Too hot or too disturbed? Temperatures more than hikers affect circadian activity of females in northern chamois

ABSTRACT

Recreational activities often result in a spatial and/or temporal activity shift in wildlife because perceived as a risk. With the concurrent development of outdoors activities and increase in temperatures due to climate change, mountain species face increasing pressures in terms of managing their activity pattern to both limit risk exposure and reduce thermal discomfort. We investigated how female northern chamois (*Rupicapra rupicapra rupicapra*) adjust their summer circadian activity to spatio-temporal variations of both temperatures and hikers. Chamois behaviour was more affected by high temperatures than by hikers' disturbance. During the hottest days, they shifted their activity peak earlier in the morning (17 minutes earlier), were more active at night (+22%), less active during daytime (-10%), and had longer morning and evening peaks (+60 minutes and +20 minutes, respectively) compared to the coldest days. These behavioural adjustments led to a global activity only slightly different during the hottest (+5%) compared to coldest days. Conversely, hikers' disturbance had weak effects on activity levels and on the timing of activity peaks. This is especially true for temporal disturbance (weekdays versus weekends and public holidays), possibly due to the fact that most weekdays in summer fell during school holidays. Only during the hottest conditions, the morning activity peak was shorter (46 minutes) and the evening peak longer (18 minutes) in female living in the most exposed areas compared to females living in the least exposed areas. One possible explanation for the overall low effect of hikers' disturbance may be that behavioural changes buffering animals from high temperatures and hikers' presence (*e.g.*, moving away from trails) allow them to just

marginally modify their activity pattern. In the context of ongoing socio-environmental changes, it is critical to conserve habitats providing thermal refuges against summer heat and preventing them from disturbance to mitigate potential detrimental consequences.

KEYWORDS: behavioural thermoregulation, circadian rhythm, climate warming, ecotourism, human disturbance, mountain ecosystem, nocturnality, recreational activities, *Rupicapra rupicapra rupicapra*

INTRODUCTION

A noticeable development and diversification of outdoor activities has been ongoing in the twenty-first century, especially in Western countries (Wheaton, 2010). While mountain ecosystems have been preserved until recently because of their low accessibility, they now face an increase of unaffiliated activities such as hiking, cross country skiing, trail running, or climbing. Those recreational activities are non-lethal, but humans can be consistently perceived as predators by wildlife (Frid & Dill, 2002), leading to a suite of negative physiological and behavioural responses (Arlettaz *et al.,* 2007; Marchand *et al.,* 2014; Larson, Reed, Merenlender, & Crooks, 2016). The consequences of repeated reactions to disturbance can be detrimental on several fitness-related components (Phillips & Alldredge, 2000; French, González-Suárez, Young, Durham, & Gerber, 2011). This is particularly true in mountain ecosystems, where the diversification of human activities challenges animals all year long, both during the period of energy acquisition from spring to autumn, and of energy loss during winter (Lindstedt & Boyce, 1985). This increased pressure on the animals is accompanied by environmental modifications, including climate change, that are particularly strong in the Alps (Pepin *et al.,* 2015). Accordingly, temperatures are rising rapidly in all seasons, with consequences such as earlier springs and plant cycles, more frequent summer

50 heatwaves and droughts, and decreased duration of snow cover associated with an augmented
51 risk of frost for plants (*e.g.,* Gobiet *et al.,* 2014). Mountain animals are therefore facing
52 concomitantly two major changes, namely an increased disturbance level and climate change.
53 To reduce their exposure to human disturbance, animals can adjust their behaviour in
54 terms of movements, habitat use and selection, and time devoted to their different activities
55 (foraging, resting, vigilance and social interactions). When facing a disturbance perceived as
56 a risk, animals can modify their activities (*e.g.,* from foraging to vigilance; Benoist, Garel,
57 Cugnasse, & Blanchard, 2013; Xu, Gong, & Wang, 2021), and move away temporarily or
58 even definitively (Rogala *et al.,* 2011). They can also modify their activity pattern by
59 delaying activities, such as foraging in disturbed places, from high- to low-risk periods
60 (Bonnot *et al.,* 2013). The benefits of such responses have been explained within the "risk
61 allocation hypothesis" framework (Lima & Bednekoff, 1999): the costs of lost opportunities
62 to forage during risky periods could be dampened if animals transfer part of their diurnal
63 activity to night-time when human activities stop for instance (*e.g.,* Marchand *et al.,* 2014;
64 Bonnot *et al.,* 2020). However, activity patterns are regulated, such as the critical
65 foraging/rumination succession in ruminants (Hamel & Côté, 2008). Any forced modification
66 of those patterns can negatively impact the fitness of individuals *via* an increased encounter
67 risk with predators (Lesmerises *et al.,* 2018) or mismatches in interactions with conspecifics
68 (Greives *et al.,* 2015), for instance.
69 At the same time, animals need to deal with climatic constraints, and behavioural
70 thermoregulation is among the most important mechanisms to avoid thermal stress. Indeed,
71 temperatures influence space use (in arctic ground squirrels *Spermophilus parryii*, Long,
72 Martin, & Barnes, 2005; in Mediterranean mouflon *Ovis gmelini musimon* x *Ovis* sp.,
73 Marchand *et al.,* 2015) and activity budget (in Japanese monkeys *Macaca fuscata*, Watanuki
74 & Nakayama, 1993), with animals having to trade off foraging and thermal cover to limit

thermoregulatory costs while keeping their energy balance (van Beest & Milner, 2013). In the same way as to avoid human disturbance, animals can shift their activity peaks earlier in the morning and later in the evening, and increase their nocturnal activity during the hottest summer days (Bourgoin *et al.*, 2008; Bourgoin *et al.*, 2011). However, in temperate ecosystems, night can be significantly shorter than day during summer, and riskier when nocturnal predators are present. Thus, the transfer of the diurnal activity to night-time does not necessarily allow to fully compensate for the loss of foraging opportunities during day and may have consequences on mass gain (Garel, Loison, Gaillard, Cugnasse & Maillard, 2004) or predation risk (Gehr *et al.*, 2017), for instance. These results highlight the importance of investigating full daily cycles to get a comprehensive picture of how animals may adjust their behaviour in the face of human-induced environmental changes (Marchand *et al.,* 2014; Marchand *et al.,* 2015).

