1 **Too disturbed or too hot: summer temperatures more**

2 **than hikers disturbance affect circadian activity of females**

3 **in northern chamois**

4

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

6 Anne[1]

7

8 **Authors details**

9 [1] Laboratoire d'Ecologie Alpine, UMR 5553 (CNRS, Université Savoie Mont--Blanc),

10 Savoie Technolac, 73376 Le Bourget-du-Lac, France.

11 [2] Laboratoire Évolution et Diversité Biologique, UMR 5174 (CNRS, Université Paul

12 Sabatier), 118 route de Narbonne, 31062 Toulouse, France.

13 [3] Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique,

14 Service Anthropisation et Fonctionnement des Ecosystèmes Terrestres, Gières, France.

15 [4] Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique,

16 Service Anthropisation et Fonctionnement des Ecosystèmes Terrestres, Juvignac, France.

17 [5] Univ Lyon, VetAgro Sup, Campus Vétérinaire de Lyon, 1 avenue Bourgelat, F-69280

18 Marcy l'Etoile, France.

19 [6] Univ Lyon, Université Lyon 1, CNRS, UMR 5558, Laboratoire de Biométrie et Biologie

20 Evolutive (LBBE), F-69622 Villeurbanne Cedex, France.

21

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

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.

48   **Keywords**: circadian rhythm, ecotourism, human disturbance, mountain ecosystem,

49   nocturnality, recreational activities, *Rupicapra rupicapra rupicapra*

50

Introduction

52   A noticeable development and diversification of outdoor activities has been ongoing in the

53   twenty-first century, especially in Western countries (Wheaton, 2010). While mountain

54   ecosystems have been preserved until recently because of their low accessibility, they now

55   face an increase of unaffiliated activities such as hiking, cross country skiing, trail running, or

56   climbing (Chanteloup, Perrin-Malterre, Duparc, & Loison, 2016). Those recreational

57   activities are non-lethal, but humans can be consistently perceived as predators by wildlife

58   (Byers, 1997; Frid & Dill, 2002), leading to a suite of physiological and behavioural

59   responses (Arlettaz *et al.,* 2007; Marchand *et al.,* 2014; Larson, Reed, Merenlender, &

60   Crooks, 2016). The consequences of repeated reactions to increasing disturbance level can be

61   detrimental on several fitness-related components (Phillips & Alldredge, 2000; French,

62   González-Suárez, Young, Durham, & Gerber, 2011). This could be particularly true in

63   mountain ecosystems, where the diversification of human activities challenges animals all

64   year long, both during the period of energy acquisition (*i.e.* spring to autumn) and loss (*i.e.*

65   winter). This increased pressure on the animals is accompanied by environmental changes,

66   including climate change, that are particularly strong in the Alps (Pepin *et al.,* 2015).

67   Accordingly, temperatures are increasing rapidly in all seasons, with consequences such as

68   earlier springs and plant cycles, more frequent summer heatwaves and droughts, and

69   decreased duration of snow cover (associated with an augmented risk of frost for plants;

70   Gobiet *et al.,* 2014). Mountain animals are therefore facing concomitantly two major changes

71   (increased disturbance level and climate change), with immediate (*e.g.* avoidance of heat and

72   disturbance) and long-term (*e.g.* through food quality or changes in habitat use) consequences

73   on their behaviour, their physiology and their energetic balance (food intake *vs.* energy

74   expenditure). Indeed, energy loss can be severe and highly detrimental for high-altitude

75   organisms undergoing harsh climatic conditions in winter and benefiting from only short

76   periods with mild weather to store enough energy to survive all year round (Lindstedt &

77   Boyce, 1985).

78   Ongoing climate change and expansion of human activities in mountain ecosystems

79   are also ultimately connected. An extended summer season or more frequent summer

80   heatwaves in valleys may, for instance, exacerbate human attendance in mountains (Scott,

81   2006). Although predicting tourism attendance under scenarios of climate change is probably

82   not straightforward (Beniston, 2003; Scott, 2006), this context raises questions on animal

83   responses to those interrelated human-induced environmental changes and on their potential

84   cumulative (even multiplicative) consequences for populations in terms of both immediate

85   and compensatory responses. One critical challenge is to understand whether behavioural

86   mechanisms used by animals to buffer them against increasing temperatures may also provide

87   a benefit against human attendance or *vice versa*.

88   Wildlife is constantly subject to the foraging/risk avoidance trade-off (Lima &

89   Bednekoff, 1999). Animals navigate and take decisions about where to be and what to do in

90   multiple layers of the landscape described as their "foodscape" (the distribution of edible

91   food resource in a landscape), their landscape of energy (the energy to be spent to move from

92   one place to another in a landscape), their thermal landscape and their landscape of fear (the

93   distribution of the risk perception in space; Laundre, Hernández, & Altendorf, 2001; Searle,

94   Hobbs, & Gordon, 2007). Individuals respond to the different values of these variables in

95   terms of movements, habitat use and selection, and time devoted to different activities

96   (foraging, resting, vigilance or social/sexual interactions). When facing a disturbance

97   perceived as a risk, animals can modify their activities (*e.g.* from foraging to vigilance;

4

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

123   influences space use (in arctic ground squirrels *Spermophilus parryii*, Long, Martin, &

124   Barnes, 2005; in Mediterranean mouflon *Ovis gmelini musimon x ovis* sp., Marchand *et al.,*

125   2015) and activity budget (in Japanese monkeys *Macaca fuscata*, Watanuki & Nakayama,

126   1993), with animals having to trade off foraging and thermal cover to limit thermoregulatory

127   costs while keeping their energy balance (van Beest & Milner, 2013). For example, female

128   Mediterranean mouflons decrease the length of their activity boots, shift their activity peaks

129   (earlier in the morning and later in the evening) and increase their nocturnal activity during

130   the hottest summer days (Bourgoin *et al.*, 2008; Bourgoin *et al.*, 2011). These results

131   highlight the importance of investigating full daily cycles to get a comprehensive picture of

132   how animals may adjust their behaviour in the face of human-induced environmental changes

133   (Marchand *et al.,* 2014; Marchand *et al.,* 2015).

