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

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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. Here we investigated daily and annual activity rhythms of Alpine chamois (Rupicapra rupicapra) by analysing high-resolution long-term data from females and males 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 significantly influenced by climatic factors and poorly affected by individual variables. As activity was strongly influenced by temperature and radiation we conjectured that it was also critically dependent upon animals' thermal balance. Our analyses showed a negative correlation between daily activity and adverse climatic conditions (i.e., precipitation and snow cover). In conclusion, our study pointed out that chamois is well adapted to Alpine environment and seasonality. However, it can be susceptible to climate change, which may produce a mismatch between its annual activity rhythms, evolved over thousands of years.

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

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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. Here we investigated daily and annual activity rhythms of Alpine chamois (*Rupicapra rupicapra*) by analysing high-resolution long-term data from females and males 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 significantly influenced by climatic factors and poorly affected by individual variables. As activity was strongly influenced by temperature and radiation we conjectured that it was also critically dependent upon animals' thermal balance. Our analyses showed a negative correlation between daily activity and adverse climatic conditions (i.e., precipitation and snow cover). In conclusion, our study pointed out that chamois is well adapted to Alpine environment and seasonality. However, it can be susceptible to climate change, which may produce a mismatch between its annual activity rhythms, evolved over thousands of years.

Key words: 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 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). Significant 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; 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; Zucker 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 on the circannual and the circadian 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 (Aschoff 1958; 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 may become out of phase with the periodic challenges posed by their environment (e.g., Pettorelli et al. 2007; Plard et al. 2014). 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 among the most vulnerable to rapid climate change (Ernakovich et al. 2014). Their climate is expected to be particularly affected by global warming: not only by rising temperatures (about 0.25 °C /decade by the mid- 21st century), but also by changes in the seasonal cycle of precipitation, global radiation, humidity,

101 temperature and precipitation extremes, as well as by closely related impacts such as floods,
102 droughts, snow cover and natural hazards (Gobiet et al. 2014).
103 Studies on the current relationship between climate and animal behaviour should shed
104 light on the species' ability to track and adapt to climate change (Dunbar 1998; Lehmann et
105 al. 2008; Korstjens et al. 2010). Alpine chamois is a relatively eurythermic mountain
106 ungulate, which has adapted to a wide range of temperatures and is distributed over a broad
107 altitudinal range (500–3100 m; Shackleton 1997; Spitzenberger et al. 2001). Indeed, this
108 species is the most widespread ungulate in the Alps (Apollonio et al. 2010) and is well
109 adapted to their environment and seasonality. It is characterised by nearly monomorphic
110 sexes, with only a weak and highly seasonal dimorphism in body mass (from approx. 40%
111 before the rut, to approx. 6% in winter and 4% in spring; Garel et al. 2009; Rughetti and
112 Festa-Bianchet 2011). The seasonal changes in body mass, together with the very high
113 survival rate of both sexes (Corlatti et al. 2012), are indicative of a conservative strategy,
114 more pronounced in males than in females. Indeed, during summer chamois accumulate fat
115 resources (Pérez-Barbería et al. 1998) to be used during the rut (i.e., November), in order to
116 reduce over-winter mortality costs. In other words, this ungulate is an ideal case-study to
117 investigate the plasticity in the response of a species to the variation in the environmental
118 conditions of mountainous regions.
119 Here we investigated daily and annual activity rhythms of Alpine chamois. In particular,
120 we compared activity levels of chamois of different sex and age class throughout the years in
121 order to investigate individual strategies of adaptation to seasonal and climatic variations.
122 Since in mountainous regions the harshest conditions occur during the winter season, we
123 focused a part of our analyses only on winter data to better understand how chamois managed
124 to control their energy balance in response to different external factors under severe
125 environmental conditions.
126

Materials 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 southeastern 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 deciduos*) 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 chrysäetos*) that typically preys upon small kids. During the study period (2010-2013), population census showed that chamois density was relatively stable: during the census of 2013, the rangers counted 6.2 individuals/Km^2 (523 females, 274 males and 267 kids + yearlings). Between 2010 and 2013, 11 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

The locomotor activity was recorded continuously from the capture of the individuals (the first one in March 2010) until the conclusion of data collection (November 2013) or until the collar stopped working. 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