Moreover, ongoing climate change and expansion of human activities in mountain ecosystems are also ultimately connected. An extended summer season or more frequent summer heatwaves in valleys may, for instance, exacerbate human attendance in mountains. Although predicting tourism attendance under scenarios of climate change is probably not straightforward (Beniston, 2003), this context raises questions on animal responses to those interrelated human-induced environmental changes and on their potential cumulative or even multiplicative consequences for populations in terms of both immediate and compensatory responses (Schmeller *et al.*, 2022). One critical challenge is therefore to understand whether the behavioural mechanisms used by animals to buffer against increasing temperatures may also provide an advantage against human attendance or *vice versa*.

Here, we relied on the GPS monitoring of 62 females of northern chamois *Rupicapra rupicapra rupicapra* to investigate at a fine scale their behavioural responses to temporal and spatial stressors during summer, through the study of their activity pattern. More specifically,

we assessed the day-to-day variation in temperatures and hikers' attendance for each chamois. We also computed an individual-specific index of spatial disturbance, combining data on the density of hiking trails in each chamois summer home range and the attendance of each trail section by hikers. A diversity of activity metrics (*e.g.*, daily activity levels, timing of activity peaks, length of activity peaks) allowed us to investigate the relative contribution of spatio-temporal variations in both temperatures and human disturbance to changes in circadian activity patterns of female chamois in summer. We expected the chamois to adjust their circadian activity pattern by avoiding being active during the hottest hours during the hottest days (**H1**) and during the most disturbed (*i.e.,* weekends and public holidays) versus less disturbed (*i.e.,* weekdays) days (**H2**), with a compensation of activity loss during daytime at night. However, as individuals were exposed to variable levels of disturbance depending on the location of their summer home range, we also expected more marked responses in chamois that were the most exposed to hikers' disturbance (**H3**), as most of them show low tolerance to hikers' presence in this population (Courbin *et al.,* 2022).

MATERIALS AND METHODS

Study Site and Species

The study took place in the National Game and Hunting Reserve of Les Bauges massif (NGHRB), a protected area in the French Alps (45°40' N, 6°13' E; 900 to 2200 m a.s.l.; 5 200 ha). The Bauges massif is made of limestone, with cold (mean annual temperature: 9.6°C, snow cover from November to April above 1 600 m, Duparc *et al.,* 2013) and wet (mean cumulative annual rainfall: 1 600 mm, Duparc *et al.,* 2013) climatic conditions (see Supporting Information 1 for details about summer temperatures). Fifty-six percent of the area is covered by forests (treeline around 1 500 m a.s.l. in the study site), dominated by beech *Fagus sylvatica* and fir *Abies alba*, 36% by grasslands, and 8% by rocks (Lopez,

2001). This heterogeneous environment leads to a huge diversity of habitats and landscapes that attracts numerous tourists every year (> 37 000, most of them during summer; 1.1 million and 0.5 million overnight stays in summer and winter respectively in 2014, Cloud Parc des Bauges, 2014). All alpine grasslands are crossed by a network of trails where nearly all hikers are concentrated due to the NGHRB restrictions, exposing chamois to a very localised disturbance (Courbin *et al.,* 2022). Other recreational activities (*e.g.,* paragliding) occur in the study site during summer, but far less frequently than hiking.

Most adult female chamois annually give birth to one young in late May. During summer, they form groups with other females, kids and yearlings, that share and keep the same home range from year to year (Loison, Jullien, & Menaut, 1999). Females play a major role in the demography of the population, particularly through fecundity and survival of young females (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000). Chamois have no natural predators in the study area during the study period, except golden eagles *Aquila chrysaetos* and red foxes *Vulpes vulpes* that may occasionally predate newborn and injured animals. The presence of very few non-resident wolves *Canis lupus* has been noticed in some years (Loupfrance.fr, 2021). Hunting performed by small groups of three to four hunters occurs in the NGHRB from the beginning of September to the end of February (Courbin *et al.,* 2022), with chamois being the main target species (~100 chamois harvested per year on average, *i.e.,* <12% of the chamois population in the area and ~70% of the total number of ungulates harvested), in addition to Mediterranean mouflon (~20%), roe deer *Capreolus capreolus* (~4%), wild boar *Sus scrofa* (~4%) and red deer *Cervus elaphus* (~2%; see Courbin *et al.,* 2022 for details).

Data Collection

We focused on summers from 2004 to 2020, between the 15th June and the 7th September. This period allows to encompass days falling in and out from the French summer break which starts in early July, but excludes the hunting season which ranges from the first weekend of September to the end of February, so that chamois were exclusively exposed to hikers' disturbance during our study period. The study period is critical for female chamois because it follows the birth season and it is characterised by high energy requirements for lactation and storage of fat reserves for winter survival (Clutton-Brock, Albon, & Guinness, 1989; Richard, Toïgo, Appolinaire, Loison & Garel 2017), so that any disturbance during this period could be particularly detrimental.