134   Here, we relied on the GPS monitoring of 62 females of northern chamois *Rupicapra*

135   *rupicapra rupicapra* to investigate at a fine scale their behavioural responses to temporal and

136   spatial stressors in a dynamic landscape of fear (Palmer *et al.,* 2022). More specifically, we

137   assessed the day-to-day variation in both temperature and hikers attendance for each

138   individual and also computed an individual-specific index of spatial disturbance combining

139   data on the attendance of each trail section by hikers, and the density of hiking trails in each

140   chamois summer home range. This allowed us to investigate individual behavioural

141   responses, using a diversity of activity metrics, to spatio-temporal variations in both

142   temperature and human disturbance, and their relative contributions to changes in summer

143   circadian activity patterns. We expected female chamois to adjust their circadian activity

144   pattern by avoiding being active during the hottest hours during the hottest days (**H1**) and

145   during the most disturbed days (**H2**), with a compensation of lost activity opportunities

146   during daytime at night. However, as individuals were exposed to variable levels of

147   disturbance depending on the location of their summer home range, we also expected more

6

148   marked responses in chamois which were the most exposed to hiker disturbance (**H3**) as most

149   of them show low tolerance to hikers presence (Courbin *et al.,* 2022).

150

151   **Materials and methods**

152   *Study site and species*

153   The study took place in the National Game and Hunting Reserve of Les Bauges massif

154   (NGHRB), in the French Alps (45°40' N, 6°13' E; 900 to 2200 m a.s.l.; 5,200 ha). The

155   Bauges massif is made of limestone, with cold (mean annual temperature: 9.6°C, snow cover

156   from November to April above 1,600 m, Duparc *et al.,* 2013) and wet (mean cumulative

157   annual rainfall: 1,600 mm, Duparc *et al.,* 2013) climatic conditions (see Supporting

158   information 1 for details about summer temperatures). Fifty-six percent of the area is covered

159   by forests, dominated by beech *Fagus sylvatica* and fir *Abies alba*, 36% by grasslands, and

160   8% by rocks (Lopez, 2001). This heterogeneous environment leads to a huge diversity of

161   habitats and landscapes that attracts numerous tourists every year (> 37,000, most of them

162   during summer). All alpine grasslands are crossed by a network of trails where nearly all

163   hikers are concentrated, so that this network is a major component of the landscape of fear

164   perceived by chamois (Courbin *et al.,* 2022). Other recreational activities (*e.g.* paragliding)

165   occur in the study site during summer, but far less frequently than hiking.

166   Most adult female chamois annually give birth to one young in late May. During

167   summer, they form groups with other females, kids and yearlings, that share and keep the

168   same home range from year to year (Loison, Jullien, & Menaut, 1999). Females play a major

169   role in the demography of the population (Gaillard, Festa-Bianchet, Yoccoz, Loison, &

170   Toigo, 2000). Chamois had no natural predators in the study area during the study period,

171   except golden eagles *Aquila chrysaetos* and red foxes *Vulpes vulpes* that may occasionally

172   predate newborns and injured animals. However, the presence of some non-resident wolves

173   *Canis lupus* has been noticed in recent years. Hunting (performed by small groups of three to

174   four hunters) occurs in the NGHRB from the beginning of September to the end of February

175   (Courbin *et al., 2022*), with chamois being the main target species (~ 100 chamois harvested

176   per year on average, *i.e.* ~ 70% of the total number of ungulates harvested), in addition to

177   Mediterranean mouflon (~ 20%), roe deer *Capreolus capreolus* (~ 4%), wild boar *Sus scrofa*

178   (~ 4%) and red deer *Cervus elaphus* (~ 2%; see Courbin *et al., 2022* for details).

179

180   *Data collection*

181   We focused on summer, *i.e.* between 15th June and 7th September, 2004-2020, when the

182   hunting season had not started yet so that chamois were exclusively exposed to hikers'

183   disturbance. This period is critical for female chamois because it follows the birth season and

184   it is characterised by high energy requirements for lactation and storage of fat reserves for

185   winter survival (Clutton-Brock, Albon, & Guinness, 1989), so that any disturbance during

186   this period could be particularly detrimental. We used a subset of 62 adult female chamois >

187   2 years old trapped during summer using falling nets baited with salt licks located in four

188   alpine grasslands near two trails highly used by hikers (Armenaz and Dent des Portes). Those

189   females were equipped with GPS collars Lotek 3300S (Lotek Engineering Inc., Carp,

190   Ontario, Canada). All captures, handling and sampling were conducted according to the

191   appropriate national laws for animal welfare, following the ethical conditions detailed in the

192   specific accreditations delivered by the Préfecture de Paris (prefectorial decree n°2009–014)

193   in agreement with the French environmental code (Art. R421-15 to 421–31 and R422-92 to

194   422–94-1).

195   Chamois locations were recorded daily and only chamois with locations during at

196   least 2/3 of the study period (*i.e.* 56 days, because deployment/recovery of GPS collars

197   occurred during summer), for which we could reliably estimate the summer home range (95%

198   kernel contour using the *adehabitatHR* package; Worton, 1989; Calenge, 2006) were

199   included in the study. Animal motion was recorded every 5 minutes by two perpendicular

200   captive-balls in the GPS collars monitoring neck movements (0: no movement, 255: highly

201   mobile) and the proportion of time the animal was head down. We discriminated each

202   chamois as "active" or "inactive" for every 5-minutes boot using the discriminant model

203   developed by Bourgoin and colleagues (2011; see also Darmon *et al.,* 2014). We used a total

204   of 4,543 complete days of activity records from the 62 previously selected chamois ($n = 137$

205   chamois-year, 1,308,384 5-minutes activity measurements in total). The activity of each

206   chamois was monitored during 18 to 132 days in total, corresponding to 1 to 49 days (*median*

207    $= 36$, $SD = 12$) during a single summer period for a given chamois.

