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

Thel Lucie[1,2], Garel Mathieu[3], Marchand Pascal[4], Bourgoin Gilles[5,6], Loison Anne[1]

Authors details

[1] Laboratoire d'Écologie Alpine, UMR 5553 (CNRS, Université Savoie Mont--Blanc), Savoie Technolac, 73376 Le Bourget-du-Lac, France.

[2] Laboratoire Évolution et Diversité Biologique, UMR 5174 (CNRS, Université Paul Sabatier), 118 route de Narbonne, 31062 Toulouse, France.

[3] Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique, Service Anthropisation et Fonctionnement des Écosystèmes Terrestres, Gières, France.

[4] Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique, Service Anthropisation et Fonctionnement des Écosystèmes Terrestres, Juvignac, France.

[5] Univ Lyon, VetAgro Sup, Campus Vétérinaire de Lyon, 1 avenue Bourgelat, F-69280 Marcy l'Etoile, France.

[6] Univ Lyon, Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie Évolutive (LBBE), F-69622 Villeurbanne Cedex, France.

Correspondence author: Thel Lucie, lucie.mc.thel@gmail.com.

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Abstract

Though non-lethal, recreational activities often result in a spatial and/or temporal shift of activity in a large range of species because they are perceived as a risk. With the concurrent development of outdoors activities and the increase of temperatures due to climate change in mountainous ecosystems, mountain species face an increasing pressure in terms of managing their activity pattern to both limit risk exposure and reduce thermal discomfort. In this context, we investigated how female northern chamois adjust their summer circadian activity to spatio-temporal variations of both temperature and hikers' disturbance. Chamois behaviour was more affected by high temperatures than by hikers' disturbance. During the hottest days (*median* ± *SD* = 17.1±1.2°C *vs.* 8.8±1.7°C during the coldest days), they shifted their activity peak earlier in the morning (- 17 minutes), and were more active at night (+ 22%) than during daytime (- 10%). Their global daily activity was slightly higher during the hottest days than during the coldest days (+ 5%). Conversely, hikers' spatial and temporal disturbance had only weak effects on activity of chamois, most likely due to a temporal mismatch with hikers, except during the hottest conditions, when the duration of the morning activity peak decreased (- 46 minutes) and the duration of the evening peak increased (+ 18 minutes) with the highest compared to the lowest disturbance. The overall low effect of hikers' disturbance on chamois activity pattern suggested that behavioural changes buffering animals from high temperature (relocation into thermal refuges) and from hikers' presence (moving away from trails) allow them to just marginally modify their activity pattern in the presence of hikers. In the context of ongoing socio-environmental changes, these findings stress the importance of

conserving habitats providing thermal refuges against summer heat and preventing them from human disturbance to mitigate their 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 heatwaves and droughts, and decreased duration of snow cover associated with an augmented

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

125 million and 0.5 million overnight stays in summer and winter respectively in 2014, Cloud
126 Parc des Bauges, 2014). All alpine grasslands are crossed by a network of trails where nearly
127 all hikers are concentrated due to the NGHRB restrictions, exposing chamois to a very
128 localised disturbance (Courbin *et al.,* 2022). Other recreational activities (*e.g.,* paragliding)
129 occur in the study site during summer, but far less frequently than hiking.

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

145

146 *Data collection*

147 We focused on summers from 2004 to 2020, between the 15th of June and the 7th of
148 September. This period allows to encompass days falling in and out from the French summer
149 holidays 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. 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 using falling nets baited with salt licks located in four alpine grasslands near two trails highly used by hikers (Armenaz and Dent des Portes). Although captures occurred during the birth and weaning period, females generally avoided drop nets (positioned on flat areas) when juveniles were particularly vulnerable (leading to the use by females of very steep slopes as an anti-predator strategy). During the weaning period, chamois form nursery groups and kids are not always closely associated with their mother, so that temporary separation between them, longer than those resulting from capture/handling, also naturally occurred in this species (Ruckstuhl & Ingold, 1998). The drop nets were triggered manually by an observer located a few dozen meters from the nets, preventing non-target captures, and chamois were processed immediately after the capture by several experienced animal handlers coordinated by the Office Français de la Biodiversité. As soon as an animal was handled, it was restrained with the eyes covered to reduce stress and legs attached to avoid injuries. An average of three individuals were captured at the same time and this number was adjusted according to the number of handlers to limit the waiting time for each chamois. All efforts were made to minimise the handling time (approximately 10 to 15 minutes per individual) to release animals on site as soon as possible. Juveniles and mothers were released at the same time to prevent them from separation. As part of a long-term Capture-Marking-Recapture monitoring, recaptures were not avoided, although unmarked individuals were targeted when