We trapped 62 adult female chamois >2 years old during summer in four alpine grasslands near two trails highly used by hikers (Armenaz and Dent des Portes). As deployment/recovery of GPS collars occurred during summer, chamois locations were not necessarily recorded daily during all the study period. Only chamois (n = 62) for which we could reliably estimate the summer home range (95% kernel contour using the *adehabitatHR* package; Worton, 1989; Calenge, 2006) were included in the study, *i.e.,* chamois with GPS locations available during at least 2/3 of the summer period, corresponding to 56 days in total. Animal motion was recorded every 5 minutes by two perpendicular captive-balls in the GPS collars monitoring neck movements (0: no movement, 255: highly mobile) and the proportion of time the animal was head down. We discriminated each chamois as "active" (*i.e.,* feeding, standing, travelling, or doing other activities such as interactions or scratching) or "inactive" (*i.e.,* sleeping, ruminating or resting) for every 5-minutes boot using the discriminant model developed by Bourgoin *et al.* (2011; see also Darmon *et al.,* 2014). From these animals, we obtained a total of 4 464 complete days of activity records in summer (*n* = 131 chamois-year, 1 285 632 5-minutes activity measurements in total). The activity of each chamois was monitored during 18 to 129 days in total, corresponding to 11 to 49 days (*mean*

174 ± *SD = 34 ± 10 days, median [Q1; Q3] = 36 [26; 42] days*) during a single summer period
175 for a given chamois (Supporting Information 2).
176
177 *Ethical Note*
178 We trapped chamois using falling nets baited with salt licks. Although captures occurred
179 during the birth and weaning period, females generally avoided drop nets (positioned on flat
180 areas) when juveniles were particularly vulnerable (leading to the use by females of very
181 steep slopes as an anti-predator strategy). During the weaning period, chamois form nursery
182 groups and kids are not always closely associated with their mother, so that temporary
183 separation between them, longer than those resulting from capture/handling, also naturally
184 occurred in this species (Ruckstuhl & Ingold, 1998). The drop nets were triggered manually
185 by an observer located a few hundred meters away from the nets, preventing from non-target
186 captures, and chamois were handled immediately after the capture by several experienced
187 people coordinated by the Office Français de la Biodiversité. As soon as an animal was
188 handled, it was restrained with the eyes covered to reduce stress and legs attached to avoid
189 injuries. An average of three individuals were captured at the same time and this number was
190 adjusted according to the number of handlers to limit the waiting time for each chamois. All
191 efforts were made to minimise the handling time (approximately 10 to 15 minutes per
192 individual) to release animals on site as soon as possible. Juveniles and mothers were
193 released at the same time to prevent them from separation. As part of a long-term Capture-
194 Marking-Recapture monitoring, recaptures were not avoided, although unmarked individuals
195 were targeted when present. Since 2003, 916 individuals have been captured or recaptured,
196 causing 5 deaths (*i.e.,* 0.55% of the individuals handled). When necessary, slaughter was
197 done by shooting a bullet in the head or by destruction of the nervous system by percussion
198 of the cranial cavity (matador), following the ethical and legal ways recommended for large

mammals after important injuries. All captures, handling and sampling were conducted according to the appropriate national laws for animal welfare, following the ethical conditions detailed in the specific accreditations delivered by the Préfecture de Paris (prefectorial decree n°2009–014) in agreement with the French environmental code (Art. R421-15 to 421–31 and R422-92 to 422–94-1).

Females were equipped with GPS collars Lotek 3300S (Lotek Engineering Inc., Carp, Ontario, Canada). The GPS collars weighed < 450 g and were deployed only on individuals > 20 kg judged to be fully healthy so that it never exceeded 2.5% of the body mass of the equipped animal (average weight of females fitted with GPS collar = 30 kg, so 1.5% of individuals body mass on average). To allow for possible seasonal variation in neck circumference, we left a gap of ~ 3 cm between the GPS collar and the animal's neck while making sure that the collar would not rotate. We retrieved the collar using a remote drop-off system triggered manually or automatically (TRRD or TRD drop-offs, respectively; Lotek Engineering Inc., Carp, Ontario, Canada) at the end of the monitoring of the individuals, nearly one year after deployment. From repeated observations of GPS-collared individuals throughout the year as part of long-term Capture-Mark-Recapture monitoring of this population, we have no indication that GPS collars cause changes in behaviour compared to other non-equipped individuals. Similarly, we did not detect any adverse effects linked to the wearing of the collars in terms of injury or reproductive activity.

Estimation of Variables of Interest

We assessed daily characteristics (see below) from 0139 hours UTC of day *d* to 0139 hours UTC of day *d+1*. This allowed us to explore potential compensation processes during the night following the day of interest. We selected the starting hour in accordance with the median value of the beginning of the crepuscular period in the morning during our study

period. We used a micro-climate model that integrates ERA5 hourly weather data produced by the Copernicus Climate Change service at ECMWF (spatial resolution 30 km x 30 km) and a digital elevation model (30 m) for downscaling atmospheric data at the population scale (micro_era5 function in NicheMapR package; Kearney & Porter, 2017; Maclean, Mosedale, & Bennie, 2019; Kearney, Gillingham, Bramer, Duffy, & Maclean, 2020). This allowed us to overcome the issue of incomplete weather data collected in the valley by local weather station and to get standardized temperatures within the population range over the study period. Mean daily temperatures were predicted from this model at 1 m high on flat terrain for a spatial location and elevation corresponding to the centroid of all chamois GPS locations. We explored the effect of temperatures on female chamois activity through a categorical variable with two levels defined according to the quantiles of the mean daily temperatures distribution. Days with mean temperature ≤ 25% quantile (*i.e.,* 10.8°C) were considered as **cold days** and days with mean temperature > 75% quantile (*i.e.,* 15.5°C) were considered as **hot days**. Cold days experienced by chamois ranged between 3.4°C and 10.8°C (mean ± SD = 8.6 ± 1.6°C, median [Q1; Q3] = 8.9 [7.6; 10.0]°C), while hot days ranged between 15.5°C and 20.9°C (mean ± SD = 17.2 ± 1.2°C, median [Q1; Q3] = 17.1 [16.2; 18.1]°C, see also Supporting Information 1).