153 (G=gravitational constant) and measured activity as the change of static acceleration (gravity)
154 and dynamic acceleration (collar) four times/second. The activity values were given within a
155 relative range between 0 and 255. Value 255 was equal to -2G / +2G and it indicated the
156 maximum acceleration, whereas 0 indicated no acceleration at all. Measurements were
157 averaged over sampling intervals of 5 minutes and stored with the date and time associated.
158 Weather data (daily mean temperature, daily mean radiation, daily precipitation
159 amount, daily mean wind speed and daily snow cover) were provided by the Swiss
160 Meteorological Institute (Begert et al. 2005) from the Buffalora station located at approx.13
161 km from the study area at an altitude of 1968 m a.s.l. (46°38'53.29" N; 10°16'1.86" E).
162
163 **Data analysis**
164 The presence of periodicity in the locomotor activity rhythms was determined by
165 means of the Lomb-Scargle periodogram (LSP) analysis and confirmed with the χ^2
166 periodogram analysis, by using the ActogramJ software for circadian analysis (Schmid et al.
167 2011). The significance was set to $p<0.05$. For each chamois, analyses were performed each
168 month with intervals of 10 days. To exclude that 8- and 12-hour periods were harmonics of
169 daily (24 hours) periods or *vice versa*, we compared the amplitude (*PN* and *Qp*) of the peaks
170 (van Oort et al. 2005). Data were presented graphically as actograms by using the Activity
171 Pattern ver. 1.3.1 software (Vectronic Aerospace GmbH, Berlin, Deutschland; Fig. 1,
172 Supplementary material Appendix 1 Fig. A1-A15).
173 On each day of data collection, mean activity (±*SD*) during the day was calculated for
174 each chamois by using the Activity Pattern ver. 1.3.1 software (Vectronic Aerospace GmbH,
175 Berlin, Deutschland). We focused on the daily mean activity (DMA) of each individual to
176 assess the effect of intrinsic and extrinsic factors on chamois activity patterns. To allow for
177 the likelihood of a non-linear response to the covariates, we chose to fit a non-parametric
178 model to the data in which the exact functional form was determined from the data

179 themselves and not specified *a priori*. Generalised Additive Mixed Models (GAMMs) are an
180 ideal tool for such analysis as they are flexible in modelling the shape of non-linear
181 relationships. Non-parametric smoothing functions are used on sections of the data and the
182 response curves are connected at their end-points to generate an overall smooth curve (Wood
183 2006). In addition to the non-parametric smoothing functions, parametric fixed and random
184 predictor terms may also be included, as in a conventional mixed-effects model. The DMA
185 was modelled as the response variable by fitting alternative GAMMs, implemented within
186 the mgcv package (version 1.7-26; Wood 2006) in R (version 3.0.2; R Core Team 2014).
187 Female and male DMA were modelled separately by using their identity as a random effect.
188 The predictor variables considered were: temperature, radiation, precipitation, wind speed,
189 snow cover and chamois age class. To subdivide our sample size homogeneously, we used
190 four uniform age classes: 1) 3-5 years old; 2) 6-8 years old; 3) 9-11 years old; 4) older than
191 11 years. Precipitation and wind speed were log-transformed in order to improve the
192 homogeneity of data distribution. Moreover, in order to identify the fluctuating pattern of
193 variation of DMA throughout the year, we inserted the Julian date as a continuous fixed
194 effect in the models. To check for multicollinearity between the explanatory variables, we
195 calculated the variance inflation factors (VIF) for each of them. Temperature was found to be
196 correlated to radiation, as well as snow cover to precipitation and, consequently, they were
197 used separately in alternative models. The VIF values of the other variables were < 3, thus
198 indicating no severe multicollinearity between them (Zuur et al. 2009). Effects of continuous
199 predictor variables were initially modelled as natural cubic spline functions and the optimal
200 roughness of the smoothing terms was determined by minimising the generalised cross-
201 validation value. When the effective degrees of freedom (*edf*) of a predictor variable were 1
202 and the graphical inspection confirmed a linear relationship with the response variable, we
203 refitted the model omitting the smoothing function. Between these two models, we selected
204 those with the lower AIC value. Effects of the Julian date were modelled as a cyclic cubic

regression spline in order to ensure 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).

Analyses were performed using the information-theoretic approach (Dochtermann and Jenkins 2011). In the light of theory, biological relevance and previous research on related species, we defined a set of alternative hypotheses, which were used to construct 47 *a priori* GAMM models (Supplementary material Appendix 2 Table A1). The alternative models were ranked and weighted with the minimum AIC criterion (Symonds and Moussalli 2011). We confirmed the global goodness-of-fit (i.e., homoscedasticity, normality of errors and independence) of the best models by visual inspection of residuals (Zuur et al. 2009).

In order to point out the influence of snow cover on female and male DMA, we constructed two sets of 24 *a priori* models (one for each sex, Supplementary material Appendix 2 Table A2) by using only data from 1 October to 30 April (i.e., the period in which snow was potentially present). Then, we followed the same approach described above, in order to identify the best model among 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. All chamois showed a clear daily rhythm of locomotor activity entrained to the natural light-dark cycle (Fig. 1, Supplementary material Appendix 1 Fig. A1-A15). Their activity was not exclusively diurnal and a nocturnal activity was also present during most of the year (Fig. 1-2, Supplementary material Appendix 1 Fig. A1-A15). The pattern of locomotor activity showed a marked seasonal variation in both females males and gradually changed from unimodal (with a single peak in December-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 hours ($P<0.05$, LSP; Fig. 2B, F) for both males and females. The bimodal pattern of activity peaked at dawn and dusk, with the

231 activity at dusk being higher than that at dawn (Fig. 1, Supplementary material Appendix 1
232 Fig. A1-A15). During autumn, the period shorted to 8 hours (P<0.05, LSP; Fig. 2C, G) and
233 the pattern of activity showed a marked increase of nocturnal activity with a peak at midnight
234 (Fig. 1, Supplementary material Appendix 1 Fig. A1-A15).