208   We assessed daily characteristics (see below) from 03:00 UTC of day *d* to 03:00 UTC

209   of day *d+1*. This allowed us to explore potential compensation processes during the night

210   following the day of interest. We selected the starting hour in accordance with the beginning

211   of the chamois activity peak during summer mornings (Darmon *et al.,* 2014). We used ERA5

212   reanalysis combined with a micro-climatic model (Kearney & Porter, 2017; Maclean,

213   Mosedale, & Bennie, 2019; Kearney, Gillingham, Bramer, Duffy, & Maclean, 2020) to

214   retrieve the mean daily temperatures within alpine pastures used by chamois during summer

215   months instead of the closest weather station located in the valley. We explored the effect of

216   temperature on female chamois activity pattern through a categorical variable with two levels

217   defined according to the quantiles of the mean daily temperature distribution. Days with

218   mean temperature ≤ 25% quantile (*i.e.* 10.7°C) were considered as **cold days** and days with

219   mean temperature > 75% quantile (*i.e.* 15.5°C) were considered as **hot days**. Cold days

220   experienced by chamois ranged between 3.4°C and 10.7°C (*median* = 8.9°C, *SD* = 1.6°C),

221   while hot days ranged between 15.5°C and 21.0°C (*median* = 17.1°C, *SD* = 1.2°C, see also

222   Supporting information 1).

223   Temporal disturbance associated with hiking practice was defined as a categorical

224   variable with two levels. Week-ends and public holidays (*i.e.* vacation days such as

225   Ascension Day) were considered as **highly disturbed days**, whereas days between Monday

226   and Friday (*i.e.* working days, including weekdays during school holidays) were considered

227   as **weakly disturbed days**. To check for the reliability of these two categories in the field, we

228   compared the daily attendance of hikers (number of hikers recorded on the trail) between

229   03:00 UTC and 23:00 UTC and the hour of first arrival for both temporal disturbance levels

230   using an eco-counter (PYRO sensor Eco-Compteur, www.eco-compteur.com; 90 cm above

231   ground) located on Armenaz trail (45°37'18.60" N, 6°13'2.53" E), on a subset of the study

232   period (2016 and 2017 summers). Our study period encompassed 193 theoretically highly

233   disturbed days and 442 weakly disturbed days. Hikers were almost two times more on the

234   trails during highly (*median* = 73 hikers, *SD* = 53 hikers) than during weakly (*median* = 40

235   hikers, *SD* = 34 hikers) disturbed days (*Mann-Whitney test statistic* = 2,565, *p-value* = 0.005).

236   Hikers also tended to arrive one hour earlier during highly (*median* = 07:00 UTC, *SD* = 2

237   hours) compared to weakly (*median* = 08:00 UTC, *SD* = 3 hours) disturbed days although

238   this difference was not statistically significant (*Mann-Whitney test statistic* = 1,447, *p-value* =

239   0.071).

240   Potential spatial exposure to hikers disturbance was evaluated within each female

241   chamois home range using frequentation rates of the trails extracted from Strava Global

242   Heatmap (Strava, 2022; www.strava.com, download date: 2022/03/09, data from the two

243   previous years, see also Courbin *et al.,* 2022 for a similar approach on this study site). Strava

244   heatmap provides a value ranging from 0 for no attendance to 255 for the highest attendance

245   for each pixel of the map and is a good proxy of relative human frequentation (Supporting

246   information 2, see also Thorsen *et al.,* 2022). The lowest value recorded for a trail pixel in

247   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

11

273   temperature classes, levels of temporal disturbance and of spatial disturbance, in interaction

274   with the *time of the day*. The levels were ordered, with the reference level corresponding to a

275   chamois living in a weakly exposed area during a cold and weakly disturbed day. We defined

276   the unique annual id-year ID of each chamois as a random effect. We set the maximum

277   number of knots for the smoothing functions to 24. We also fitted the null model, which was

278   similar to the model described above but excluded the *temperature-disturbance* variable, for

279   comparison purposes.

280   We used the predictions of the model to investigate the effect of temperature and

281   hikers disturbance on several activity metrics derived from this model (described below). We

282   controlled for the effect of *day length* by fixing it to the median of the complete dataset (*i.e.*

283   963 minutes) when predicting chamois activity for each level of the *temperature-disturbance*

284   combination. We derived the *diurnal*, *nocturnal* and *total activity* as the area under the

285   activity curve for each level of the *temperature-disturbance* variable. We defined daytime as

286   the period elapsed between two hours after dawn and two hours before dusk, and night-time

287   as the period elapsed between two hours after dusk and two hours before dawn (see Bonnot *et*

288   *al., 2020* for a similar approach). We assessed the *timing of the morning* and *evening activity*

289   *peak* (time when the highest activity level occurs in the morning and the evening

290   respectively). We calculated confidence intervals around these values using bootstraps

291   method (Supporting information 4). We then calculated the deviation from the reference level

292   by subtracting the value for the reference level to the value for the level of interest (*i.e.* each

293   level of the *temperature-disturbance* variable) for each activity metric. The percentage of

294   variation between two situations was calculated as *(value$_{end}$ - value$_{strat}$)/value$_{start}$*100*. We

295   performed all analyses using the R software (R Core Development Team 2022).

296

297

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

13

320   (*i.e.* slightly above 40%), whereas the activity level at the same hours was lower and more

321   variable during hot days (Fig. 1).