Temporal disturbance associated with hiking was defined as a categorical variable with two levels. Weekends and public holidays, *i.e.,* vacation days such as National Day, were considered as the most disturbed days, hereafter called **weekends and public holidays**. Days between Monday and Friday, *i.e.,* working days including weekdays during school holidays, were considered as the least disturbed days and hereafter called **weekdays**. To check for the reliability of these two categories in the field, we compared the daily attendance of hikers (number of hikers recorded on the trail) between 0000 hours UTC and 2359 hours UTC and the hour of first arrival for both temporal disturbance levels using an eco-counter

(PYRO sensor Eco-Compteur, www.eco-compteur.com; 90 cm above ground) located on Armenaz trail (45°37'18.60" N, 6°13'2.53" E) and present during two consecutive summers (2016 and 2017). Our study period encompassed 189 weekends and public holidays and 440 weekdays. During the same period of the year in 2016 and 2017, hikers were almost two times more on the trails during weekends and public holidays (*mean* ± *SD* = *74* ± *53* hikers, *median* [Q1; Q3] = 73 [39; 106] hikers) than during weekdays (*mean* = 47 ± 34 hikers, median = 40 [25; 73] hikers; Mann-Whitney: *test statistic* = 2 558, *N1* = 41, *N2* = 96, *p-value* = 0.006). Hikers also tended to arrive 60 minutes earlier during weekends and public holidays (mean ± SD = 0744 ± 120 minutes UTC, median [Q1; Q3] = 0700 [0700; 0900] hours UTC) compared to weekdays (mean ± SD = 0813 ± 180 minutes UTC, median [Q1; Q3] = 0800 [0700; 0900] hours UTC), although this difference was not statistically significant (Mann-Whitney: *test statistic* = 1 559, *N1* = 40, *N2* = 91, *p-value* = 0.188; Supporting Information 1). We also conducted a Mann-Whitney test to assess if hikers' attendance was affected by temperatures (see *Results* section).

Potential spatial exposure to hikers' disturbance was evaluated within each female chamois home range using attendance rates of the trails extracted from Strava Global Heatmap (Strava, 2022; www.strava.com, download date: 2022/03/09, data from the two previous years; see also Courbin *et al.,* 2022 for a similar approach on this study site). Strava heatmap provides a value ranging from 0 for no attendance to 255 for the highest attendance for each pixel (pixel size = 25 m x 25 m) and is a good proxy of relative human attendance (Supporting Information 3; Thorsen *et al.,* 2022; Venter, Gundersen, Scott & Barton, 2023). The lowest and highest values recorded for a trail pixel in our study site were 51 and 255 respectively. We thus defined attendance classes according to the quantiles of the [51; 255] distribution in order to cover trail pixels exclusively: 1 = [51; 119] (between 0% and 33% quantile, low attendance); 2 =]119; 187] (between 33% and 66% quantiles, intermediate

attendance); 3 =]187; 255] (between 66% and 100% quantiles, high attendance). We counted the number of trail pixels of each class in a given home range, and multiplied this number by the corresponding class value (*i.e.,* 1, 2 or 3) to give a different weight to each trail pixel according to its attendance level. We then summed these values for a given home range and normalised the total by dividing it by the home range surface to obtain our spatial disturbance index. We used the median spatial disturbance index (*i.e.,* 0.00577) as a threshold to discriminate between **most exposed chamois** and **least exposed chamois**.

As our study period ran over almost three months, day length varied widely and is known to influence chamois activity (Brivio *et al.*, 2016; Fattorini *et al.,* 2019). We accounted for this effect by including day length in our models (for a similar approach, see Semenzato *et al.*, 2021). We evaluated day length as the time elapsed between dawn and dusk using the *crepuscule* function from the *maptools* package (Bivand & Lewin-Koh, 2022; reference angle of the sun below the horizon = 6°, *i.e.,* civil dawn/dusk).

Statistical Analyses: Predicting Activity Patterns and Calculating Activity Metrics

We first modelled the daily activity of chamois as a series of values of either 0 (inactive) or 1 (active) for each 5-minutes boot using a generalised additive mixed model (GAMM) with a binomial distribution of errors (*mgcv* package, Wood, 2011; Wood, Goude, & Shaw 2015; Wood, 2017). We included three fixed effects in the model: 1) *time of the day*, *i.e.,* exact time every 5 minutes, and 2) *day length*, as well as their interaction (using the *ti* function dedicated to interactions in generalised additive models), as continuous variables with a cyclic cubic regression splines as smoothing basis for terms including *day length* exclusively; 3) a synthesis 8-levels categorical variable representing all possible combinations between temperatures classes, levels of temporal disturbance and of spatial disturbance, in interaction with the *time of the day* (using the *by* argument of the *s* function in the implementation of the

GAMM). The levels were ordered, with the reference level corresponding to a chamois living in the least exposed areas during a cold and weekdays (Supporting Information 2). The interaction between *day length* and *time of the day* allowed us to account for the fact that the activity pattern is determined by the timing of sunrise and sunset (Ashby, 1972; Cederlund, 1989), which varies widely according to the date. We defined the unique annual id-year ID of each chamois as a random effect (using the parameter "re" for the *bs* argument in the *s* function in the implementation of the GAMM) to account for inter-individual variations in circadian activity pattern (Supporting Information 4). We set the maximum number of knots for the smoothing functions to 24. We also fitted the null model, which was similar to the model described above but excluded the *temperatures-disturbance* variable, for comparison purposes. All details about model fitting are provided in Supporting Information 5.

We used the predictions of the model to investigate the effect of temperatures and hikers' disturbance on several activity metrics derived from this model (described below). We controlled for the effect of *day length* by fixing it to the median of the complete dataset (*i.e.,* 963 minutes) when predicting chamois activity for each level of the *temperatures-disturbance* combination. We derived the *total*, *diurnal*, *nocturnal* and both *morning* and *evening crepuscular activity* as the area under the activity curve (*AUC* function of the *DescTools* package; Signorell, 2023) for each level of the *temperatures-disturbance* variable. We defined daytime as the period elapsed between 120 minutes after dawn and 120 minutes before dusk, and night-time as the period elapsed between 120 minutes after dusk and 120 minutes before dawn (see Bonnot *et al.,* 2020 for a similar approach). Crepuscular periods corresponded to the remaining periods between daytime and night-time. We assessed the *timing of the morning* and *evening activity peaks* as the time when the highest activity probability occurs in the morning and the evening, respectively. We finally evaluated *morning* and *evening peak duration* as the period elapsed between the first time when the

activity probability reached 0.5 and the last time before it went underneath 0.5 for both activity peaks (for a similar approach see Bourgoin *et al.*, 2011). The percentage of variation between two situations was calculated as $100*(value_2 - value_1)/value_1$. We performed all analyses using the R software (R Core Development Team 2022, version R 4.3.0). Data is available from the Zenodo Repository: https://zenodo.org/record/8123239.