235 *Global models* – The best model selected (with the lowest AIC value) for females
236 included all predictor variables: age class, day of the year, temperature, precipitation and
237 wind speed. For males, the best model included all variables except wind speed (Table 1).
238 Results showed that age class did not significantly affect the DMA of both female and male
239 chamois. Throughout the year, the DMA of both sexes followed a bell-shaped pattern, with a
240 maximum of activity at the beginning of summer (females: peak on the 178th day of the year
241 – 27 June; males: peak on the 185th day of the year – 1 July) and minimum values in January
242 (Fig 3A). A second peak of activity was detected from mid-October to the end of November.
243 This second peak was higher in males than in females. Temperatures significantly affected
244 chamois DMA. The pattern of the relationship was similar for females and males: DMA
245 increased with increasing daily mean temperatures until 3-5 °C and then decreased with a
246 slight difference between the two sexes (Fig. 3B). Female and male DMA was also
247 significantly influenced by precipitation: DMA decreased linearly with increasing daily
248 precipitation (females: ß= -2.93 ± 0.68; males: ß= - 1.02 ± 0.14). Finally, female DMA
249 decreased linearly with increasing wind speed (ß= -3.79 ± 0.68).

250 *Winter models* – For both sexes the best models selected included: radiation, wind
251 speed and snow cover (Table 2). Only for females, the model selected contained also age
252 class but with no significant statistical effect. Results showed that in this period (1 October –
253 1 April) the variation in chamois DMA was better explained by radiation than by
254 temperature, with a positive non-linear effect for female (Fig. 4A) and a positive linear effect
255 for males (ß= 0.03 ± 0.002). Chamois DMA considerably decreased with increasing snow
256 cover (Fig. 4B), while the relationship between DMA and wind speed followed a hump-

shaped pattern, with a peak of activity around 1.19 m/s for females and around 1.18 m/s for males (Fig. 4C).

Discussion

This first detailed field study on Alpine chamois activity showed that this species exhibited clear daily and annual activity rhythms entrained to the light-dark cycle. Daily activity was significantly influenced by climatic factors (i.e., temperature, radiation, snow cover and wind speed) and poorly affected by individual variables, such as sex and age class. As a matter of fact, even though females were more active during all seasons, the two sexes had a similar reaction to the environmental factors analysed, with no significant difference among individuals of different ages.

Daily activity rhythms varied from a unimodal pattern during winter to a bimodal pattern during summer and autumn. It is no coincidence that the findings on DMA showed that chamois were more active during spring and early 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, the variation in the activity patterns indicated 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 (April–June; earlier at lower altitudes), thus providing an abundant and protein-rich source of 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, in fact, 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, if

283 the forage is protein-rich, the digestion is faster so that animals are able to engage in a second
284 bout of foraging activity during the day (VanSoest 1994). Moreover, even the modifications
285 in chamois daily activity levels pointed out by our analyses resulted to be a good strategy of
286 adaptation to the availability of food resources. As reported for other northern-temperate
287 mammals (Tyler and Blix 1990; Adamczewski et al. 1997; Parker et al. 2009), the peak of
288 activity during the spring-summer months may be an adaptation that enables chamois to use
289 the most favourable forage conditions in order to storage fat tissue to survive during long,
290 cold and snowy winters. Accordingly, the reduction of activity during winter and the use of
291 the unimodal pattern showed by our analyses may be seen as an adaptation strategy to
292 conserve energy in response to the unfavourable conditions (i.e., harsh weather, decline in
293 forage quality and decreased food availability due to snow cover). For both female and male
294 chamois, the decrease in forage quality and quantity may be offset by a decrease in metabolic
295 rate and the use of the stored energy reserves. The reduction of food intake and, in general, of
296 metabolic rate during winter is widespread amongst northern ungulates as a strategy to cope
297 with cold conditions and low availability of food resources (reviewed in Arnold et al. 2004).
298 At first glance, seasonal variations in the activity pattern coincided with the variation in
299 the photoperiod, thus suggesting that the latter is the main *Zeitgeber*. Nevertheless,
300 throughout the year activity rhythms can deviate from the photoperiod cycle, therefore
301 suggesting that other biological and environmental factors may act as time cues for the
302 activity regulation of chamois. In November, for example, a peak of activity -more
303 pronounced in males than in females- disrupted the pattern of decrease from mid-summer to
304 winter. Indeed, the chamois' mating season occurs in this period, with a peak between 16 and
305 25 November (Corlatti et al. 2013b). This peak of activity could not be ascribed to foraging
306 behaviour as males typically reduce forage intake during the rut (Willisch and Ingold 2007).
307 Therefore, in accordance with Corlatti et al. (2013b), the high activity levels found in this
308 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 detected at midnight. Thus, our analyses match with the previous knowledge on this species and contribute to explain why males lose weight faster than females during the rutting period (Garel et al. 2009; Rughetti and Festa-Bianchet 2011). In fact, during the rut they spent significantly less time foraging (reduction of food intake; Willisch and Ingold 2007; Corlatti et al. 2013a) and were active for a longer period (i.e., increase in energy expenditure).