322

323   *Hikers disturbance*

324   All the summer home ranges used by the studied chamois were crossed by at least one hiking

325   trail, more or less used by hikers. Our spatial disturbance index ranged between 0.00317 and

326   0.02912 (*median* = 0.00577, *SD* = 0.00433), with only seven chamois above 0.01000

327   (Supporting information 1). Chamois living in highly exposed areas always had a

328   significantly higher total activity than those living in weakly exposed areas of *approx.* 0.1

329   unit (almost 1% variation; Table 1, Fig. 2.a), except during cold highly disturbed days where

330   they were similar. However, most exposed chamois significantly decreased their diurnal

331   activity during hot days by *approx.* 0.1 unit (more than 2% variation) as compared to weakly

332   exposed ones and both did not extensively modify their nocturnal activity (Table 1, Fig. 2.b

333   and 2.c). Similarly, chamois did not significantly modify the timing of their activity peaks

334   according to the level of hikers exposure of their summer home range (consider large

335   confidence intervals in Table 2 and Fig. 3).

336   Chamois significantly increased their total activity level of *approx.* 0.1 unit (1%

337   variation) during highly disturbed days compared to weakly disturbed days, except for

338   chamois living in highly exposed areas during cold days, where it is the opposite (Table 1,

339   Fig. 2.a). In terms of nocturnal/diurnal activity, patterns were less clear regarding the effect of

340   temporal disturbance. Chamois living in highly disturbed areas tended to slightly reduce their

341   diurnal activity during highly disturbed compared to weakly disturbed days by less than 0.1

342   unit (less than 1% variation). To the contrary, chamois living in weakly disturbed areas

343   increased their diurnal activity by *approx.* 0.1 unit (more than 1% variation). The amount of

14

344 nocturnal activity did not change extensively according to temporal disturbance (Fig. 2.b and

345 2.c). Moreover, the timing of morning and evening activity peaks was not affected by the

346 level of temporal disturbance (consider large confidence intervals in Table 2 and Fig. 3).

347

Discussion

349 *General results*

350 Our objective was to determine and compare the relative contribution of summer

351 temperatures and hikers disturbance on the activity pattern of a wild ungulate, the northern

352 chamois. In agreement with **H1**, chamois adjusted their circadian activity to temperature by

353 shifting their activity peak earlier in the morning (and to a lesser extent, later in the evening),

354 and by being more active at night and less active during daytime during hot days.

355 Surprisingly, their total daily activity was higher during hot than cold days owing to a

356 significant increase of activity level during the activity peaks. Furthermore, even if this

357 response was less pronounced, chamois living in areas highly exposed to hikers also adjusted

358 their activity pattern, particularly during hot days, as expected from **H3**. When living in

359 disturbed areas and during disturbed days, they slightly decreased their activity during

360 daytime and increased it during the following night, confirming **H2**. Although they also

361 slightly delayed the morning activity peak during cold days, hikers disturbance had very little

362 effect on timing of activity peaks, most likely due to a temporal mismatch with hiker arrival

363 and departure (*e.g.* more than 2 hours after the morning peak). We also revealed

364 modifications of the activity levels in chamois living in areas weakly exposed to hikers

365 disturbance.

366

367

368

15

369 *Additional effect of potential versus actual exposure to hikers disturbance*

370 Even during weakly disturbed days (*i.e.* week days), chamois highly exposed to hikers

371 disturbance, due to the presence of highly used trails in their home range, generally

372 demonstrated stronger responses than those living in weakly exposed areas, *i.e.* home ranges

373 where trails were less used and/or less represented. For instance, during hot days, chamois

374 living in highly exposed areas decreased their diurnal activity compared to chamois living in

375 weakly exposed areas, either during highly or weakly disturbed days. During highly disturbed

376 days (*i.e.* week-ends), chamois living in highly disturbed areas decreased their activity even

377 more, demonstrating a cumulative effect of potential exposure to disturbance and actual

378 disturbance itself, directly illustrating the effect of the landscape of fear (Laundre,

379 Hernández, & Altendorf, 2001). But contrary to our expectations, most of the activity metrics

380 explored also varied for chamois living in weakly exposed areas according to the level of

381 temporal disturbance they experienced. Samia and colleagues showed that weakly exposed

382 populations among birds, mammals and lizards can be less tolerant to human disturbance

383 because they are less used to it (Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015). In

384 our population, most of the individuals (85%) move temporarily away from trails every day

385 when hikers are present (Courbin *et al.,* 2022). This low tolerance might explain the weak

386 difference between most/less disturbed chamois either through a similar response to human

387 presence whatever the encounter risk (human being almost present everyday) or through the

388 relocation of their activity in habitats farther away from the main source of disturbance (*i.e.*

389 trails). Cumulative effects of exposure to human disturbance and actual disturbance are far

390 more important than they seem, particularly because they can induce a delayed response

391 instead of a direct, easily observable one (Chassagneux *et al.,* 2020).

392

393

16

Interaction between human disturbance and temperature

Though chamois seem to be less sensitive to high temperatures than other wild ungulate species (see Darmon *et al.,* 2014 for a comparison between chamois and mouflon), 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 (Malagnino *et al.,* unpublished). This may explain that chamois responded much less strongly to human disturbance than to temperature. Moreover, in our study site, hiker attendance was significantly higher when temperature was high (42 ± 55 SD hikers during cold days, 61 ± 37 SD hikers during hot days; *Mann-Whitney test statistic* = 322.5, *p-value* = 0.003). Hence, the response to human disturbance could be lower than expected as the behavioural changes to buffer from high temperatures may also prevent 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 increase their behavioural response as disturbance factors accumulate (Benoist, Garel, Cugnasse, & Blanchard, 2013).