RESULTS

Model Adjustment

The full generalised additive mixed model (*AIC* = 1 578 865, *explained deviance* = 11.4%, *adjusted R2* = 0.149) was better than the null model including *time of the day* and *day length* effects and excluding the *temperatures-disturbance* variable (*AIC* = 1 591 999, *explained deviance* = 10.7%, *adjusted R2* = 0.140, Supporting Information 5) to predict activity pattern (Fig. 1). All smooth terms (fixed and random effects) were significant (*p-values* < 0.001).

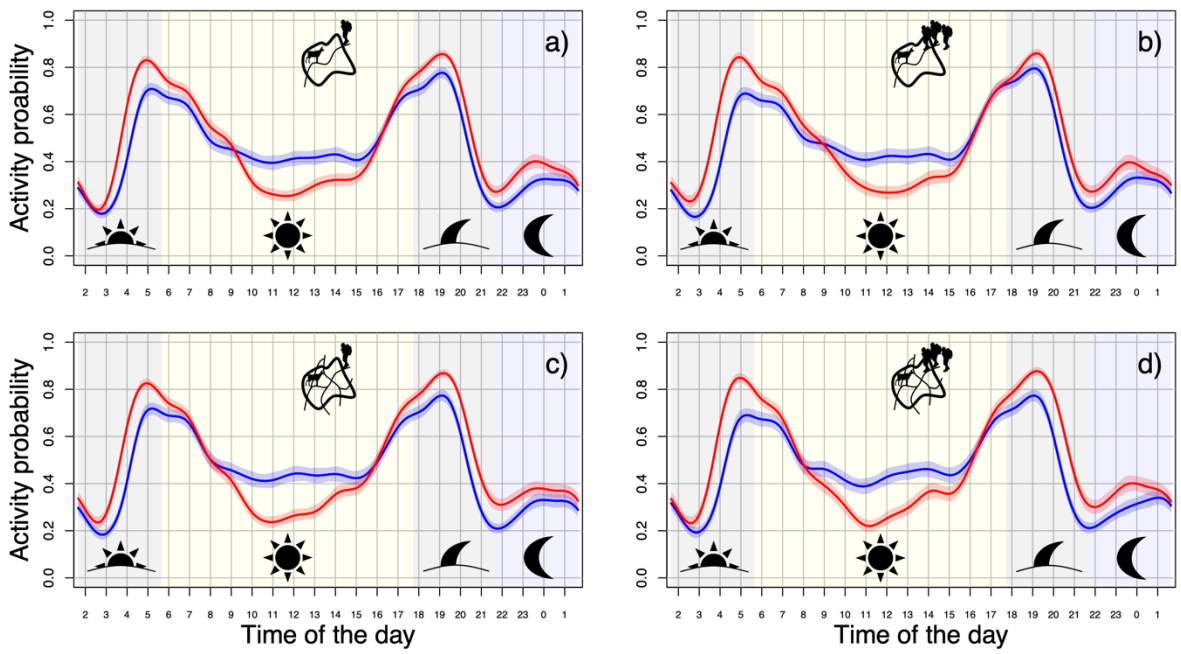

Figure 1: predicted circadian activity patterns (activity ranges between 0 for inactivity, to 1 for full-time activity) of 62 female northern chamois in the National Game and Hunting Reserve of Les Bauges massif, in summer (15th June to 7th September, 2004-2020), according to temperatures (blue: cold day; red: hot day) and human disturbance: a) chamois living in the least exposed areas during weekdays; b) chamois living in the least exposed areas during weekends and public holidays; c) chamois living in the most exposed areas during weekdays; d) chamois living in the most exposed areas during weekends and public holidays (see also pictograms directly in the figure). Solid lines represent predicted values from the model, shaded areas around the curves represent 95% confidence intervals. Background shades represent the periods used to calculate the area under the activity curve for morning and evening crepuscules (grey), daytime (yellow) and night-time (blue; see also pictograms directly in the figure). Time of the day represents hours in Coordinated Universal Time (UTC).

Temperatures

Whatever the level of spatial exposure and temporal disturbance, chamois increased their total activity during hot days compared to cold days, by 5% on average (Fig. 2). This change corresponds to an average increase of 22% in the nocturnal activity and a decrease of 10% in the diurnal activity, from cold to hot days (Fig. 2). In addition, crepuscular activity increased from cold to hot days by more than 31% in the morning and 18% in the evening on average (Fig. 2). Chamois also advanced their morning peak by 17 minutes from cold to hot days, and they only slightly delayed their evening peak by 5 minutes on average (Fig. 3). Morning and evening peaks lasted longer during hot compared to cold days of almost 60 minutes and of 20 minutes respectively, on average (Fig. 4). Chamois maintained a certain amount of activity in

the middle of the day during cold days (*i.e.,* above 40%), whereas the activity probability at the same hours was much lower and more variable during hot days (Fig. 1).

