Too disturbed or too hot: summer temperatures more than hikers disturbance affect circadian activity of females in northern chamois

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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 stress. In this context, we investigated how female northern chamois adjust their summer circadian activity to spatio-temporal variations of both temperature and hikers disturbance. We found that 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 (50 minutes earlier; and to a lesser extent, later in the evening), and were more active at night (+ 21.5% *approx.*) than during daytime (- 10.10% *approx.*). Their global daily activity was higher (+ 4.54% *approx.*) during the hottest than coldest days owing to a significant increase of activity level during the activity peaks. Conversely, hikers disturbance had almost no effect on activity peaks of chamois most likely due to a temporal mismatch with hikers arrival and departure. Spatial and temporal disturbance had also a weak effect on chamois activity level, except when considered together and during the hottest days (*i.e.* the most disturbed conditions) exacerbating the temporal report of activity at night those days. Low tolerance of chamois to hikers presence might have led to the pattern reported with a similar response whatever the intensity of encounter risk. These results might also suggest that behavioural changes buffering animals from high temperature (relocation into refuge areas) and/or from hikers presence (moving away temporarily from trails) allow them to marginally modify their activity pattern. In the context of ongoing socio-environmental changes, these findings stress the importance of conserving habitats providing both shelter against summer heat and human disturbance to mitigate their potential detrimental consequences.

Keywords: circadian rhythm, 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 (Chanteloup, Perrin-Malterre, Duparc, & Loison, 2016). Those recreational activities are non-lethal, but humans can be consistently perceived as predators by wildlife (Byers, 1997; Frid & Dill, 2002), leading to a suite of physiological and behavioural responses (Arlettaz *et al.,* 2007; Marchand *et al.,* 2014; Larson, Reed, Merenlender, & Crooks, 2016). The consequences of repeated reactions to increasing disturbance level can be detrimental on several fitness-related components (Phillips & Alldredge, 2000; French, González-Suárez, Young, Durham, & Gerber, 2011). This could be particularly true in mountain ecosystems, where the diversification of human activities challenges animals all year long, both during the period of energy acquisition (*i.e.* spring to autumn) and loss (*i.e.* winter). This increased pressure on the animals is accompanied by environmental changes, including climate change, that are particularly strong in the Alps (Pepin *et al.,* 2015). Accordingly, temperatures are increasing 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 risk of frost for plants; Gobiet *et al.,* 2014). Mountain animals are therefore facing concomitantly two major changes (increased disturbance level and climate change), with immediate (*e.g.* avoidance of heat and disturbance) and long-term (*e.g.* through food quality or changes in habitat use) consequences

on their behaviour, their physiology and their energetic balance (food intake *vs.* energy expenditure). Indeed, energy loss can be severe and highly detrimental for high-altitude organisms undergoing harsh climatic conditions in winter and benefiting from only short periods with mild weather to store enough energy to survive all year round (Lindstedt & Boyce, 1985).

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 (Scott, 2006). Although predicting tourism attendance under scenarios of climate change is probably not straightforward (Beniston, 2003; Scott, 2006), this context raises questions on animal responses to those interrelated human-induced environmental changes and on their potential cumulative (even multiplicative) consequences for populations in terms of both immediate and compensatory responses. One critical challenge is to understand whether behavioural mechanisms used by animals to buffer them against increasing temperatures may also provide a benefit against human attendance or *vice versa*.

Wildlife is constantly subject to the foraging/risk avoidance trade-off (Lima & Bednekoff, 1999). Animals navigate and take decisions about where to be and what to do in multiple layers of the landscape described as their "foodscape" (the distribution of edible food resource in a landscape), their landscape of energy (the energy to be spent to move from one place to another in a landscape), their thermal landscape and their landscape of fear (the distribution of the risk perception in space; Laundre, Hernández, & Altendorf, 2001; Searle, Hobbs, & Gordon, 2007). Individuals respond to the different values of these variables in terms of movements, habitat use and selection, and time devoted to different activities (foraging, resting, vigilance or social/sexual interactions). When facing a disturbance perceived as a risk, animals can modify their activities (*e.g.* from foraging to vigilance;

