, Figure S1.2); this could possibly explain the weaker  
284 effect of temperature on this sex.

285 As regards NMA, then, the analysis detected a weak influence of moonlight, with chamois  
286 females and males being slightly more active when the available moonlight was more intense  
287 (Figure 2a). Finally, results showed that chamois NMA did not correlate to the diurnal activity of the  
288 previous day (Figure 2b). In order to ascertain whether NMA was related to the activity during the  
289 previous daylight hours when environmental conditions were more demanding in terms of energy

290 expenditure (i.e., in summer, winter, and mating season – Supplementary materials 3), we refitted  
291 the best model for NMA considering the respective subsets only. Surprisingly, in summer only the  
292 males' NMA was negatively affected by their diurnal activity: when the DMA exceeded the  
293 threshold of 0.43, the nocturnal activity decreased. NMA of females were not influenced by their  
294 DMA (Figure 3a). In winter, conversely, the NMA of both sexes was positively related to their DMA  
295 (Figure 3b). We did not find any relationship between DMA and NMA during the mating season  
296 (Supplementary materials 3, Figure S3.1); surprisingly, though, we detected a significant increase  
297 in male activity during bright moonlit nights (Supplementary materials 3, Figure S3.2).

298 The analysis also detected a significant relationship between nocturnal acrophase, i.e. the  
299 peak of activity during the night, and Julian date for both males and females. However, no clear  
300 biological effect was detectable. (Figure 4). For females, the range of the acrophase throughout  
301 the year covered only 24 minutes, being comprised between 74 to 50 minutes before midnight (i.e.,  
302 22:46-23:10). Whereas the males' range was larger (50 minutes): the acrophase occurred between  
303 87 to 37 minutes before midnight (i.e., hours 22:33-23:23).

304

## 305 **DISCUSSION**

306 To date, the role of nocturnal activity in the daily activity budget of mammals has been  
307 seldom investigated (Hetem et al., 2012). Our study points out that a species which is active both  
308 during day and night – i.e. cathemeral species – has a high behavioural plasticity to cope with  
309 demanding environmental conditions by modifying the distribution of activity between daylight and  
310 darkness hours. While Alpine chamois has generally been considered a diurnal species, the  
311 present study showed that nocturnal activity plays a relevant role in its activity budget, especially  
312 when diurnal activity decreases due to unfavourable environmental conditions. Additionally, we  
313 showed that, over the whole year, nocturnal activity reached the acrophase – i.e., the peak of  
314 activity – during the first half of the night, constantly and without significant sexual differences  
315 (prediction 2c). Previous investigations on Alpine chamois reported that nocturnal activity peaked  
316 around midnight (Ingold et al., 1998), or during the second half of the night (Carnevali et al., 2016).  
317 Such small differences in the timing of acrophase could depend either on the methodology of  
318 activity recording or on external factors, such as date of sampling, geographical location and  
319 environmental conditions. Overall, these results strongly indicate a stable entrainment of nocturnal  
320 activity. Which environmental cue contributed to maintaining such stable entrainment is not clear.  
321 However, changes in light intensity and spectrum occurring at sunset could be suitable entraining  
322 signals, as they are present all year round (Walmsley et al., 2015). Consistently with these findings  
323 and the results of Brivio et al. (2016), showing seasonal variations of daily activity periodicity,  
324 Alpine chamois should be considered as a cathemeral species.

325 As regards our specific predictions, findings pointed out that nocturnal activity is relevant for  
326 chamois. We expected nocturnal activity to be marginal, or to play an exclusively compensatory  
327 role when diurnal activity was limited (prediction 2a), and we expected it not to be affected by  
328 external factors (prediction 1). Instead, findings showed that the same factors similarly affected  
329 nocturnal and diurnal patterns, with the only exception of ambient temperature. During daylight  
330 hours, when temperature typically reached the highest values, chamois increased their activity  
331 levels when temperature increased up to the threshold of 8° C ca. When temperature exceeded  
332 this threshold value, however, DMA decreased, more sharply in males than in females. The  
333 reduction in activity levels in response to increasing air temperature as a strategy against  
334 overheating has previously been detected in ungulates (e.g., Belovsky and Slade, 1986; Brivio et  
335 al., 2017; Shi et al., 2003), including chamois (Brivio et al., 2016). Our separate investigation on  
336 diurnal and nocturnal hours, on the other hand, showed that ambient temperature positively  
337 affected NMA. In the Alps, animals do not risk overheating during the night. Rather, they typically  
338 face the risk of hypothermia, which they cope with by reducing their activity levels (Brivio et al.,  
339 2016). Thus, we may hypothesise that chamois take advantage of milder nights to increase their  
340 activity and, as a consequence, their energy intake. More in general, we may argue that chamois  
341 have evolved to take advantage of favourable periods: when the phenological cycle of vegetation  
342 was better, precipitation was low, and wind was calm, chamois increased their activity and, as a  
343 result, their food intake. Such plasticity in chamois behavioural patterns, already suggested by  
344 Brivio et al. (2016), was also supported by our analyses concerning the most demanding periods of  
345 the year (prediction 2b). Chamois adapted its nocturnal activity to respond to the seasonality of the  
346 environmental pressures typical of the Alps. During winter, nocturnal activity was positively related  
347 to the diurnal one and, therefore, served as a cumulative opportunity for energy intake when food  
348 availability and quality were scarce. Conversely, during summer it was compensatory: male  
349 chamois were less active in the warmest days and they had higher nocturnal activity in days of low  
350 diurnal activity, likely to improve energy intake. Surprisingly, this compensatory role was observed  
351 in males only. Further analyses are needed to understand why it was not detected in females.