Climate is another time cue for chamois activity: they adjusted their activity responding to variations in temperature, as well as to changes in precipitation levels, wind speed and, during winter, snow cover and solar radiation. Air temperature appeared to significantly influence chamois activity rhythms, either reducing or stirring daily activity levels. Similar correlations between daily activity and air temperature have been found for other ungulate species (Belovsky and Slade 1986; Beier and McCullough 1990; Schmitz 1991; Owen-Smith 1998; Loe et al. 2007; Pipia et al. 2008; Signer et al. 2011). The response of chamois activity to temperature was parabolic, with the highest activity levels at temperatures between 3 and 5°C and a decline in activity levels at higher and lower temperatures for both sexes (Fig. 3B). Therefore, activity appeared to be strictly dependent upon animal thermal balance. On the one hand, when air temperatures are significantly below the animals' thermoneutral zone, decreased 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 reduce heat loss. Accordingly, Moen (1976) and Gates and Hudson (1979) showed that lying position and inactivity significantly reduce the metabolic costs of thermoregulation during cold weather. On the other hand, when the air temperature rises significantly above the species' thermoneutral zone, the reduction of activity is likely an attempt to avoid thermal overload, by reducing heat-generating activities (i.e., feeding, moving and maybe even social interaction). This last result is consistent with a previous observational study on Alpine chamois, which reported that animals allocated less

time to foraging with increasing temperatures during summer (Mason et al. 2014). Several authors showed that thermal stress places an upper limit on the time animals may devote to daily activity (e.g., Orthoptera: Parker 1982; Chappell 1983; *Corvus brachyrhynchos*, *Sciurus carolinensis*: Kilpatrick 2003; *Castor Canadensis*: Belovsky 1984b; *Lepus americanus*: Belovsky 1984a; *Alces alces*: Belovsky 1978; *Tragelaphus strepsiceros*: Owen-Smith 1998). Each species 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 Jordan 1978; Belovsky and Slade 1986; Owen-Smith 1998). Our results showed that chamois started to decrease their activity already at 3-5°C. Given the rapid alteration in the seasonal cycle of climatic variables characterising the last decades, the annual activity rhythms of chamois, which have evolved over thousands of years, 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 (about 0.25 °C / decade, Gobiet et al. 2014), chamois daily activity is expected to decrease, particularly during summer, likely compromising their ability to accumulate body reserves. This may affect the animals' ability to cope with the food shortages of the Alpine winter season, and therefore it may have important effects on individual life history. This scenario could be worsened by the forecasts on global radiation along the Alpine ridge, which indicate an increase of 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 managed to reduce the amount of

361 endogenous heat produced to maintain constant body temperature. Consistently, Signer et al.
362 (2011) showed that radiant heat-assisted rewarming play a key-role as a strategy to endure
363 harsh over-wintering conditions in Alpine ibex. In this framework, it is useful to note the role
364 of the black coat of chamois during the winter season. Our findings suggested that this
365 specific evolutionary characteristic favoured a greater absorption of solar radiation
366 (exogenous heat) and thus an increase of daily activity.
367 Conversely, chamois winter activity may benefit from the significant decrease in alpine
368 snow duration and abundance resulting from the global climate change (Gobiet et al. 2014).
369 Our analyses on winter data highlighted a strong negative correlation between daily activity
370 and snow cover. Several studies analysed the effect of snow cover on spatial behaviour
371 (Tyler and Blix 1990), activity rhythms (Cederlund 1981; Beier and McCullough 1990), life
372 history and population dynamics (Jacobson et al. 2004; Apollonio et al. 2013; Willisch et al.
373 2013). It is well known that deep snow causes a higher energy expenditure for large
374 mammals, likely as a consequence of both lower food availability and increased energy
375 expenditure related to locomotion. Our study showed that chamois reduced their activity
376 when the thickness of snow increased: indeed, when snow cover was thicker, chamois
377 adopted a safe strategy by reducing their total activity, likely because of the reduced food
378 availability, but also to avoid mobility problems and to reduce accident risks (i.e.,
379 avalanches). As chamois have an interdigital membrane to increase the distribution of weight
380 and favour mobility on snow surfaces, we may expect a reduced effect of snow cover on their
381 behaviour. Nonetheless, this anatomic adaptation to snow surfaces does not seem sufficient
382 to maintain regular activity rhythms in case of deep snow cover. Further research should
383 assess the effect of such activity reduction on individual life history and population
384 dynamics.
385 In conclusion, our study pointed out that well-detailed information on activity may be
386 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.