98 Benoist, Garel, Cugnasse, & Blanchard, 2013; Xu, Gong, & Wang, 2021), and move away
99 temporarily or even definitively (Rogala *et al.,* 2011; Courbin *et al.,* 2022). Another way to
100 face disturbance is to modify their activity pattern by delaying their activities, such as
101 foraging in disturbed places, from high- to low-risk periods (Bonnot *et al.,* 2013). The benefit
102 of such responses to disturbances have been explained within the "risk allocation hypothesis"
103 framework (Lima & Bednekoff, 1999). Indeed, the costs of lost opportunities to forage during
104 risky periods could be dampened if animals transfer part of their diurnal activity to night-time
105 when human activities usually stop (*e.g.* Marchand *et al.,* 2014, Bonnot *et al.,* 2020) or adjust
106 their activity hour by hour (Li *et al.,* 2009) when disturbed.
107 However, as night can be significantly shorter than day (*e.g.* in summer), the transfer
108 of the diurnal activities to night-time does not necessarily allow to fully compensate for the
109 loss of foraging opportunities during day and may have consequences, for instance, on mass
110 gain (Bourgoin *et al.*, 2011). More generally, activity patterns are precisely regulated (such as
111 the critical foraging/rumination balance in ruminants, Hamel & Côté, 2008), and any
112 modification of those patterns can negatively impact individual's fitness, *e.g.* by increasing
113 encounter risk with predators (Lesmerises *et al.,* 2018), by leading to mismatches in
114 interactions with conspecifics (Greives *et al.,* 2015), or by increasing risk of diseases
115 infection (Takahashi, Hong, Ko, & McDearmon, 2008). At a coarse time scale, activity
116 patterns are seasonally structured, driven by photoperiod, environmental conditions and
117 species life-cycle (Bourgoin *et al.*, 2008). At a fine pace of time, such as a day, they depend
118 on internal drivers (Saper, Lu, Chou, & Gooley, 2005), fine scale weather conditions (*e.g.*
119 wind speed, Bourgoin *et al.*, 2011) or activity patterns of other species (*e.g.* insect harassment
120 disrupt activity budget in reindeer *Rangifer tarandus tarandus*, Hagemoen & Reimers, 2002).
121 At both coarse and fine time scales, temperature is among the most important regulators of
122 activity patterns (*e.g.* in Alpine ibex *Capra ibex*, Semenzato *et al.,* 2021). Temperature

influences space use (in arctic ground squirrels *Spermophilus parryii*, Long, Martin, & Barnes, 2005; in Mediterranean mouflon *Ovis gmelini musimon x ovis* sp., Marchand *et al.,* 2015) and activity budget (in Japanese monkeys *Macaca fuscata*, Watanuki & 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). For example, female Mediterranean mouflons decrease the length of their activity boots, 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). 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).

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 in a dynamic landscape of fear (Palmer *et al.,* 2022). More specifically, we assessed the day-to-day variation in both temperature and hikers attendance for each individual and also computed an individual-specific index of spatial disturbance combining data on the attendance of each trail section by hikers, and the density of hiking trails in each chamois summer home range. This allowed us to investigate individual behavioural responses, using a diversity of activity metrics, to spatio-temporal variations in both temperature and human disturbance, and their relative contributions to changes in summer circadian activity patterns. We expected female 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 lost activity opportunities 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 which were the most exposed to hiker disturbance (**H3**) as most of them show low tolerance to hikers presence (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), 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, 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). All alpine grasslands are crossed by a network of trails where nearly all hikers are concentrated, so that this network is a major component of the landscape of fear perceived by chamois (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 (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000). Chamois had 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 newborns and injured animals. However, the presence of some non-resident wolves

Canis lupus has been noticed in recent years. 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.* ~ 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 summer, *i.e.* between 15th June and 7th September, 2004-2020, when the hunting season had not started yet so that chamois were exclusively exposed to hikers' disturbance. This 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), so that any disturbance during this period could be particularly detrimental. We used a subset of 62 adult female chamois > 2 years old trapped 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). Those females were equipped with GPS collars Lotek 3300S (Lotek Engineering Inc., Carp, Ontario, Canada). 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).

Chamois locations were recorded daily and only chamois with locations during at least 2/3 of the study period (*i.e.* 56 days, because deployment/recovery of GPS collars occurred during summer), 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. 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" or "inactive" for every 5-minutes boot using the discriminant model developed by Bourgoin and colleagues (2011; see also Darmon *et al.,* 2014). We used a total of 4,543 complete days of activity records from the 62 previously selected chamois (n = 137 chamois-year, 1,308,384 5-minutes activity measurements in total). The activity of each chamois was monitored during 18 to 132 days in total, corresponding to 1 to 49 days (*median* = 36, *SD* = 12) during a single summer period for a given chamois.