present. Since 2003, 916 individuals have been (re)captured, causing 5 deaths (*i.e.,* 0.55% of the individuals handled, generally euthanised using recommended ethical/legal ways 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 used 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). 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 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.

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 locations available during at least 2/3 of their monitoring 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 (*median* = 36, *SD* = 10) during a single summer period for a given chamois (Supporting Information 2).

We assessed daily characteristics (see below) from 01:39 UTC of day d to 01:39 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 north-facing terrain for a spatial location and elevation corresponding to the centroid of all chamois GPS locations. We explored the effect of temperature on female chamois activity through a categorical

variable with two levels defined according to the quantiles of the mean daily temperature 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 (*median* = 8.9°C, *SD* = 1.6°C), while hot days ranged between 15.5°C and 20.9°C (*median* = 17.1°C, *SD* = 1.2°C, see also Supporting Information 1).

Temporal disturbance associated with hiking practice was defined as a categorical variable with two levels. Weekends and public holidays, *i.e.,* vacation days such as Ascension Day, were considered as **highly disturbed days**. Days between Monday and Friday, *i.e.,* working days including weekdays during school holidays, were considered as **weakly disturbed days**. 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 00:00 UTC and 23:59 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), on a subset of the study period (2016 and 2017 summers). Our study period encompassed 189 theoretically highly disturbed days and 440 weakly disturbed days. During the same period of the year in 2016 and 2017, hikers were almost two times more on the trails during highly (*median* = 73 hikers, *SD* = 53 hikers) than during weakly (*median*= 40 hikers, *SD* = 34 hikers) disturbed days (*Mann-Whitney test statistic* = 2,558, *p-value* = 0.006). Hikers also tended to arrive one hour earlier during highly (*median* = 07:00 UTC, *SD* = 2 hours) compared to weakly (*median* = 08:00 UTC, *SD* = 3 hours) disturbed days although this difference was not statistically significant (*Mann-Whitney test statistic* = 1,559, *p-value* = 0.188; Supporting Information 1).

Potential spatial exposure to hikers' disturbance was evaluated within each female chamois home range using frequentation 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 frequentation (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 frequentation 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 frequentation); 2 =]119; 187] (between 33% and 66% quantiles, intermediate frequentation); 3 =]187; 255] (between 66% and 100% quantiles, high frequentation). 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 frequentation 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 **highly exposed chamois** and **weakly 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). Similarly to Semenzato *et al.* 2021, we accounted for this effect by including day length in our models. 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 temperature 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 a weakly exposed area during a cold and weakly disturbed day. 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 on 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 *temperature-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 temperature 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 *temperature-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 *temperature-disturbance* variable. We defined daytime as the period elapsed between two hours after dawn and two hours before dusk, and night-time as the period elapsed between two hours after dusk and two hours 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 *temperature-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).