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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.

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Figure captions

Figure 1: Representative actograms of daily activity of one A) radio-collared female Alpine chamois and B) one radio-collared male Alpine chamois in the Swiss National Park (Switzerland). Vertical bars represent their activity levels (over intervals of 5 minutes), the color 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 hours time scale to help the interpretation.

Figure 2: Periodogram analysis of locomotor activity rhythms of one radio-collared female Alpine chamois (g500: A, B, C, D) and one radio-collared male Alpine chamois (g319: E, F, G, H) in the Swiss National Park (Switzerland). Lomb-Scargle periodogram analysis (confidence level, 95%) for actograms shown in Figure 1 performed over intervals of 10 days in 4 different periods of the year. Periodogram analysis showed the presence and periodicity of rhythms of locomotor activity. Periodicity confirmed the presence of unimodal (A, D, E, H), bimodal (B,F) and trimodal (C,G) patterns in both the male and the female 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 hours. The straight horizontal lines represent the threshold of significance, set at $P=0.05$. Amplitudes of the peaks are used to indicate the main period (dotted lines).

Figure 3: Value predicted by the best Generalised Additive Mixed Model (see the text for more details) of daily mean activity of Alpine chamois in the Swiss National Park (Switzerland). The figure A) shows the effect of Julian day and B) daily mean temperature. In the graphs males are represented by continuous line, females by broken line.

Figure 4: Value predicted by the best Generalised Additive Mixed Model (see the text for more details) of Alpine chamois daily activity during winter months (1 October-30 April) in the Swiss National Park (Switzerland). The figure A) shows the effect of radiation, B) snow cover, and C) wind speed. In the graphs males are represented by continuous line, females by broken line.

Tables

Table 1: Top 5 Generalised Additive Mixed Models predicting daily mean activity in Alpine chamois throughout the year in the Swiss National Park, Switzerland.

model #	variables in the model	AIC	deltaAIC
FEMALES			
45	**age class+ temperature+ precipitation+ wind speed+ Julian day**	**42086.07**	**0**
38	age class+ temperature+ precipitation+ Julian day	42104.48	18.41
43	temperature+ precipitation+ wind speed+ Julian day	42141.61	55.54
31	temperature+ precipitation+ Julian day	42156.78	70.71
37	age class+ temperature+ wind speed+ Julian day	42172.75	86.68
MALES			
38	**age class+ temperature+ precipitation+ Julian day**	**19479.10**	**0**
45	age class+ temperature+ precipitation+ wind speed+ Julian day	19479.34	0.24
43	temperature+ precipitation+ wind speed+ Julian day	19486.58	7.48
31	temperature+ precipitation+ Julian day	19486.62	7.52
37	age class+ temperature+ wind speed+ Julian day	19522.41	43.31

Best models were selected with the $\Delta AIC \geq 2$ criterion. [*AIC* = Akaike information criterion; ΔAIC = difference in AIC value between the AIC of a given model and the best model (lowest AIC)].

Table 2: Top 5 Generalised Additive Mixed Models predicting daily mean activity in Alpine chamois during winter months (1 October-30 April) in the Swiss National Park, Switzerland.

model #	variables in the model	AIC	deltaAIC
FEMALES			
23	**age class + radiation + wind speed + snow cover**	**16012.37**	**0**
21	radiation + wind speed + snow cover	16050.52	38.15
18	age class + radiation + snow cover	16051.61	39.24
13	radiation + snow cover	16088.83	76.46
22	age class + temperature + wind speed + snow cover	16300.02	287.65
MALES			
21	**radiation + wind speed + snow cover**	**8875.483**	**0**
23	age class + radiation + wind speed + snow cover	8877.079	1.596
13	radiation + snow cover	8886.038	10.555
18	age class + radiation + snow cover	8887.877	12.394
22	age class + temperature + wind speed + snow cover	8950.037	74.554

Best models were selected with the $\Delta AIC \geq 2$ criterion. [*AIC* = Akaike information criterion; ΔAIC = difference in AIC value between the AIC of a given model and the best model (lowest AIC)].