We assessed daily characteristics (see below) from 03:00 UTC of day d to 03:00 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 beginning of the chamois activity peak during summer mornings (Darmon *et al.,* 2014). We used ERA5 reanalysis combined with a micro-climatic model (Kearney & Porter, 2017; Maclean, Mosedale, & Bennie, 2019; Kearney, Gillingham, Bramer, Duffy, & Maclean, 2020) to retrieve the mean daily temperatures within alpine pastures used by chamois during summer months instead of the closest weather station located in the valley. We explored the effect of temperature on female chamois activity pattern 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.* 10.7°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 10.7°C (*median* = 8.9°C, *SD* = 1.6°C), while hot days ranged between 15.5°C and 21.0°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. Week-ends and public holidays (*i.e.* vacation days such as Ascension Day) were considered as **highly disturbed days**, whereas 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 03:00 UTC and 23:00 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 193 theoretically highly disturbed days and 442 weakly disturbed days. 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* = 2,565, *p-value* = 0.005). 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* = 1,447, *p-value* = 0.071).

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 of the map and is a good proxy of relative human frequentation (Supporting information 2, see also Thorsen *et al.,* 2022). The lowest value recorded for a trail pixel in our study site was 51, so we defined frequentation classes according to the quantiles of the

248 [51; 255] distribution (*i.e.* covering trail pixels exclusively): 1 = [51; 119] (between 0% and
249 33% quantile, low frequentation); 2 =]119; 187] (between 33% and 66% quantiles,
250 intermediate frequentation); 3 =]187; 255] (between 66% and 100% quantiles, high
251 frequentation). We counted the number of trail pixels of each class in a given home range,
252 and multiplied this number by the corresponding class value (*i.e.* 1, 2 or 3) to give a different
253 weight to each trail pixel according to its frequentation level. We then summed these values
254 for a given home range and normalised the total by dividing it by the home range surface to
255 obtain our spatial disturbance index. We used the median spatial disturbance index (*i.e.*
256 0.00577) as a threshold to discriminate between **highly exposed chamois** and **weakly**
257 **exposed chamois**.
258 As our study period ran over almost three months, day length varied widely and is
259 known to influence chamois activity (Fattorini *et al.,* 2019). We evaluated day length as the
260 time elapsed between dawn and dusk using the *crepuscule* function from the *maptools*
261 package (Bivand & Lewin-Koh, 2022; reference angle of the sun below the horizon = 6°, *i.e.*
262 civil dawn/dusk).
263
264 *Statistical analyses: predicting activity patterns and calculating activity metrics*
265 To account for the effect of day length and inter-individual variations on circadian activity
266 patterns (see Supporting information 3), we first modelled the daily activity of chamois as a
267 series of values of either 0 (no activity) or 1 (highly active) for each 5-minutes boot. We used
268 a generalised additive mixed model with a binomial distribution of errors (*mgcv* package,
269 Wood, 2011; Wood, Goude, & Shaw 2015; Wood, 2017). We included three fixed effects in
270 the model: 1) *time of the day* (*i.e.* exact time every 5 minutes) and 2) *day length* (and their
271 interaction) as continuous variables with a cyclic cubic regression splines as smoothing basis;
272 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*. 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. We defined the unique annual id-year ID of each chamois as a random effect. 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.

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 *diurnal*, *nocturnal* and *total activity* as the area under the activity curve 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). We assessed the *timing of the morning* and *evening activity peak* (time when the highest activity level occurs in the morning and the evening respectively). We calculated confidence intervals around these values using bootstraps method (Supporting information 4). We then calculated the deviation from the reference level by subtracting the value for the reference level to the value for the level of interest (*i.e.* each level of the *temperature-disturbance* variable) for each activity metric. The percentage of variation between two situations was calculated as $(value_{end} - value_{strat})/value_{start}*100$. We performed all analyses using the R software (R Core Development Team 2022).

Results

Model adjustment

The full generalised additive mixed model (*AIC* = 1,606,766, *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* = 1,619,884, *explained deviance* = 10.7%, *adjusted R2* = 0.140) to predict activity pattern (Fig. 1). All smooth terms (fixed and random effects) were significant (*p-values* < 0.001).