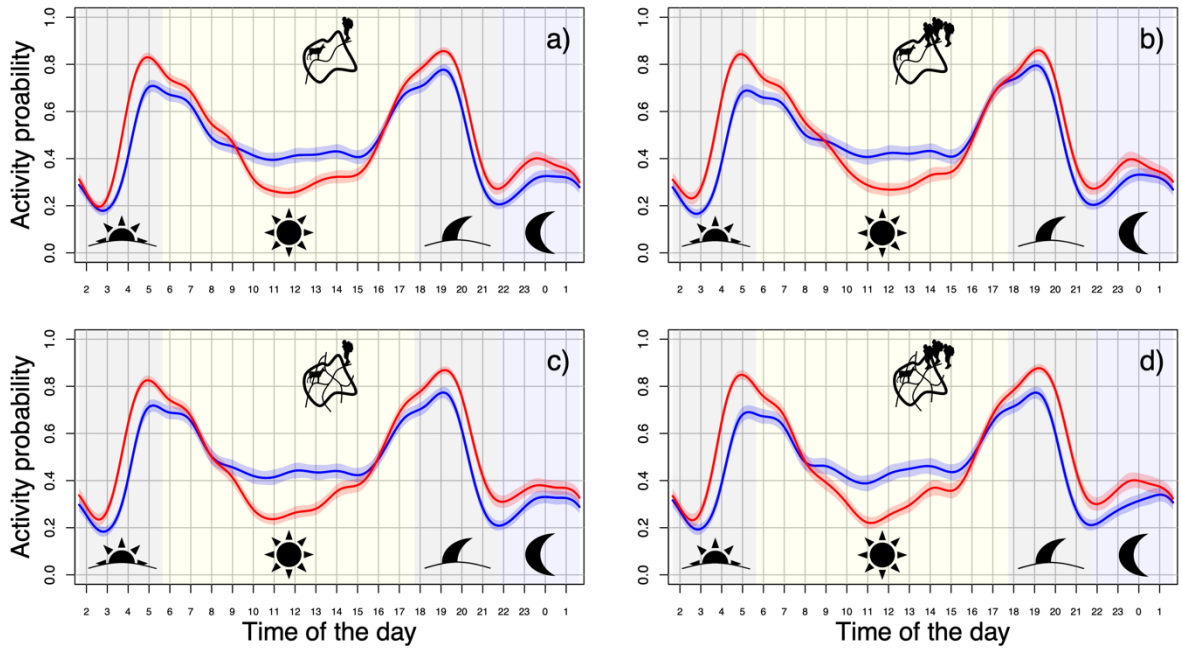

Figure 1: predicted circadian activity patterns (activity ranges between 0 for inactivity, to 1 for active) of 62 female northern chamois in the National Game and Hunting Reserve of Les Bauges massif, in summer (15th June to 7th September, 2004-2020), according to temperature (blue: cold day; red: hot day) and human disturbance: a) chamois living in a weakly exposed area during a weakly disturbed day; b) chamois living in a weakly exposed area during a highly disturbed day; c) chamois living in a highly exposed area during a weakly disturbed day; d) chamois living in a highly exposed area during a highly disturbed day (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).

Temperature

Whatever the level of spatial exposure and temporal disturbance, chamois increased their total activity during hot days compared to cold days of 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 was 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 (Fig. 3). Morning and evening peaks lasted longer during hot compared to cold days of almost 1 hour and of 20 minutes respectively (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 lower and more variable during hot days (Fig. 1).