Figure 1
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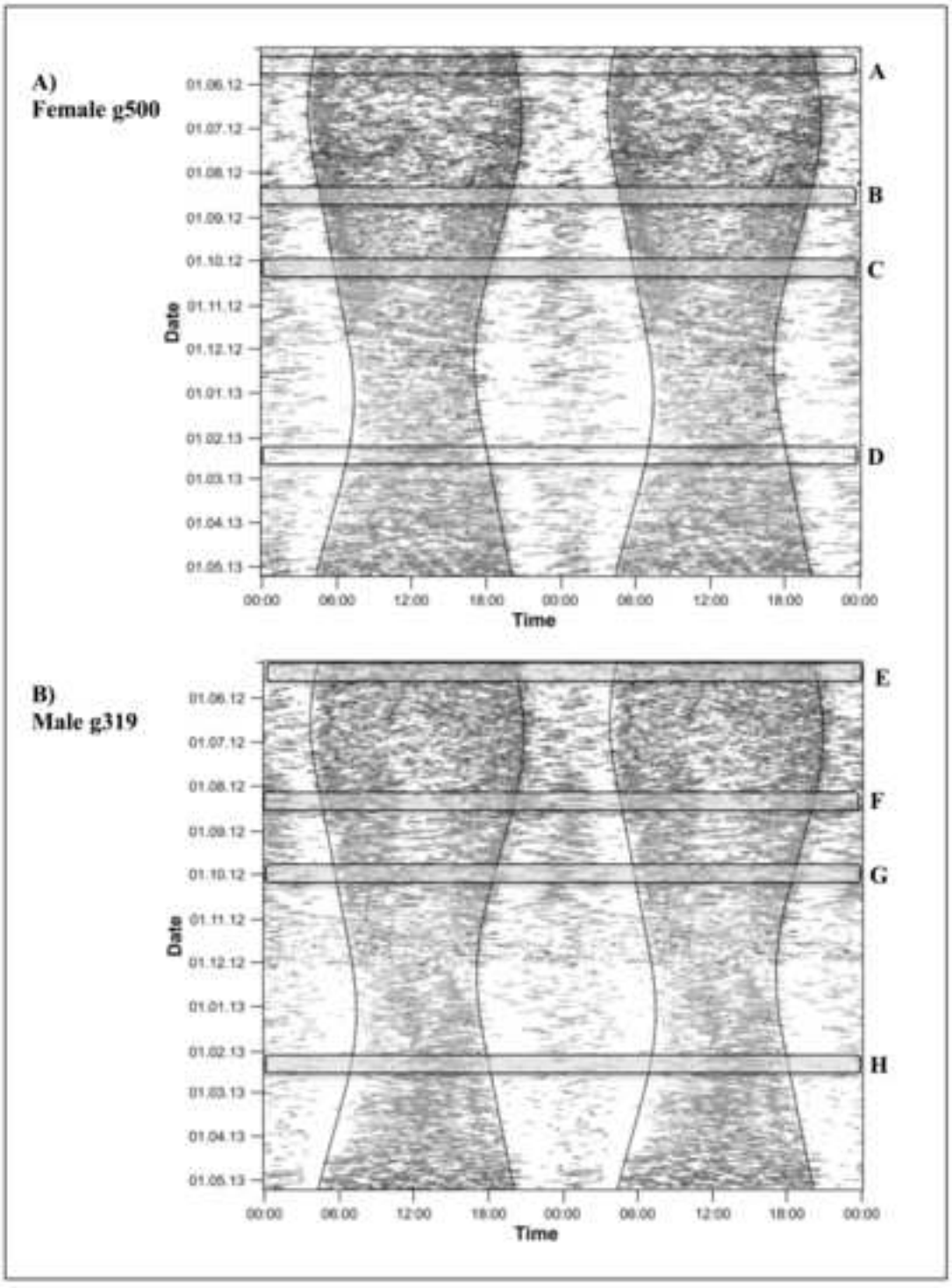