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 activity when exposed to high temperatures and/or hikers 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 study site 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

444 *Management implications*

445 As ecosystem engineers, wild ungulates play a major role in mountain landscapes, by their

446 movements (*e.g.* seed dispersal via zoochory, Albert *et al.,* 2015) and grazing (*e.g.* plant

447 selection via grazing, Austrheim & Eriksson, 2001). Most of the populations of large

448 mammals living in the Alps and surrounding massifs have to face several kinds of

449 disturbance, ranging from hiking to cable car ebb and flow, while constrained by increasing

450 temperature during summer due to climate change (Brivio *et al.,* 2016). As tourism

451 development is often a pillar of the local economy, the right balance must be found between

452 natural environment and tourism management (Reynolds & Braithwaite, 2001). Human

453 impact on chamois could become an issue given that it may decrease the size of their suitable

454 habitats (Peksa & Ciach, 2015), generate a necessary reorganisation of their circadian activity

455 patterns, and reduce their ability to satisfactorily cope with thermal stress, particularly in the

456 context of increasing temperatures. The interaction between those factors could eventually

457 jeopardise their demography if particular attention is not paid in conserving habitats

458 providing both shelter against summer heat and human disturbance (Frid & Dill, 2002;

459 Chirichella, Stephens, Mason, & Apollonio, 2021). Our study contributes to filling the

460 knowledge gap on the cumulative effects of weather and human disturbance on chamois

461 circadian activity in this context of ongoing socio-environmental changes (Corlatti *et al.,*

462 2022).

19

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.

Acknowledgments

Conflict of Interest

The authors declared they have no conflict of interest.

Data availability statement

Data will be available after acceptance of the manuscript.

References

Albert, A., Auffret, A. G., Cosyns, E., Cousins, S. A. O., D'hondt, B., Eichberg, C., Eycott, A. E., Heinken, T., Hoffmann, M., Jaroszewicz, B., & others. (2015). Seed dispersal by ungulates as an ecological filter: A trait-based meta-analysis. Oikos, 124(9), 1109–1120.

Anderwald, P., Campell Andri, S., & Palme, R. (2021). Reflections of ecological differences? Stress responses of sympatric Alpine chamois and red deer to weather, forage quality, and human disturbance. Ecology and Evolution, 11(22), 15740–15753. https://doi.org/10.1002/ece3.8235

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., & Jenni-Eiermann, S. (2007). Spreading free-riding snow sports represent a novel serious threat for wildlife. Proceedings of the Royal Society B: Biological Sciences, 274(1614), 1219–1224.

Austrheim, G., & Eriksson, O. (2001). Plant species diversity and grazing in the Scandinavian mountains-patterns and processes at different spatial scales. Ecography, 24(6), 683–695.

Beniston, M. (2003). Climatic change in mountain regions: a review of possible impacts. Climate Variability and Change in High Elevation Regions: Past, Present & Future, 5–31.

Benoist, S., Garel, M., Cugnasse, J.-M., & Blanchard, P. (2013). Human disturbances, habitat characteristics and social environment generate sex-specific responses in vigilance of Mediterranean mouflon. PLoS One, 8(12), e82960.

Bivand, R., & Lewin-Koh, N. (2022). maptools: Tools for Handling Spatial Objects. https://cran.r-project.org/package=maptools

Bonnot, N. C., Couriot, O., Berger, A., Cagnacci, F., Ciuti, S., De Groeve, J. E., Gehr, B., Heurich, M., Kjellander, P., Kröschel, M., & others. (2020). Fear of the dark?

511   Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe.

512   Journal of Animal Ecology, 89(1), 132–145. https://doi.org/10.1111/1365-2656.13161

513   Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., & Hewison,

514   A. J. (2013). Habitat use under predation risk: hunting, roads and human dwellings

515   influence the spatial behaviour of roe deer. European Journal of Wildlife Research,

516   59(2), 185–193.

517   Bourgoin, G, Garel, M., Van Moorter, B., Dubray, D., Maillard, D., Marty, E., & Gaillard, J.-

518   M. (2008). Determinants of seasonal variation in activity patterns of mouflon. Canadian

519   Journal of Zoology, 86(12), 1410–1418.

520   Bourgoin, G., Garel, M., Blanchard, P., Dubray, D., Maillard, D., & Gaillard, J.-M. (2011).

521   Daily responses of mouflon (Ovis gmelini musimon x Ovis sp.) activity to summer

522   climatic conditions. Canadian Journal of Zoology, 89(9), 765–773.

523   https://doi.org/10.1139/Z11-046

524   Brivio, F., Bertolucci, C., Tettamanti, F., Filli, F., Apollonio, M., & Grignolio, S. (2016). The

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

526   conditions. Behavioral Ecology and Sociobiology, 70(8), 1291–1304.

527   Byers, J. A. (1997). American pronghorn: social adaptations and the ghosts of predators past.

528   University of Chicago Press.

529   Calenge, C. (2006). The package adehabitat for the R software: tool for the analysis of space

530   and habitat use by animals. Ecological Modelling, 197, 1035.

531   Carnevali, L., Lovari, S., Monaco, A., & Mori, E. (2016). Nocturnal activity of a diurnal

532   species, the northern chamois, in a predator-free Alpine area. Behavioural Processes,

533   126, 101–107.

534   Chanteloup, L., Perrin-Malterre, C., Duparc, A., & Loison, A. (2016). Quels points de vue sur

535   les espaces partagés entre humains et animaux sauvages? Espaces et Sociétés, 1, 33–47.

536   Chassagneux, A., Calenge, C., Marchand, P., Richard, E., Guillaumat, E., Baubet, E., & Saïd,

537   S. (2020). Should I stay or should I go? Determinants of immediate and delayed

538   movement responses of female red deer (Cervus elaphus) to drive hunts. Plos One,

539   15(3), e0228865.

540   Chirichella, R., Stephens, P. A., Mason, T. H. E., & Apollonio, M. (2021). Contrasting

541   effects of climate change on Alpine chamois. The Journal of Wildlife Management,

542   85(1), 109–120.

543   Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1989). Fitness costs of gestation and

544   lactation in wild mammals. Nature, 337(6204), 260–262.

545   https://doi.org/10.1038/337260a0

546   Corlatti, L., Iacolina, L., Safner, T., Apollonio, M., Buzan, E., Ferretti, F., Hammer, S. E.,

547   Herrero, J., Rossi, L., Serrano, E., & others. (2022). Past, present and future of chamois

548   science. Wildlife Biology, e01025. https://doi.org/10.1002/wlb3.01025

549   Courbin, N., Garel, M., Marchand, P., Duparc, A., Debeffe, L., Börger, L., & Loison, A.

550   (2022). Interacting lethal and nonlethal human activities shape complex risk tolerance

551   behaviors in a mountain herbivore. Ecological Applications, e2640.