Temperature

Whatever the level of spatial exposure and temporal disturbance, chamois always significantly increased their total activity during hot days compared to cold days of about 0.5 unit (area under curve, see Table 1, see also Fig. 2.a). This change corresponds to a significant increase of *approx.* 0.2 unit (more than 21% variation) in the nocturnal activity and decrease of *approx.* 0.6 unit (more than 10% variation) in the diurnal activity, from cold to hot days (Table 1, Fig. 2.b and 2.c). Chamois also significantly advanced their morning peak, *i.e.* by slightly less than 1h from cold to hot days ($Timing_{morn.\ peak\ cold}$ ranging between 05:40 [05:15; 05:40] UTC and 05:55 [05:30; 05:55] UTC, $Timingm_{orn.\ peak\ hot}$ ranging between 04:45 [04:40; 05:10] UTC and 04:55 [04:45; 05:10] UTC), but they only slightly delayed their evening peak (difference not significant for chamois living in a weakly exposed area during weakly disturbed days, Table 2, Fig. 3). Both morning and evening peaks were more intense (*i.e.* higher activity level) of about 14% during hot compared to cold days (Fig. 1). Chamois maintained a certain amount of activity in the middle of the day during cold days

(*i.e.* slightly above 40%), whereas the activity level at the same hours was lower and more variable during hot days (Fig. 1).

Hikers disturbance

All the summer home ranges used by the studied chamois were crossed by at least one hiking trail, more or less used by hikers. 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). Chamois living in highly exposed areas always had a significantly higher total activity than those living in weakly exposed areas of *approx.* 0.1 unit (almost 1% variation; Table 1, Fig. 2.a), except during cold highly disturbed days where they were similar. However, most exposed chamois significantly decreased their diurnal activity during hot days by *approx.* 0.1 unit (more than 2% variation) as compared to weakly exposed ones and both did not extensively modify their nocturnal activity (Table 1, Fig. 2.b and 2.c). Similarly, chamois did not significantly modify the timing of their activity peaks according to the level of hikers exposure of their summer home range (consider large confidence intervals in Table 2 and Fig. 3).

Chamois significantly increased their total activity level of *approx.* 0.1 unit (1% variation) during highly disturbed days compared to weakly disturbed days, except for chamois living in highly exposed areas during cold days, where it is the opposite (Table 1, Fig. 2.a). In terms of nocturnal/diurnal activity, patterns were less clear regarding the effect of temporal disturbance. Chamois living in highly disturbed areas tended to slightly reduce their diurnal activity during highly disturbed compared to weakly disturbed days by less than 0.1 unit (less than 1% variation). To the contrary, chamois living in weakly disturbed areas increased their diurnal activity by *approx.* 0.1 unit (more than 1% variation). The amount of

nocturnal activity did not change extensively according to temporal disturbance (Fig. 2.b and 2.c). Moreover, the timing of morning and evening activity peaks was not affected by the level of temporal disturbance (consider large confidence intervals in Table 2 and Fig. 3).

Discussion

General results

Our objective was to determine and compare the relative contribution of summer temperatures and hikers disturbance on the activity pattern of a wild ungulate, the northern chamois. In agreement with **H1**, chamois adjusted their circadian activity to temperature by shifting their activity peak earlier in the morning (and to a lesser extent, later in the evening), and by being more active at night and less active during daytime during hot days. Surprisingly, their total daily activity was higher during hot than cold days owing to a significant increase of activity level during the activity peaks. Furthermore, even if this response was less pronounced, chamois living in areas highly exposed to hikers also adjusted their activity pattern, particularly during hot days, as expected from **H3**. When living in disturbed areas and during disturbed days, they slightly decreased their activity during daytime and increased it during the following night, confirming **H2**. Although they also slightly delayed the morning activity peak during cold days, hikers disturbance had very little effect on timing of activity peaks, most likely due to a temporal mismatch with hiker arrival and departure (*e.g.* more than 2 hours after the morning peak). We also revealed modifications of the activity levels in chamois living in areas weakly exposed to hikers disturbance.