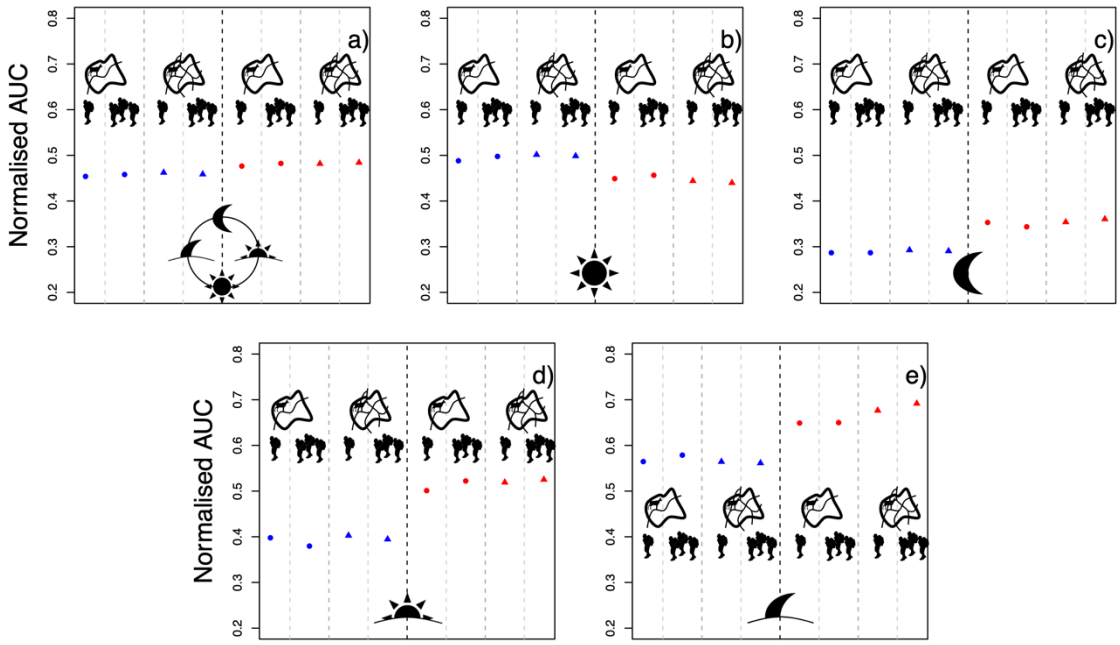

Figure 2: Area Under Curve (AUC, unitless) normalised by the duration of each period for each situation of interest, namely a combination of different levels of temperature (blue: cold day; red: hot day), spatial (dot: low exposure; triangle: high exposure) and temporal (low: week days; high: weekends; see also pictograms directly in the figure) disturbance: a) total

(24 hours), b) diurnal (12.08 hours), c) nocturnal (3.92 hours), d) morning crepuscular (4 hours) and e) evening crepuscular (4 hours) 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 (June to September, 2004-2020). We defined "diurnal" as the period elapsed between two hours after dawn and two hours before dusk, "nocturnal" as the period elapsed between two hours after dusk and two hours before dawn, and "crepuscule" as the remaining periods in the morning and in the evening (see text for details).

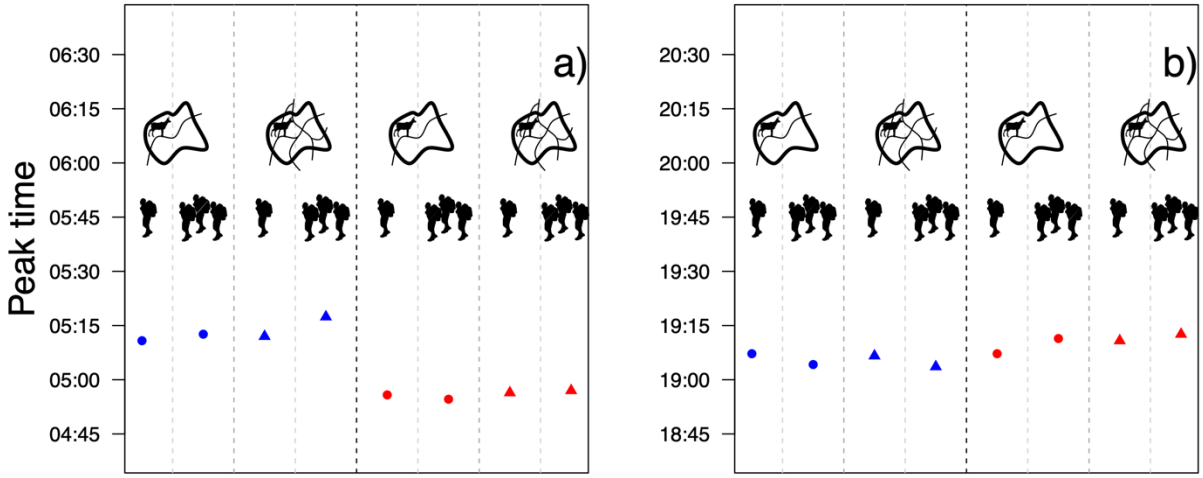

Figure 3: Timing of the Activity Peak (APT, time of the day when the activity peaks happen, *i.e.*, the time when the highest probability of activity occurs) for each situation of interest, namely a combination of different levels of temperature (blue: cold day; red: hot day), spatial (dot: low exposure; triangle: high exposure) and temporal (low: week days; high: weekends; see also pictograms directly in the figure) disturbance: a) morning peak and b) evening peak. APT are calculated from predicted circadian activity patterns of northern chamois of National Game and Hunting Reserve of Les Bauges massif, in summer (June to September, 2004-

2020). Note the change of interval on the y axis between figures, although the scale stays the same.