552   https://doi.org/10.1002/eap.2640

553   Darmon, G., Bourgoin, G., Marchand, P., Garel, M., Dubray, D., Jullien, J.-M., & Loison, A.

554   (2014). Do ecologically close species shift their daily activities when in sympatry? A

555   test on chamois in the presence of mouflon. Biological Journal of the Linnean Society,

556   111(3), 621–626. https://doi.org/10.1111/bij.12228

557   Duparc, A. (2016). Dynamiques spatio-temporelles des ressources alimentaires et des

558   activités humaines: impacts sur la sélection d'habitat d'un grand herbivore de

559   montagne. Université Grenoble Alpes.

560   Duparc, A., Redjadj, C., Viard-Crétat, F., Lavorel, S., Austrheim, G., & Loison, A. (2013).

561   Co-variation between plant above-ground biomass and phenology in sub-alpine

562   grasslands. Applied Vegetation Science, 16(2), 305–316.

563   Fattorini, N., Brunetti, C., Baruzzi, C., Chiatante, G., Lovari, S., & Ferretti, F. (2019).

564   Temporal variation in foraging activity and grouping patterns in a mountain-dwelling

565   herbivore: Environmental and endogenous drivers. Behavioural Processes, 167,

566   103909.

567   French, S. S., González-Suárez, M., Young, J. K., Durham, S., & Gerber, L. R. (2011).

568   Human disturbance influences reproductive success and growth rate in California sea

569   lions (Zalophus californianus). PloS One, 6(3), e17686.

570   https://doi.org/10.1371/journal.pone.0017686

571   Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk.

572   Conservation Ecology, 6(1). https://doi.org/10.5751/es-00404-060111

573   Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toigo, C. (2000).

574   Temporal variation in fitness components and population dynamics of large herbivores.

575   Annual Review of Ecology and Systematics, 31(1), 367–393.

576   https://doi.org/10.1146/annurev.ecolsys.31.1.367

577   Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of

578   human disturbance on wildlife nocturnality. Science, 360(6394), 1232–1235.

579   https://doi.org/10.1126/science.aar7121

580   Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., & Stoffel, M. (2014). 21st

581   century climate change in the European Alps - A review. Science of the Total

582   Environment, 493, 1138–1151.

583   Greives, T. J., Kingma, S. A., Kranstauber, B., Mortega, K., Wikelski, M., van Oers, K.,

584   Mateman, A. C., Ferguson, G. A., Beltrami, G., & Hau, M. (2015). Costs of sleeping in:

585   circadian rhythms influence cuckoldry risk in a songbird. Functional Ecology, 29(10),

586   1300–1307.

587   Hagemoen, R. I. M., & Reimers, E. (2002). Reindeer summer activity pattern in relation to

588   weather and insect harassment. Journal of Animal Ecology, 71(5), 883–892.

589   Hamel, S., & Côté, S. D. (2008). Trade-offs in activity budget in an alpine ungulate:

590   contrasting lactating and nonlactating females. Animal Behaviour, 75(1), 217–227.

591   Kearney, M. R., Gillingham, P. K., Bramer, I., Duffy, J. P., & Maclean, I. M. D. (2020). A

592   method for computing hourly, historical, terrain-corrected microclimate anywhere on

593   Earth. Methods in Ecology and Evolution, 11(1), 38–43.

594   Kearney, M. R., & Porter, W. P. (2017). NicheMapR - an R package for biophysical

595   modelling: the microclimate model. Ecography, 40(5), 664–674.

596   Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of recreation

597   on animals revealed as widespread through a global systematic review. PloS One,

598   11(12), e0167259.

599   Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison:

600   reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian

601   Journal of Zoology, 79(8), 1401–1409.

602   Lesmerises, F., Déry, F., Johnson, C. J., & St-Laurent, M.-H. (2018). Spatiotemporal

603   response of mountain caribou to the intensity of backcountry skiing. Biological

604   Conservation, 217, 149–156.

605   Li, C., Jiang, Z., Feng, Z., Yang, X., Yang, J., & Chen, L. (2009). Effects of highway traffic

606   on diurnal activity of the critically endangered Przewalski gazelle. Wildlife Research,

607   36(5), 379–385.

608   Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator

609   behavior: the predation risk allocation hypothesis. The American Naturalist, 153(6),

610   649–659.

611   Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in

612   mammals. The American Naturalist, 125(6), 873–878. https://doi.org/10.1086/284385

613   Loison, A., Jullien, J.-M., & Menaut, P. (1999). Subpopulation structure and dispersal in two

614   populations of chamois. Journal of Mammalogy, 80(2), 620–632.

615   Long, R. A., Martin, T. J., & Barnes, B. M. (2005). Body temperature and activity patterns in

616   free-living arctic ground squirrels. Journal of Mammalogy, 86(2), 314–322.

617   Lopez, J. F. (2001). Inventaire systématique de la flore et de la végétation du Massif des

618   Bauges.

619   Maclean, I. M. D., Mosedale, J. R., & Bennie, J. J. (2019). Microclima: An r package for

620   modelling meso-and microclimate. Methods in Ecology and Evolution, 10(2), 280–290.

621   Marchand, P., Garel, M., Bourgoin, G., Dubray, D., Maillard, D., & Loison, A. (2014).

622   Impacts of tourism and hunting on a large herbivores spatio-temporal behavior in and

623   around a French protected area. Biological Conservation, 177, 1–11.

624   Marchand, P., Garel, M., Bourgoin, G., Dubray, D., Maillard, D., & Loison, A. (2015). Sex-

625   specific adjustments in habitat selection contribute to buffer mouflon against summer

626   conditions. Behavioral Ecology, 26(2), 472–482.