Additional effect of potential versus actual exposure to hikers disturbance

Even during weakly disturbed days (*i.e.* week days), chamois highly exposed to hikers disturbance, due to the presence of highly used trails in their home range, generally demonstrated stronger responses than those living in weakly exposed areas, *i.e.* home ranges where trails were less used and/or less represented. For instance, during hot days, chamois living in highly exposed areas decreased their diurnal activity compared to chamois living in weakly exposed areas, either during highly or weakly disturbed days. During highly disturbed days (*i.e.* week-ends), chamois living in highly disturbed areas decreased their activity even more, demonstrating a cumulative effect of potential exposure to disturbance and actual disturbance itself, directly illustrating the effect of the landscape of fear (Laundre, Hernández, & Altendorf, 2001). But contrary to our expectations, most of the activity metrics explored also varied for chamois living in weakly exposed areas according to the level of temporal disturbance they experienced. Samia and colleagues showed that weakly exposed populations among birds, mammals and lizards can be less tolerant to human disturbance because they are less used to it (Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015). In our population, most of the individuals (85%) move temporarily away from trails every day when hikers are present (Courbin *et al.,* 2022). This low tolerance might explain the weak difference between most/less disturbed chamois either through a similar response to human presence whatever the encounter risk (human being almost present everyday) or through the relocation of their activity in habitats farther away from the main source of disturbance (*i.e.* trails). Cumulative effects of exposure to human disturbance and actual disturbance are far more important than they seem, particularly because they can induce a delayed response instead of a direct, easily observable one (Chassagneux *et al.,* 2020).

394 *Interaction between human disturbance and temperature*

395 Though chamois seem to be less sensitive to high temperatures than other wild ungulate
396 species (see Darmon *et al.,* 2014 for a comparison between chamois and mouflon), their
397 faecal glucocorticoid metabolites concentration increases during drought conditions in
398 summer (Anderwald, Campell Andri, & Palme 2021), as well as the time they spend in
399 thermal refuges (Malagnino *et al.*, unpublished). This may explain that chamois responded
400 much less strongly to human disturbance than to temperature. Moreover, in our study site,
401 hiker attendance was significantly higher when temperature was high (42 ± 55 SD hikers
402 during cold days, 61 ± 37 SD hikers during hot days; *Mann-Whitney test statistic* = 322.5, *p-*
403 *value* = 0.003). Hence, the response to human disturbance could be lower than expected as
404 the behavioural changes to buffer from high temperatures may also prevent chamois from
405 hikers disturbance, as both factors are correlated. Animals have to face several sources of
406 disturbance (*e.g.* human disturbance, predation, high temperatures) and they eventually
407 cannot indefinitely increase their behavioural response as disturbance factors accumulate
408 (Benoist, Garel, Cugnasse, & Blanchard, 2013).

409 Recent studies provided evidence of a non-negligeable nocturnal activity peak in
410 chamois (Carnevali, Lovari, Monaco, & Mori, 2016). Here, we also highlighted that
411 nocturnal activity significantly increased while diurnal activity decreased during hot days,
412 confirming the influence of high temperatures and human disturbance on chamois activity.
413 Similarly to numerous other species, chamois decreased their activity when exposed to high
414 temperatures and/or hikers disturbance and attempted to compensate for the activity loss
415 when it is absent (*e.g.* later in the day or at night, Gaynor, Hojnowski, Carter, & Brashares,
416 2018). However, an increase in nocturnal activity could expose individuals to other threats,
417 such as nocturnal predators (Bonnot *et al.,* 2020). This is particularly true in our study site
418 with the progressive return of wolves recorded since the end of the study period. Large

419 herbivores may face the difficult challenge of avoiding being exposed to high temperature in
420 the middle of the day while limiting their exposure to human disturbance during the rest of
421 the day, but without shifting completely their activity at night because of predation risk.
422 Chamois can spatially adjust to dampen the impact of hiker disturbance (Duparc,
423 2016; Courbin *et al.,* 2022). These diel migrations (Courbin *et al.,* 2022) allow chamois to
424 maintain a certain level of activity during disturbed periods. Unfortunately, our data provides
425 no clue about the nature of the behaviours displayed (*i.e.* foraging, resting, moving or social
426 behaviours). But contrary to high temperatures for which any kind of behaviour is costly and
427 should thus be reduced, leading to a lower activity level, some behaviours are favoured in the
428 context of human disturbance and could produce inconsistent activity patterns. For instance,
429 an escape movement is a response to risk which leads to an increase in the activity level,
430 while resting in a refuge area can also be a response to risk (through avoidance) but leads to a
431 lower activity level.
432 Mountain animals face increasing temperatures through the ongoing climate warming,
433 and modifications of their landscape of fear through the development of recreational activities
434 and the return of predators in these landscapes. Both constraints can lead either to similar
435 responses (*e.g.* rest in refuge areas), or to opposite reactions (*e.g.* reduce activity to avoid
436 thermal stress or escape to limit predation risk), which complicates their behavioural response
437 (Courbin *et al.,* 2022). That is why identifying the effect of human disturbance on wildlife
438 remains a difficult task (Tablado & Jenni, 2017), and an integrated approach is needed to take
439 into account all the covariables affecting chamois activity, such as temperature and predation.
440 Such an approach will be possible in our study site in the forthcoming years (consider
441 Courbin *et al.,* 2022 and Malagnino *et al.*, unpublished together with this study).
442
443