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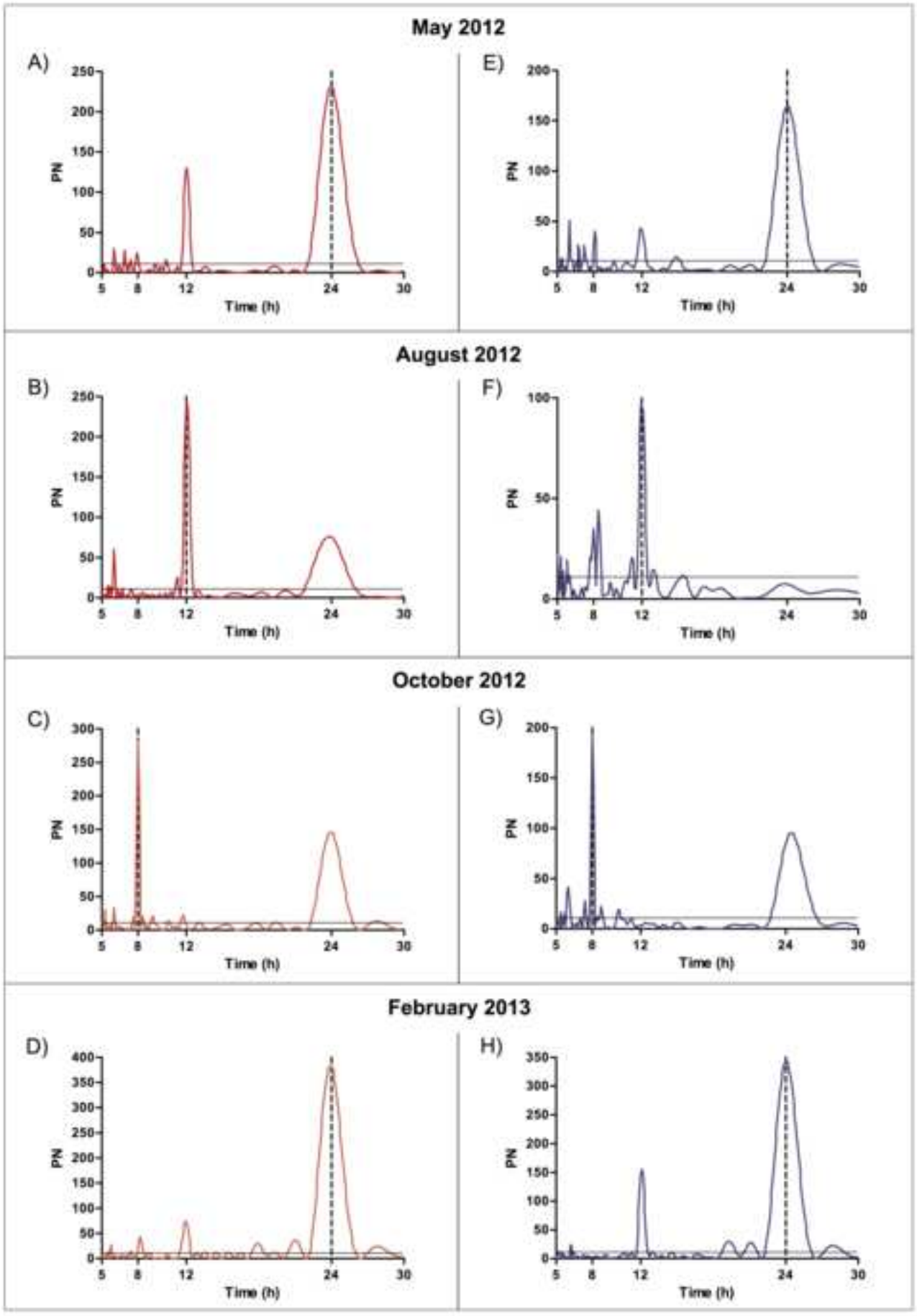

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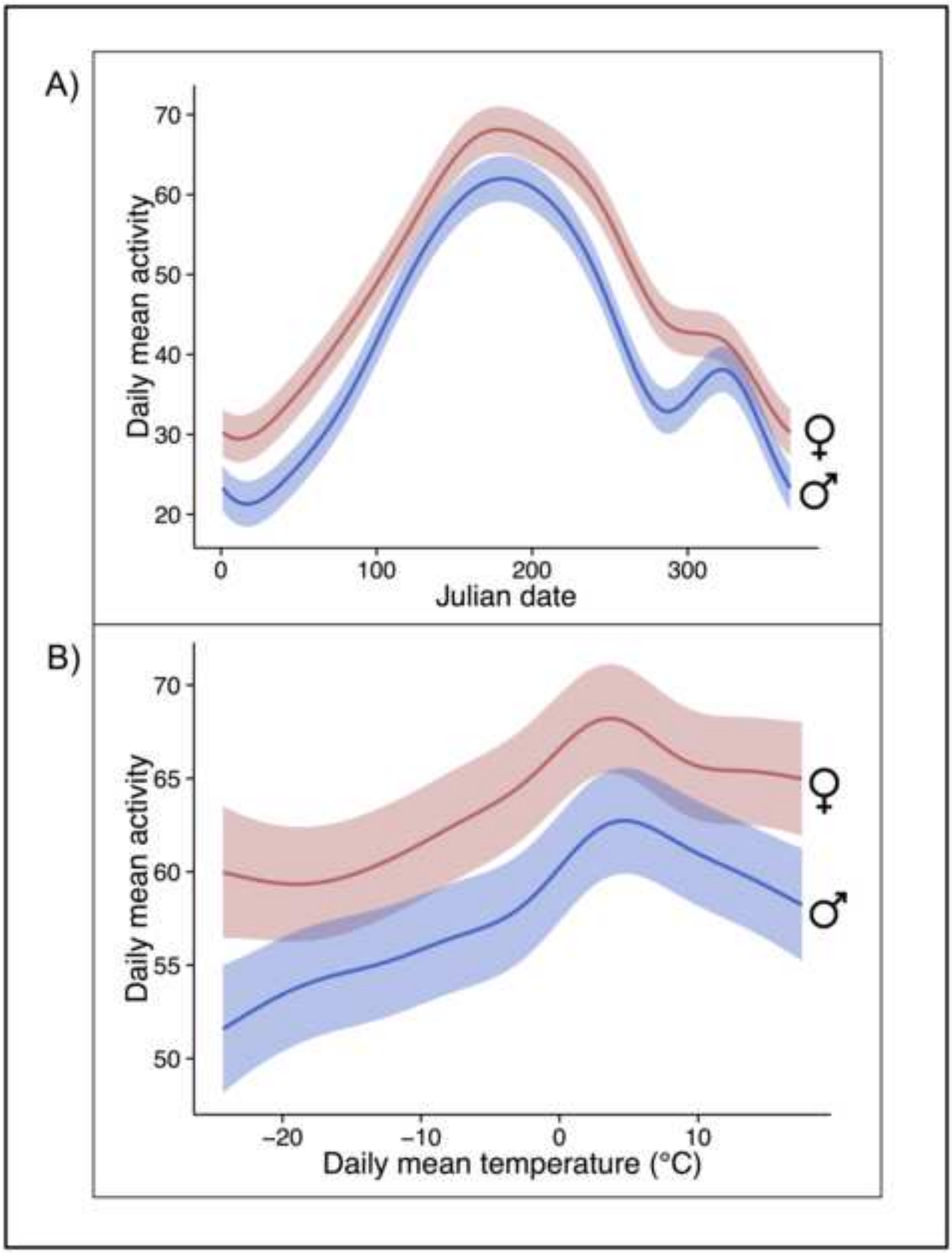