627   Pęksa, Ł., & Ciach, M. (2015). Negative effects of mass tourism on high mountain fauna: the

628   case of the Tatra chamois Rupicapra rupicapra tatrica. Oryx, 49(3), 500–505.

629   Palmer M. S., Gaynor K. M., Becker J. A., Abraham J. O., Mumma M. A., & Pringle R. M.

630   (2022). Dynamic landscapes of fear: understanding spatiotemporal risk. Trends in

631   Ecology & Evolution. https://doi.org/10.1016/j.tree.2022.06.007

632 Pepin, N., Bradley, R. S., Diaz, H. F., Baraër, M., Caceres, E. B., Forsythe, N., Fowler, H.,

633   Greenwood, G., Hashmi, M. Z., Liu, X. D., & others. (2015). Elevation-dependent

634   warming in mountain regions of the world. Nature Climate Change, 5(5), 424–430.

635 Phillips, G. E., & Alldredge, A. W. (2000). Reproductive success of elk following

636   disturbance by humans during calving season. The Journal of Wildlife Management,

637   521–530.

638 Reynolds, P. C., & Braithwaite, D. (2001). Towards a conceptual framework for wildlife

639   tourism. Tourism Management, 22(1), 31–42.

640 Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J., & Musiani, M.

641   (2011). Human activity differentially redistributes large mammals in the Canadian

642   Rockies National Parks. Ecology and Society, 16(3).

643 Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015).

644   Increased tolerance to humans among disturbed wildlife. Nature Communications, 6(1),

645   1–8.

646 Saper, C. B., Lu, J., Chou, T. C., & Gooley, J. (2005). The hypothalamic integrator for

647   circadian rhythms. Trends in Neurosciences, 28(3), 152–157.

648 Scott, D. (2006). Global environmental change and mountain tourism. Tourism and Global

649   Environmental Change, 54–75.

650 Searle, K. R., Hobbs, N. T., & Gordon, I. J. (2007). It's the" foodscape", not the landscape:

651   using foraging behavior to make functional assessments of landscape condition. Israel

652   Journal of Ecology and Evolution, 53(3–4), 297–316.

653 Semenzato, P., Cagnacci, F., Ossi, F., Eccel, E., Morellet, N., Hewison, A. J. M., Sturaro, E.,

654   & Ramanzin, M. (2021). Behavioural heat-stress compensation in a cold-adapted

655   ungulate: Forage-mediated responses to warming Alpine summers. Ecology Letters,

656   24(8), 1556–1568.

657   Strava. 2022. Strava Global Heatmap. https://www.strava.com/heatmap.

658   Tablado, Z., & Jenni, L. (2017). Determinants of uncertainty in wildlife responses to human

659   disturbance. Biological Reviews, 92(1), 216–233.

660   Takahashi, J. S., Hong, H.-K., Ko, C. H., & McDearmon, E. L. (2008). The genetics of

661   mammalian circadian order and disorder: implications for physiology and disease.

662   Nature Reviews Genetics, 9(10), 764–775.

663   Thorsen, N. H., Bischof, R., Mattisson, J., Hofmeester, T. R., Linnell, J. D. C., & Odden, J.

664   (2022). Smartphone app reveals that lynx avoid human recreationists on local scale, but

665   not home range scale. Scientific Reports, 12(1), 1–13.

666   van Beest, F. M., & Milner, J. M. (2013). Behavioural responses to thermal conditions affect

667   seasonal mass change in a heat-sensitive northern ungulate. PloS One, 8(6), e65972.

668   Watanuki, Y., & Nakayama, Y. (1993). Age difference in activity pattern of Japanese

669   monkeys: effects of temperature, snow, and diet. Primates, 34(4), 419–430.

670   Wheaton, B. (2010). Introducing the consumption and representation of lifestyle sports. Sport

671   in Society, 13(7–8), 1057–1081.

672   Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood

673   estimation of semiparametric generalized linear models. Journal of the Royal Statistical

674   Society (B), 73(1), 3–36.

675   Wood, S. N. (2017). Generalized Additive Models: An Introduction with R (2nd ed.).

676   Chapman and Hall/CRC.

677   Wood, S. N, Goude, Y., & Shaw, S. (2015). Generalized additive models for large data sets.

678   Journal of the Royal Statistical Society: Series C (Applied Statistics), 64(1), 139–155.

679   Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-

680   range studies. Ecology, 70(1), 164–168.

681   Xu, W., Gong, Y., & Wang, H. (2021). Alert time reflects the negative impacts of human

682   disturbance on an endangered bird species in Changbai Mountain, China. Global

683   Ecology and Conservation, 28, e01709.

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]

695 Table 2: Timing of the morning and evening peaks (UTC) estimated from predicted circadian

696 activity patterns (median value of the bootstraps distribution, $n = 1001$) of northern chamois

697 of the National Game and Hunting Reserve of Les Bauges massif, in summer (June to

698 September, 2004-2020), according to temperature and human disturbance. Values between

699 brackets correspond to 2.5% and 97.5% quantiles (95% confidence intervals) estimated with

700 bootstraps.

701

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]

702

703   Figure 1: predicted circadian activity patterns (activity ranges between 0 for no activity, to 1

704   for the highest level of activity) of female northern chamois in the National Game and

705   Hunting Reserve of Les Bauges massif, in summer (15th June to 7th September, 2004-2020),

706   according to temperature (blue: cold day; red: hot day) and human disturbance: a) chamois

707   living in a weakly exposed area during a weakly disturbed day; b) chamois living in a weakly

708   exposed area during a highly disturbed day; c) chamois living in a highly exposed area during

709   a weakly disturbed day; d) chamois living in a highly exposed area during a highly disturbed

710   day. Solid lines represent predicted values from the model, shaded areas represent 95%