Management implications

As ecosystem engineers, wild ungulates play a major role in mountain landscapes, by their movements (*e.g.* seed dispersal via zoochory, Albert *et al.,* 2015) and grazing (*e.g.* plant selection via grazing, Austrheim & Eriksson, 2001). Most of the populations of large mammals living in the Alps and surrounding massifs have to face several kinds of disturbance, ranging from hiking to cable car ebb and flow, while constrained by increasing temperature during summer due to climate change (Brivio *et al.,* 2016). As tourism development is often a pillar of the local economy, the right balance must be found between natural environment and tourism management (Reynolds & Braithwaite, 2001). Human impact on chamois could become an issue given that it may decrease the size of their suitable habitats (Peksa & Ciach, 2015), generate a necessary reorganisation of their circadian activity patterns, and reduce their ability to satisfactorily cope with thermal stress, particularly in the context of increasing temperatures. The interaction between those factors could eventually jeopardise their demography if particular attention is not paid in conserving habitats providing both shelter against summer heat and human disturbance (Frid & Dill, 2002; Chirichella, Stephens, Mason, & Apollonio, 2021). Our study contributes to filling the knowledge gap on the cumulative effects of weather and human disturbance on chamois circadian activity in this context of ongoing socio-environmental changes (Corlatti *et al.,* 2022).

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.

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Conflict of Interest

The authors declared they have no conflict of interest.

Data availability statement

Data will be available after acceptance of the manuscript.

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Tables and Figures

Table 1: Total, diurnal and nocturnal Area Under Curve (unitless) estimated from predicted circadian activity patterns (median value of the bootstraps distribution, n = 1001) of northern chamois of the National Game and Hunting Reserve of Les Bauges massif, in summer (June to September, 2004-2020), according to temperature and human disturbance. We defined "diurnal" as the period elapsed between two hours after dawn and two hours before dusk, and "nocturnal" as the period elapsed between two hours after dusk and two hours before dawn (see text for details). Values between brackets correspond to 2.5% and 97.5% quantiles (95% confidence intervals) estimated with bootstraps.

Disturbance-Temperature variable levels			**Total activity**	**Diurnal activity**	**Nocturnal activity**
Potential exposure	**Hikers disturbance**	**Temperature**			
Low	Low	Low	10.89 [10.72; 11.06]	5.89 [5.77; 6.01]	1.09 [1.08; 1.09]
Low	High	Low	11.03 [10.86; 11.19]	5.98 [5.87; 6.11]	1.10 [1.08; 1.10]
Low	Low	High	11.41 [11.23; 11.54]	5.39 [5.28; 5.51]	1.34 [1.31; 1.34]
Low	High	High	11.53 [11.35; 11.66]	5.46 [5.36; 5.59]	1.31 [1.28; 1.31]
High	Low	Low	11.07 [10.90; 11.24]	6.03 [5.91; 6.15]	1.11 [1.09; 1.11]
High	High	Low	11.03 [10.86; 11.20]	5.99 [5.87; 6.12]	1.12 [1.10; 1.12]
High	Low	High	11.50 [11.32; 11.63]	5.33 [5.22; 5.45]	1.34 [1.31; 1.34]
High	High	High	11.58 [11.40; 11.72]	5.30 [5.19; 5.42]	1.38 [1.35; 1.38]

Table 2: Timing of the morning and evening peaks (UTC) estimated from predicted circadian activity patterns (median value of the bootstraps distribution, n = 1001) of northern chamois of the National Game and Hunting Reserve of Les Bauges massif, in summer (June to September, 2004-2020), according to temperature and human disturbance. Values between brackets correspond to 2.5% and 97.5% quantiles (95% confidence intervals) estimated with bootstraps.