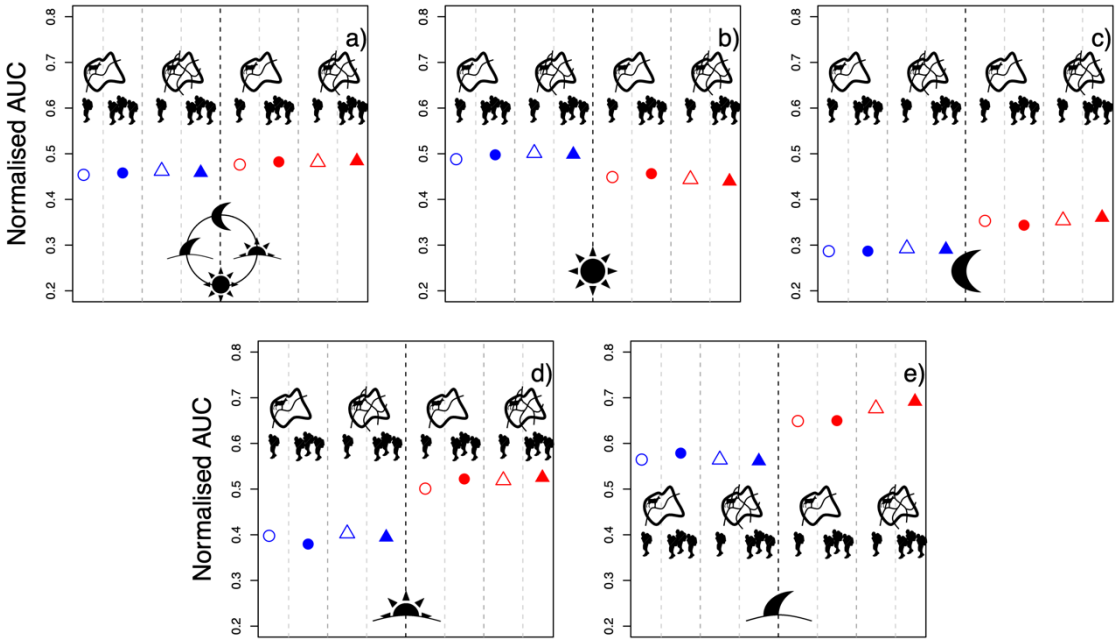

Figure 2: Area Under Curve (AUC, unitless) normalised by the duration of each period for each situation of interest, namely a combination of different levels of temperatures (blue: cold day; red: hot day), spatial (dot: low exposure; triangle: high exposure) and temporal (empty symbol: weekdays; filled symbol: weekends and public holidays; see also pictograms directly in the figure) disturbance: a) total (1 440 minutes), b) diurnal (724.8 minutes), c) nocturnal (235.2 minutes), d) morning crepuscular (240 minutes) and e) evening crepuscular (240 minutes) activity (see also pictograms directly in the figure). AUC are calculated from predicted circadian activity patterns of northern chamois of the National Game and Hunting Reserve of Les Bauges massif, in summer (15th June to 7th September, 2004-2020). We defined "diurnal" as the period elapsed between 120 minutes after dawn and 120 minutes before dusk, "nocturnal" as the period elapsed between 120 minutess after dusk and 120 minutes before dawn, and "crepuscule" as the remaining periods in the morning and in the evening (see text for details).

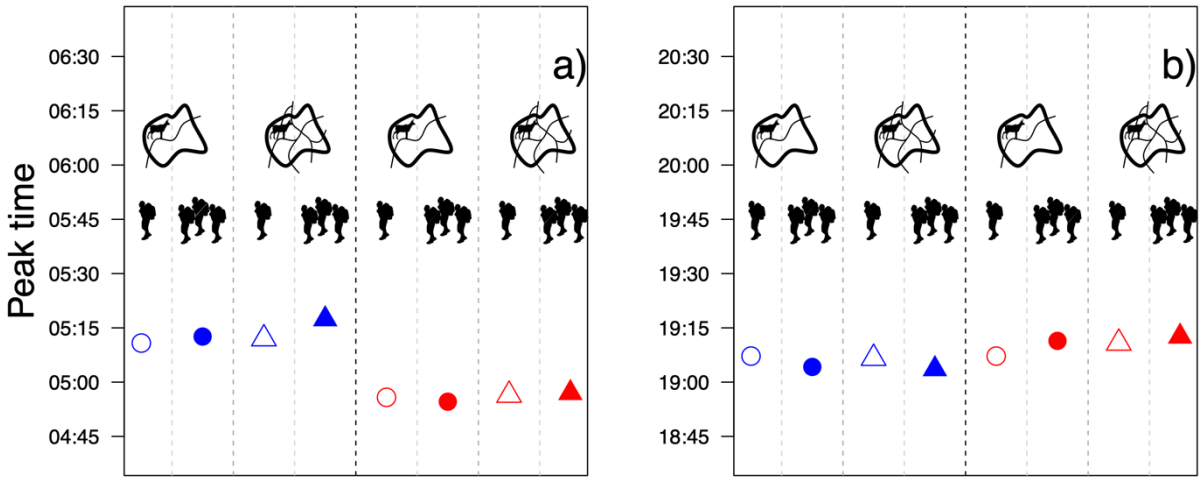

Figure 3: Timing of the Activity Peak (TAP, time of the day when the activity peaks happen, *i.e.*, the time when the highest probability of activity occurs) for each situation of interest, namely a combination of different levels of temperatures (blue: cold day; red: hot day), spatial (dot: low exposure; triangle: high exposure) and temporal (empty symbol: weekdays; filled symbol: weekends and public holidays; see also pictograms directly in the figure) disturbance: a) morning peak and b) evening peak. TAP are calculated from predicted circadian activity patterns of northern chamois of National Game and Hunting Reserve of Les Bauges massif, in summer (15th June to 7th September, 2004-2020). Note the change of interval on the y axis between figures, although the scale stays the same.