711   confidence intervals. Time of the day represents hours in Coordinated Universal Time (UTC).
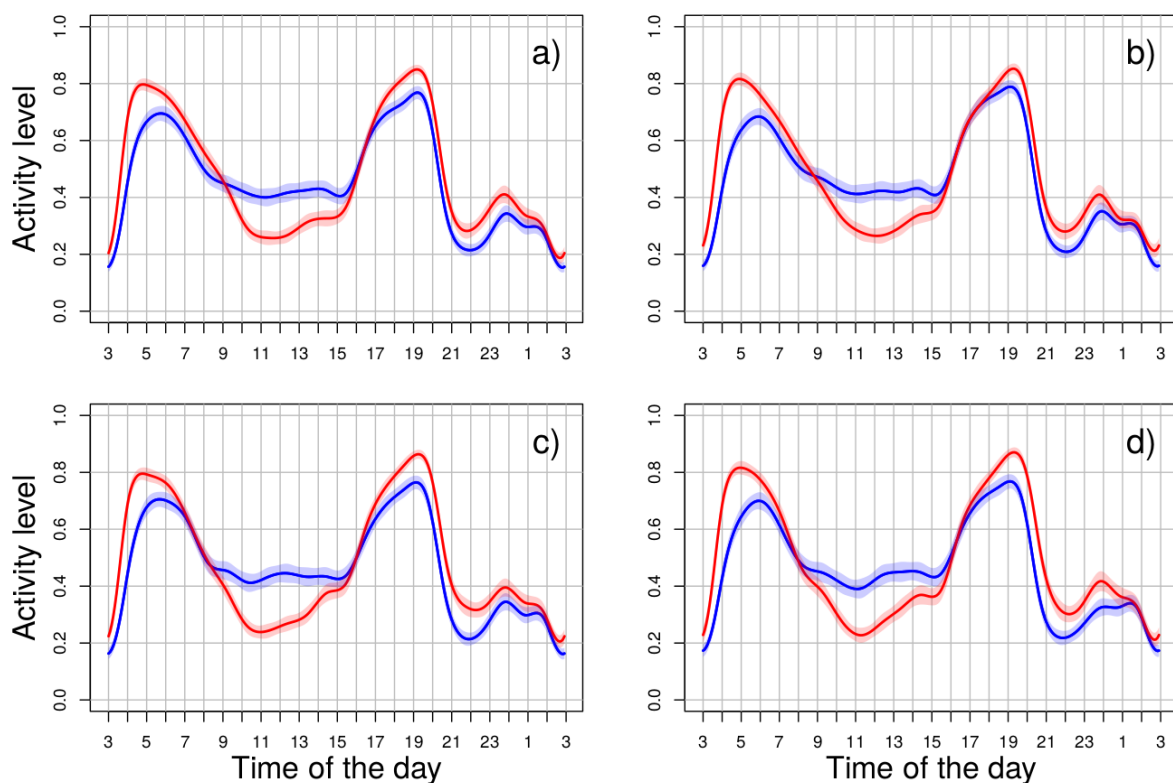
712

713

714   Figure 2: Area Under Curve (AUC) differential (unitless) between the reference situation (*i.e.*

715   chamois living in a weakly exposed area during a cold weakly disturbed day) and the

716   situation of interest, a combination of different levels of temperature (blue: cold day; red: hot

717   day), spatial (dot: low exposure; triangle: high exposure) and hikers attendance (low = week

718   days; high = week-ends): a) total, b) diurnal and c) nocturnal activity. AUC are calculated

719   from predicted circadian activity patterns of northern chamois of the National Game and

720   Hunting Reserve of Les Bauges massif, in summer (June to September, 2004-2020; see Fig.

721   1). The central point represents the median, and the vertical bars represent the 2.5% and

722   97.5% quantiles of the bootstraps distribution ($n = 1001$). Note the change of scale between

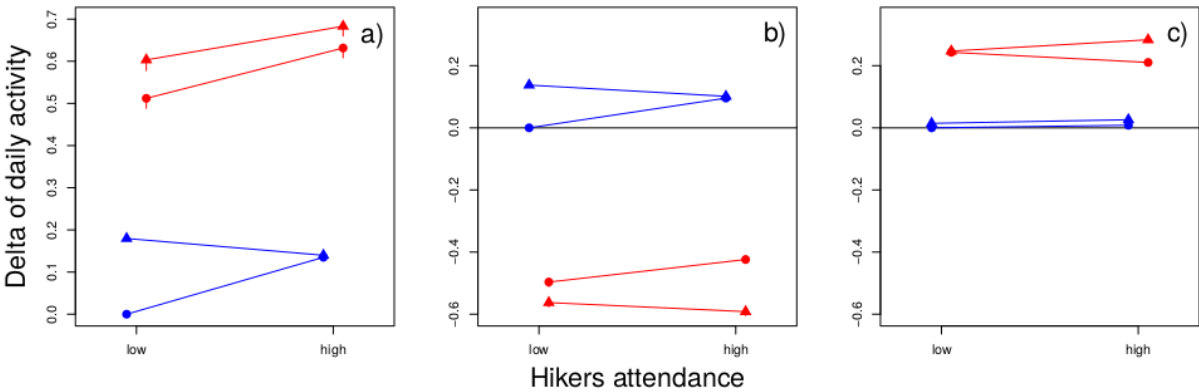723   Fig. 2.a and Fig. 2.b and 2.c.

724

725

726 Figure 3: Activity Peak Timing (APT) differential (in minutes) between the reference

727 situation (*i.e.* chamois living in a weakly exposed area during a cold weakly disturbed day)

728 and the situation of interest, a combination of different levels of temperature (blue: cold day;

729 red: hot day), spatial (dot: low exposure; triangle: high exposure) and temporal human

730 disturbance: a) morning and b) evening peak. APT are calculated from predicted circadian

731 activity patterns of northern chamois of National Game and Hunting Reserve of Les Bauges

732 massif, in summer (June to September, 2004-2020). The central point represents the median,

733 and the vertical bars represent the 2.5% and 97.5% quantiles of the bootstraps distribution (*n*

734 = 1001). The points have been shifted on both sides to improve readability.

735

736