Disturbance-Temperature variable levels			**Morning peak timing**	**Evening peak timing**
Potential exposure	**Hikers disturbance**	**Tempera-ture**		
Low	Low	Low	05:40 [05:10; 05:45]	19:10 [19:10; 19:15]
Low	High	Low	05:50 [05:25; 05:55]	19:05 [19:05; 19:10]
Low	Low	High	04:50 [04:40; 05:05]	19:10 [19:10; 19:15]
Low	High	High	04:55 [04:45; 05:05]	19:15 [19:15; 19:20]
High	Low	Low	05:40 [05:15; 05:40]	19:10 [19:05; 19:10]
High	High	Low	05:55 [05:30; 05:55]	19:05 [19:05; 19:10]
High	Low	High	04:45 [04:40; 05:10]	19:15 [19:15; 19:15]
High	High	High	04:55 [04:45; 05:10]	19:20 [19:20; 19:20]

Figure 1: predicted circadian activity patterns (activity ranges between 0 for no activity, to 1 for the highest level of 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 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. Solid lines represent predicted values from the model, shaded areas represent 95% confidence intervals. Time of the day represents hours in Coordinated Universal Time (UTC).

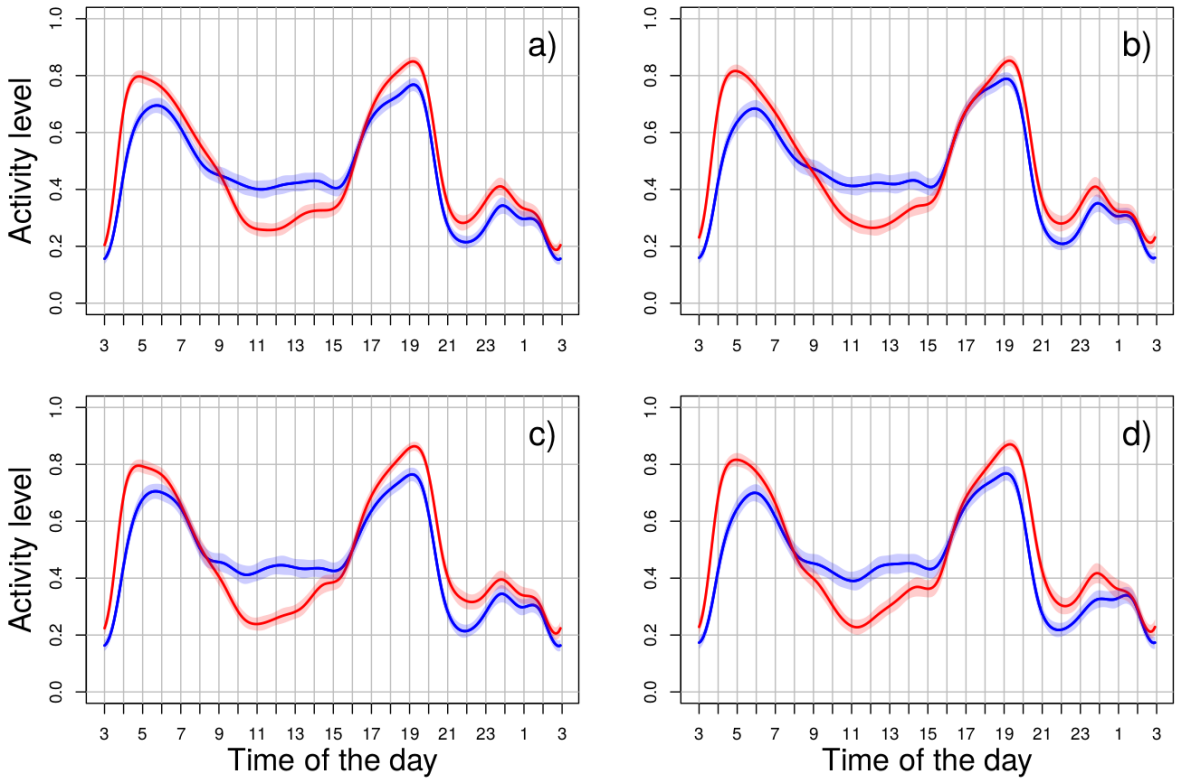

Figure 2: Area Under Curve (AUC) differential (unitless) between the reference situation (*i.e.* chamois living in a weakly exposed area during a cold weakly disturbed day) and the situation of interest, a combination of different levels of temperature (blue: cold day; red: hot day), spatial (dot: low exposure; triangle: high exposure) and hikers attendance (low = week days; high = week-ends): a) total, b) diurnal and c) nocturnal activity. 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; see Fig. 1). The central point represents the median, and the vertical bars represent the 2.5% and 97.5% quantiles of the bootstraps distribution (n = 1001). Note the change of scale between Fig. 2.a and Fig. 2.b and 2.c.