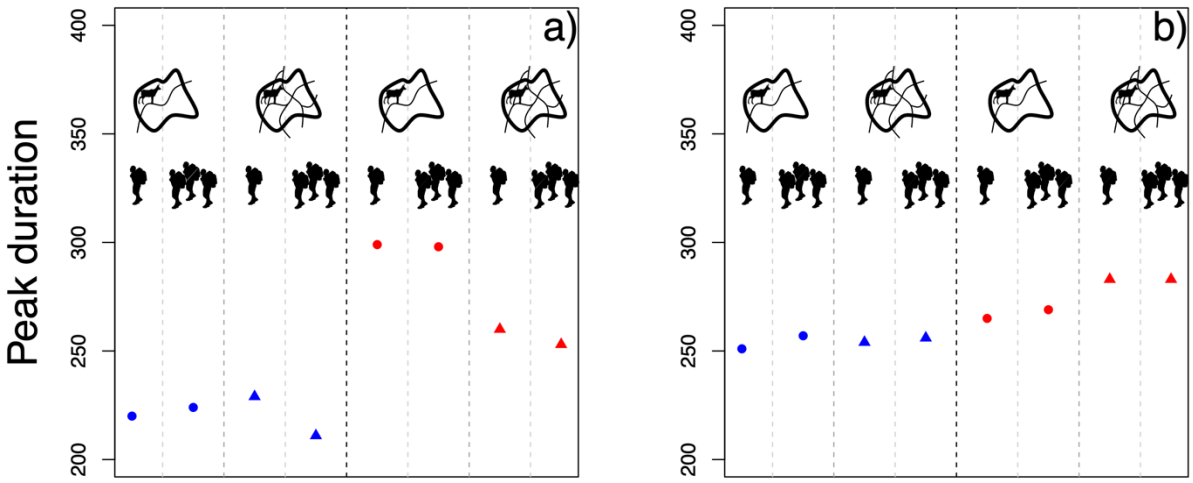

Figure 4: Peak Duration (PD, in minutes) for each situation of interest, namely a combination of different levels of temperature (blue: cold day; red: hot day), spatial (dot: low exposure; triangle: high exposure) and temporal (low: week days; high: weekends; see also pictograms directly in the figure) 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 (June to 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 (*median* = 0.00577, *SD* = 0.00433), with only seven chamois above 0.01000 (Supporting Information 1). Overall, the effect of temperature was much more pronounced than the effect of disturbance and very little difference between the general activity patterns was discernible between the different levels of hikers' disturbance for a given temperature (Figs. 1 and 5). This translated by 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). However, the duration of the activity peaks during hot days seemed to be affected by the level of hikers' disturbance (Fig. 4). Indeed, the morning activity peak decreased by 46 minutes from chamois living in a weakly disturbed area during weakly disturbed days to chamois living in a highly disturbed area during highly disturbed days. The evening activity peak increased by almost 20 minutes for the same groups.