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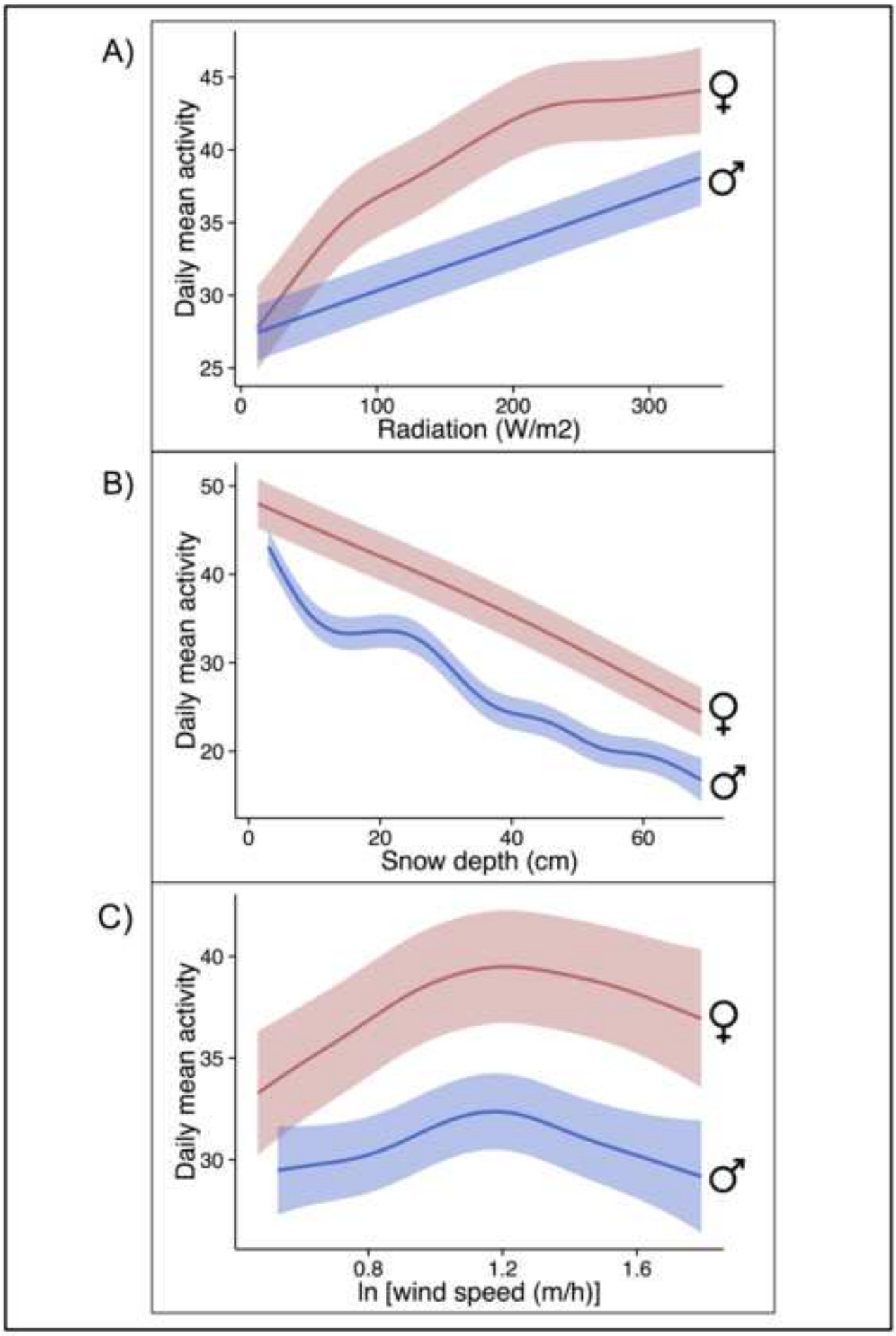

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