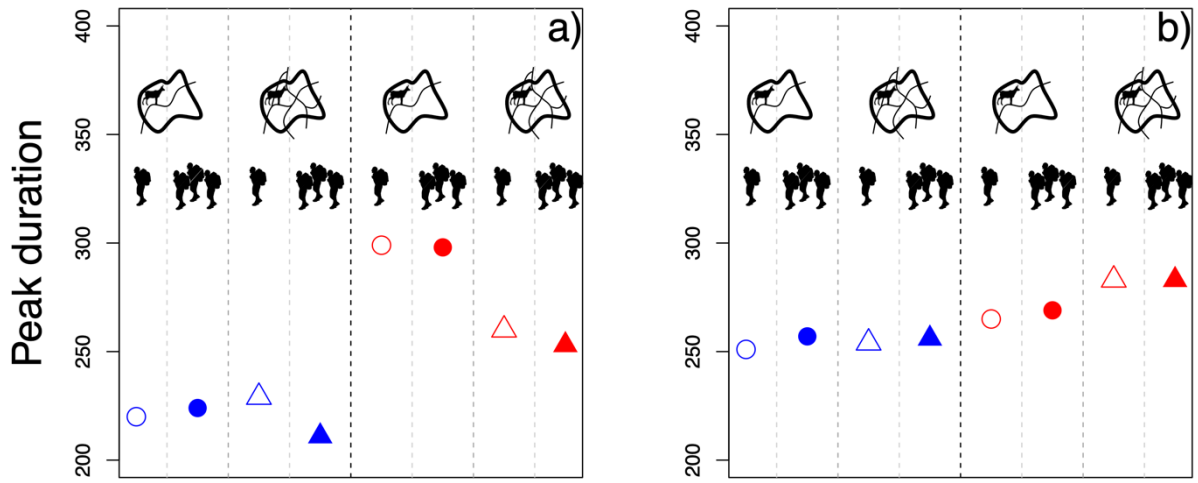

Figure 4: Peak Duration (PD, in minutes) for each situation of interest, namely a combination of different levels of temperatures (blue: cold day; red: hot day), spatial (dot: low exposure; triangle: high exposure) and temporal (empty symbol: weekdays; filled symbol: weekends and public holidays; see also pictograms directly in the figure) disturbance: a) morning and b) evening peak. PD are calculated from predicted circadian activity patterns of northern chamois of National Game and Hunting Reserve of Les Bauges massif, in summer (15th June to 7th September, 2004-2020).

Hikers' Disturbance

All the summer home ranges used by the studied chamois were crossed by at least one hiking trail. Our spatial disturbance index ranged between 0.00317 and 0.02912 (mean ± SD = 0.00699 ± 0.00433, median [Q1; Q3] = 0.00577 [0.00458; 0.00774]), with only seven chamois above 0.01000 (Supporting Information 1). In 2016 and 2017, hikers' attendance was significantly higher when temperatures were high (mean ± SD = 45 ± 56 hikers, median [Q1; Q3] = 21 [7; 63] hikers during cold days; mean ± SD = 62 ± 37 hikers, median [Q1; Q3] = 54 [31; 84] hikers during hot days; Mann-Whitney: *test statistic* = 333, *N1* = 23, *N2* = 48, *p-value* = 0.007).

Overall, the effect of temperatures was much more pronounced than the effect of disturbance and very few differences between the general activity patterns were discernible between the different levels of hikers' disturbance for a given temperature (Figs. 1 and 5). Our analyses revealed very similar amounts of total, diurnal, nocturnal and crepuscular activity whatever the level of disturbance (Fig. 2). Similarly, the changes in terms of timing of the activity peaks according to hikers' disturbance was not biologically significant (< 7 minutes, Fig. 3). Only the duration of the activity peaks during hot days (also the most disturbed days) was affected by the spatial exposure to hikers' disturbance (Fig. 4) with the

morning peak being 46 minutes shorter and the evening peak 20 minutes longer for chamois living in the most exposed areas compared to chamois living in the least exposed areas. On the contrary, temporal disturbance (*i.e.*, weekdays which are the least disturbed days versus weekends and public holidays which are the most disturbed days) had almost no effect on the length of activity peaks (Fig. 4).

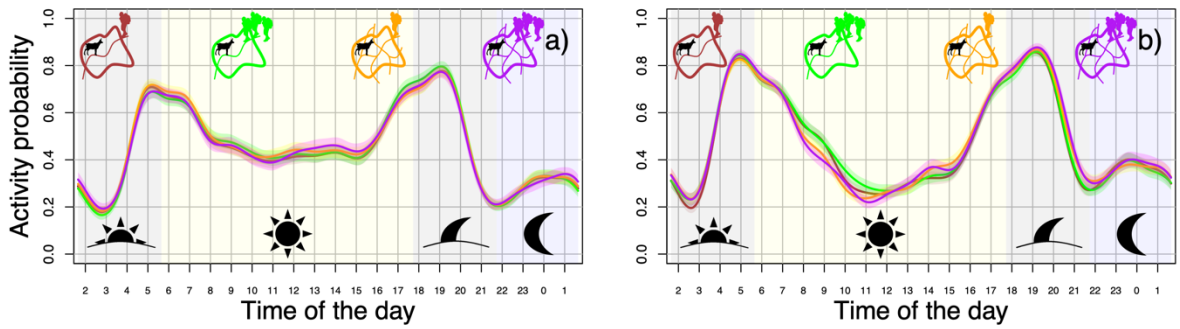

Figure 5: predicted circadian activity patterns (activity ranges between 0 for inactivity, to 1 for full-time activity) of female northern chamois in the National Game and Hunting Reserve of Les Bauges massif, in summer (15th June to 7th September, 2004-2020), according to temperatures and human disturbance: a) cold day and b) hot day. In both panels, brown represents chamois living in the least exposed areas during weekdays; green represents chamois living in the least exposed areas during weekends and public holidays; orange represents chamois living in the most exposed areas during weekdays; purple represents chamois living in the most exposed areas during weekends and public holidays (see also pictograms directly in the figure). Solid lines represent predicted values from the model, shaded areas around the curves represent 95% confidence intervals. Background shades represent the periods used to calculate the area under the curve for morning and evening crepuscules (grey), daytime (yellow) and night-time (blue; see also pictograms directly in the figure). Time of the day represents hours in Coordinated Universal Time (UTC).