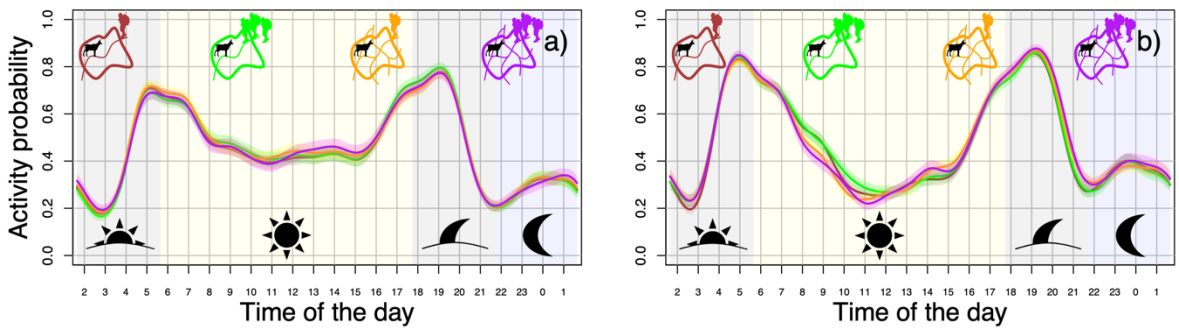

Figure 5: predicted circadian activity patterns (activity ranges between 0 for inactivity, to 1 for active) of female northern chamois in the National Game and Hunting Reserve of Les Bauges massif, in summer (15th June to 7th September, 2004-2020), according to temperature and human disturbance: a) cold day and b) hot day. In both panels, brown represents chamois living in a weakly exposed area during a weakly disturbed day; green represents chamois living in a weakly exposed area during a highly disturbed day; orange represents chamois living in a highly exposed area during a weakly disturbed day; purple represents chamois living in a highly exposed area during a highly disturbed day (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).

Discussion

Our objective was to determine and compare the relative contribution of summer temperatures and hikers' disturbance on the activity pattern of females of a wild ungulate, the northern chamois. During hot days, chamois adjusted their circadian activity by shifting their activity peak earlier in the morning and by increasing its duration. During hot days, they also increased their nocturnal and crepuscular activity while being less active during the hottest hours of daytime (in agreement with **H1** stating that chamois should adjust their circadian activity pattern by avoiding being active during the hottest hours during the hottest days, with a compensation of activity loss during daytime). Surprisingly, their total daily activity was higher during hot than cold days. On the other hand, chamois only seldomly adjust their activity pattern according to hikers' disturbance, disproving **H2** stating that chamois should adjust their circadian activity pattern by avoiding being active during the most disturbed days. Nevertheless, during hot days, we observed a decrease in the duration of the morning activity peak and a slight increase in the duration of the evening activity peak from the less exposed chamois to the most exposed chamois, as well as a tenuous increase in the nocturnal and crepuscular activity at the expense of the diurnal activity. Hikers' disturbance had very little effect on chamois activity peaks. These results provide only a partial support for **H3** stating that the chamois the most exposed to hikers' disturbance should have a more marked response.

Though chamois seem to be less sensitive to high temperatures than other alpine ungulate species (see Darmon *et al.,* 2014 for a comparison between chamois and mouflon; see also Semenzato *et al.* 2021 for Alpine ibex), their faecal glucocorticoid metabolites

concentration increases during drought conditions in summer (Anderwald, Campell Andri, & Palme 2021), as well as the time they spend in thermal refuges during hot days (Loison *et al.*, 2022). This may explain that chamois responded much more strongly to temperature than to hikers' disturbance. Moreover, in our study site, hikers' attendance was significantly higher when temperature was high (*median* = 21, *SD* = 56 hikers during cold days; *median* = 54, *SD* = 37 hikers during hot days; *Mann-Whitney test statistic* = 333, *p-value* = 0.007). Hence, the behavioural changes to buffer from high temperatures may also protect chamois from hikers' disturbance, as both factors are correlated. Animals have to face several sources of disturbance (*e.g.,* human disturbance, predation, high temperatures) and they eventually cannot indefinitely adjust their behavioural response as disturbance factors accumulate (Benoist, Garel, Cugnasse, & Blanchard, 2013). Such a limitation seems to appear in our population when chamois highly exposed to disturbance experience high hikers' frequentation during hot days. Instead of maintaining a longer morning activity peak to compensate for the loss of diurnal activity due to the heat, they reduce it likely because of hikers already present on the trails (mainly between 08:00 UTC and 15:00 UTC, Supporting Information 1).