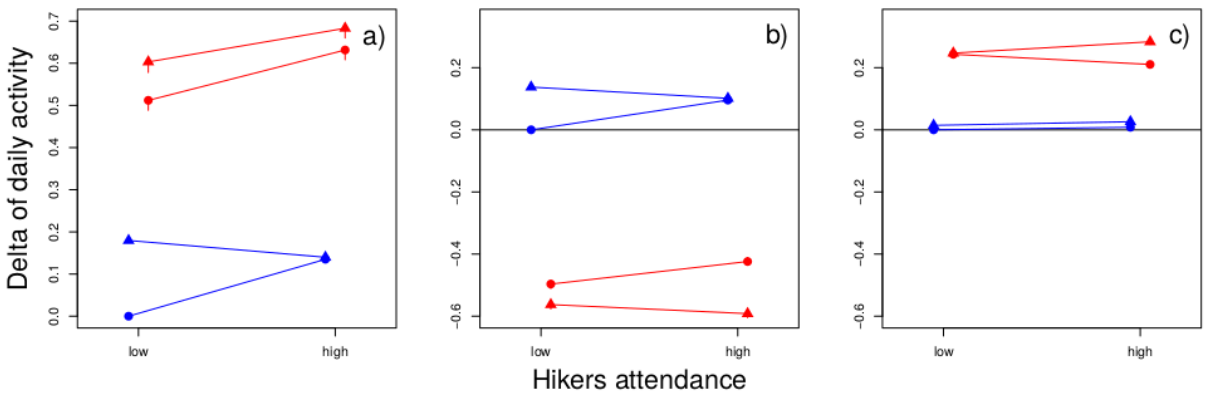
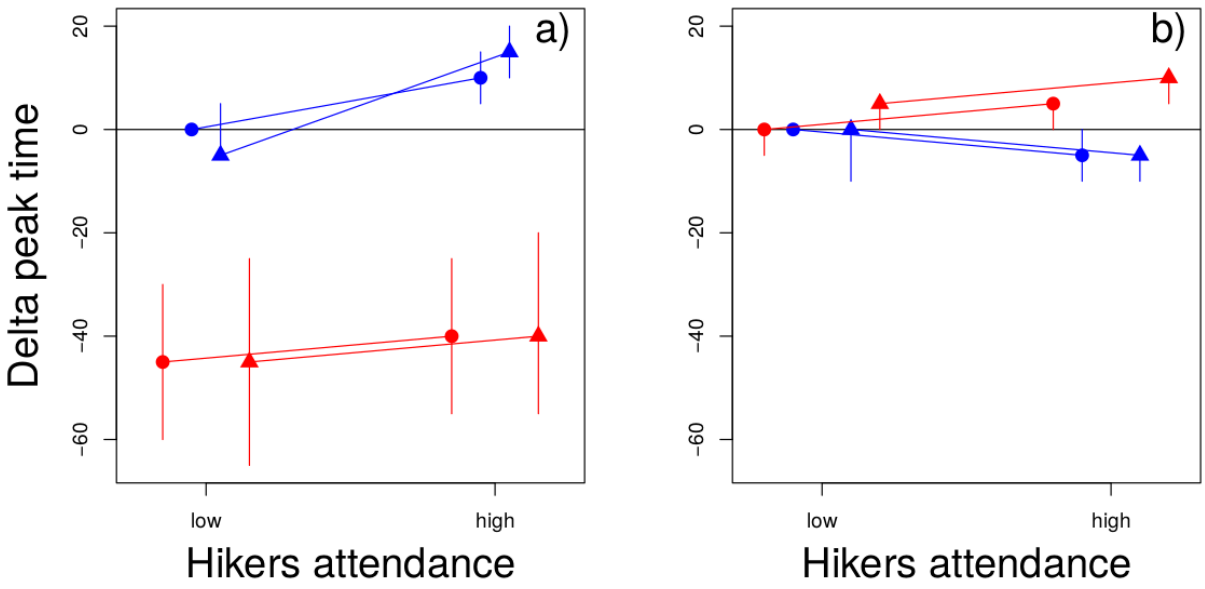
Figure 3: Activity Peak Timing (APT) differential (in minutes) between the reference situation (*i.e.* chamois living in a weakly exposed area during a cold weakly disturbed day) and the situation of interest, a combination of different levels of temperature (blue: cold day; red: hot day), spatial (dot: low exposure; triangle: high exposure) and temporal human disturbance: a) morning 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). The central point represents the median, and the vertical bars represent the 2.5% and 97.5% quantiles of the bootstraps distribution (n = 1001). The points have been shifted on both sides to improve readability.