438 **DISCUSSION**

439 Our objective was to determine and compare the relative contribution of summer
440 temperatures and hikers' disturbance on the activity pattern of females of a mountain
441 ungulate, the northern chamois. During hot days, chamois adjusted their circadian activity by
442 shifting their activity peak earlier in the morning and by increasing its duration. As expected
443 during hot days, they also increased their nocturnal and crepuscular activity while being less
444 active during the hottest hours of daytime. These behavioural adjustments allowed females to
445 maintain a similar level of total daily activity between cold and hot days. On the other hand,
446 and contrary to our expectations, chamois only rarely adjust their activity pattern according to
447 hikers' disturbance. Only during hot days (also the most disturbed days), we observed a
448 decrease in the duration of the morning activity peak and a slight increase in the duration of
449 the evening activity peak for chamois living in the most exposed areas compared to chamois
450 living in the least exposed areas, as well as a tenuous increase in the nocturnal and
451 crepuscular activity at the expense of the diurnal activity. Temporal disturbance (*i.e.*,
452 weekends and public holidays *versus* weekdays) had almost no effect on chamois activity
453 peaks.

454 Though chamois seem to be less sensitive to high temperatures than other alpine
455 ungulate species (see Darmon *et al.,* 2014 for a comparison between chamois and mouflon;
456 see also Semenzato *et al.* 2021 for Alpine ibex), their faecal glucocorticoid metabolites
457 concentration increases during drought conditions in summer (Anderwald, Campell Andri, &
458 Palme 2021), as well as the time they spend in thermal refuges during hot days (Malagnino,
459 2022). This may explain that chamois responded much more strongly to temperatures than to
460 hikers' disturbance. Moreover, in our study site, hikers' attendance was significantly higher
461 when temperatures were high. Hence, the behavioural changes to buffer from high
462 temperatures may also protect chamois from hikers' disturbance, as both factors were related.

463 Animals have to face several stressors (*e.g.,* human disturbance, predation, high
464 temperatures) and they eventually cannot indefinitely adjust their behavioural response as
465 stressors accumulate (Benoist, Garel, Cugnasse, & Blanchard, 2013). Moreover, most of the
466 response to human disturbance in our population seems to happen at the spatial level rather
467 than the temporal level (Fig. 4a) and only during the hot days (when hiker's attendance was
468 at its highest level), causing a marked decline in the duration of the morning activity peak in
469 chamois living in the most versus least exposed areas.

470 Recent studies provided evidence of a non-negligeable nocturnal activity peak in
471 chamois (Carnevali, Lovari, Monaco, & Mori, 2016). Here, we also highlighted that
472 nocturnal activity significantly increased while diurnal activity decreased during hot days,
473 confirming the influence of high temperatures on chamois activity. As in numerous other
474 species, chamois decreased their diurnal activity when exposed to high temperatures and/or
475 human disturbance and attempted to compensate for the activity loss when they are absent
476 (*e.g.,* later in the day or at night, Gaynor, Hojnowski, Carter, & Brashares, 2018). However,
477 an increase in nocturnal activity could expose individuals to other threats, such as nocturnal
478 predators (Bonnot *et al.,* 2020). This is particularly true in our study site with the progressive
479 return of wolves recorded since 2020. Large herbivores may face the difficult challenge of
480 avoiding being exposed to high temperatures while limiting their exposure to human
481 disturbance, but without shifting completely their activity at night because of predation risk.
482 The shift to more crepuscular activity observed in this study could be an answer to this trade-
483 off.

484 Interestingly and in contrast with Brivio *et al.* (2016) and Grignolio *et al.* (2018) in
485 another chamois population, total activity was slightly higher (+5%) during hot than cold
486 days in our chamois population. Such a finding is not necessarily surprising as other studies
487 have found similar results (in the same population, Malagnino, 2022; in Alpine ibex

maintaining a constant activity both during cold and hot days, Semenzato *et al.*, 2021). In addition, this does not necessarily translate into an increase in feeding behaviour, but might be because chamois display diel migrations between refuges and feeding spots (Courbin *et al.,* 2022), particularly if both habitats are distant or heterogeneous. With the increasing temperatures in summer, chamois could be forced to commute more frequently or move further to find shelter from the heat while maintaining the same level of feeding activity, eventually leading to the overall increase observed. Unfortunately, our data provides no clue about the nature of the behaviours displayed (*i.e.,* foraging, moving or social behaviours) and we cannot ascertain if this rise of activity effectively corresponds to spatial displacement.

We observed only minor differences between the most and least disturbed chamois, either because chamois respond similarly to human presence regardless of the encounter risk because hikers are present almost every day even if at different level (especially during summer with summer school break), or because they shift their activity in habitats further away from the main source of disturbance, *i.e.,* the trails (Courbin *et al.* 2022). In our population, 85% of the individuals move temporarily away from trails every day when hikers are present (Courbin *et al.,* 2022), demonstrating that even the less exposed chamois adjust their behaviour to human disturbance. This low tolerance affects the whole population and not just the most exposed individuals and might explain the weak difference observed between groups.

Mountain animals face both rising temperatures from ongoing climate warming, and modifications in their exposure to actual and perceived risks from the development of recreational activities and the return of predators in these landscapes. The interaction between those factors could eventually jeopardise their demography if particular attention is not paid in conserving habitats providing both refuge against summer heat and human disturbance (Frid & Dill, 2002; Chirichella, Stephens, Mason, & Apollonio, 2021). Moreover, both

constraints can lead either to similar responses (*e.g.,* rest in refuge areas), or to opposite reactions (*e.g.,* reduce activity to avoid thermal stress, increase movement to reach thermal refuges or escape to limit predation risk), which complicates our understanding of their behavioural response. Here we highlight a strong effect of temperatures but low effects of hikers' disturbance on the activity pattern of northern female chamois. Identifying the effect of human disturbance on wildlife remains a difficult task, particularly at the population scale (Tablado & Jenni, 2017), and an integrated approach is needed to consider all forms of response, such as variations in activity level and timing, behavioural budgets and spatial displacements.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo Repository: https://zenodo.org/record/8123239.

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