352 In a more general perspective, our findings support the theory proposed by Bennie et al.  
353 (2014), who stated that light and temperature combine to define available temporal niches. In a  
354 biogeographical perspective, diurnal activity patterns are expected to be the most frequent at high  
355 altitude areas, where nocturnal temperatures are very low; whereas crepuscular and cathemeral  
356 activity patterns should be prevalent in the Arctic regions, which are characterized by long hours of  
357 twilight and high seasonal variation in the hours of daylight (Bennie et al., 2014). Our results  
358 stressed that seasonality –rather than altitude - seems to be the key factor affecting activity  
359 rhythms in the Alpine region and that behavioural plasticity, which is intrinsic of cathemerality, may  
360 contribute to increase the energy intake. In fact, heat-sensitive species may rely largely on  
361 responding to overheating by means of behavioural strategies (du Plessis et al., 2012; Stelzner

362 and Hausfater, 1986), such as decreasing their activity level when ambient temperature increases  
363 over a certain critical threshold during the day (Terrien et al., 2011). Researchers showed that a  
364 reduction in activity levels entails a decrease in energy intake and they investigated how ungulates  
365 could compensate for the energetic demands imposed by global warming (Mason et al., 2017). In  
366 view of foregoing, we suppose that the possibility to switch from diurnal to nocturnal activity will  
367 favour cathemeral species facing global climate change.

368 As to our third prediction, our findings on the effect of moonlight on activity patterns seems  
369 to support the idea that chamois increase their activity in favourable nocturnal conditions  
370 (prediction 3). Even though the increase in activity during moonlit nights was weak, this result  
371 supports the visual acuity hypothesis formulated by Prugh and Golden (2014), who maintained that  
372 moonlight increases the foraging efficiency and favours the detection of predators, so that prey  
373 species relying on vision to locate food and predators are more active in the moonlight than on  
374 darker nights. Our study area was free from predators and human harassment – including hunting  
375 and poaching – was absent or very scarce. Accordingly, moonlight could only favour foraging  
376 efficiency and not predators detection. This may contribute to explaining the weak effect of  
377 moonlight on activity patterns. Conversely, our results did not support the “habitat-mediated  
378 predation risk” hypothesis, which predicts that, in open habitats, predators detect prey more easily  
379 during moonlit nights (Prugh and Golden, 2014). According to the latter hypothesis, in prey species  
380 lunar phobia and its negative effect on activity should decrease as habitat cover increases.  
381 Surprisingly, moonlight positively affected male NMA during the mating season, even though the  
382 rut occurs in late autumn when climatic conditions are severe and, possibly, there is snow cover on  
383 the terrain. We may conjecture that the reproductive efforts stimulate males to be active whenever  
384 the environmental conditions are favourable in order to increase their reproductive opportunity. Our  
385 findings on the moonlight effect on NMA are in accordance with other recent findings (Carnevali et  
386 al., 2016), even though the magnitude of these patterns was found to be weaker, maybe due either  
387 to the use of a different equipment in collecting data (VHF signal vs. accelerometer data), or to  
388 different environmental conditions.

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

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407

408 **AUTHOR CONTRIBUTIONS**

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

412

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558 **FIGURES CAPTIONS**

559

560 Figure 1: Values predicted by the best generalised additive model of mean activity of Alpine  
561 chamois in the Swiss National Park. The figure shows the effects of Julian date (A-B),  
562 maximum daily temperature (C-D), daily precipitation (E-F), and wind speed (G-H) on  
563 diurnal (left side of the figure) and nocturnal (right side of the figure) mean activity. The  
564 predictions are given according to the mean of all other covariates in the model. In the  
565 graphs, females are represented by the red line, males by the blue line, while the coloured  
566 shaded areas are the estimated standard errors. The values on the y axes for nocturnal  
567 activity have been back transformed from the arcsin square root values used to calculate  
568 the best models (see the text for more details).

569

570 Figure 2: Values predicted by the best generalised additive model of nocturnal mean activity of  
571 Alpine chamois in the Swiss National Park. The figure shows the effects of moonlight (A)  
572 and diurnal mean activity (B). The predictions are given according to the mean of all other  
573 covariates in the model. In the graphs, females are represented by the red line, males by  
574 the blue line, while the coloured shaded areas are the estimated standard errors. The  
575 values on the y axes have been back transformed from the arcsin square root values used  
576 to calculate the best models (see the text for more details).

577

578 Figure 3: Values predicted by the best generalised additive model of nocturnal mean activity of  
579 Alpine chamois in the Swiss National Park during summer (A) and winter (B). The  
580 predictions are given according to the mean of all other covariates in the model. In the  
581 graphs, females are represented by the red line, males by the blue line, while the coloured  
582 shaded areas are the estimated standard errors. The values on the y axes have been  
583 back transformed from the arcsin square root values used to calculate the best models  
584 (see the text for more details).

585

586 Figure 4: Values predicted by the best Generalised Additive Model (see the text for more details) of  
587 Alpine chamois nocturnal acrophase in Swiss National Park. In the graphs, females are  
588 represented by the red line, males by the blue line, while the coloured shaded areas are  
589 the estimated standard errors.

590