Recent studies provided evidence of a non-negligeable nocturnal activity peak in chamois (Carnevali, Lovari, Monaco, & Mori, 2016). Here, we also highlighted that nocturnal activity significantly increased while diurnal activity decreased during hot days, confirming the influence of high temperatures and human disturbance on chamois activity. Similarly to numerous other species, chamois decreased their diurnal activity when exposed to high temperatures and/or human disturbance and attempted to compensate for the activity loss when it is absent (*e.g.,* later in the day or at night, Gaynor, Hojnowski, Carter, & Brashares, 2018). However, an increase in nocturnal activity could expose individuals to other threats, such as nocturnal predators (Bonnot *et al.,* 2020). This is particularly true in our

463 study site with the progressive return of wolves recorded since the recent years. Large
464 herbivores may face the difficult challenge of avoiding being exposed to high temperature
465 while limiting their exposure to human disturbance, but without shifting completely their
466 activity at night because of predation risk. The shift to more crepuscular activity observed in
467 this study could be an answer to this necessary trade-off.

468 Interestingly and in contrast with Brivio *et al.*, (2016) and Grignolio *et al.*, (2018) in
469 another chamois population, total activity was higher during hot than cold days in our
470 chamois population. Such a finding is not necessarily surprising as other studies have found
471 similar results (in the same population; Loison *et al.*, 2022; in Alpine ibex maintaining a
472 constant activity both during cold and hot days, Semenzato *et al.*, 2021). In addition, this does
473 not necessarily translate into an increase in feeding behaviour, but might be because chamois
474 display diel migrations between refuges and feeding spots (Courbin *et al.,* 2022), particularly
475 if both habitats are distant or heterogeneous. With the increasing temperatures in summer,
476 chamois could be forced to commute more frequently or move further to find shelter from the
477 heat while maintaining the same level of feeding activity, eventually leading to the overall
478 increase observed. Unfortunately, our data provides no clue about the nature of the
479 behaviours displayed (*i.e.,* foraging, moving or social behaviours) and we cannot ascertain if
480 this rise of activity effectively corresponds to spatial displacement.

481 We observed only minor differences between the most and least disturbed chamois,
482 either because chamois respond similarly to human presence regardless of the encounter risk,
483 because hikers are present almost every day, or because they shift their activity in habitats
484 further away from the main source of disturbance, *i.e.,* the trails. Conversely, Samia,
485 Nakagawa, Nomura, Rangel, & Blumstein (2015) showed that weakly exposed populations
486 can be less tolerant to human disturbance because they are less used to it. In our population,
487 85% of the individuals move temporarily away from trails every day when hikers are present

488 (Courbin *et al.,* 2022), demonstrating that even the less exposed chamois adjust their
489 behaviour to human disturbance. This low tolerance affects the whole population and not just
490 the most exposed individuals and might explain the weak difference observed between
491 groups.

492 Mountain animals face both rising temperatures from ongoing climate warming, and
493 modifications in their exposure to actual and perceived risks from the development of
494 recreational activities and the return of predators in these landscapes. The interaction between
495 those factors could eventually jeopardise their demography if particular attention is not paid
496 in conserving habitats providing both refuge against summer heat and human disturbance
497 (Frid & Dill, 2002; Chirichella, Stephens, Mason, & Apollonio, 2021). Moreover, both
498 constraints can lead either to similar responses (*e.g.,* rest in refuge areas), or to opposite
499 reactions (*e.g.,* reduce activity to avoid thermal stress or escape to limit predation risk), which
500 complicates our understanding of their behavioural response. Here we highlight a strong
501 effect of temperature but almost no effect of hikers' disturbance on the activity pattern of
502 northern female chamois. Identifying the effect of human disturbance on wildlife remains a
503 difficult task, particularly at the population scale (Tablado & Jenni, 2017), and an integrated
504 approach is needed to consider all forms of response, such as variations in activity level and
505 timing, behavioural budgets and spatial displacements. Our study contributes to filling the
506 knowledge gap on the cumulative effects of weather and human disturbance on chamois
507 circadian activity in this context of ongoing socio-environmental changes (Corlatti *et al.,*
508 2022).

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Conflict of Interest

The authors declared they have no conflict of interest.

Data availability statement

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

Authors' contributions

LT, MG, PM, AL, GB conceived the ideas and designed methodology; MG, PM and AL organised data collection; LT analysed the data; LT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.