

# Interacting lethal and nonlethal human activities shape complex risk tolerance behaviors in a mountain herbivore

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- 1 Running head: Human-induced tolerance adjustments
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### 3 Title: Interacting lethal and nonlethal human activities shape complex risk tolerance

- 4 behaviors in a mountain herbivore
- 5
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- 22 Open Research statement: data will be deposited in Figshare upon acceptance of the manuscript.

#### 23 ABSTRACT

Animals perceive human activities as risky and generally respond with fear-induced proactive 24 behaviors, to buffer the circadian patterns of lethal and nonlethal disturbances, such as diel 25 migrations between risky places during safe nighttime and safer places during risky daytime. 26 However, such responses potentially incur costs through movement or reduced foraging time, 27 hence, individuals should adjust their tolerance when human activities are harmless, through 28 habituation. Yet this is a challenging cognitive task when lethal and nonlethal risks co-occur, 29 30 forming complex landscapes of fear. The consequences of this human-induced complexity have 31 however rarely been assessed. We studied individual diel migration dynamics of chamois (Rupicapra rupicapra rupicapra, 89 GPS-tracked individual-years) from/to trails in the French 32 33 Alps, in areas with co-occurring lethal (hunting) and nonlethal (hiking and skiing) disturbances, 34 with different intensities across seasons. We developed a conceptual framework relying on the 35 risk-disturbance hypothesis and habituation to predict tolerance adjustments of chamois under 36 various disturbance contexts and across contrasted seasonal periods. Based on spatial and 37 statistical analyses combining periodograms and multinomial logistic models, we found that diel migration in relation to distance to a trail was a consistent response by chamois (~85% of 38 individuals) to avoid human disturbance during daytime, especially during the hiking and hunting 39 40 periods. Such behavior unveiled a low tolerance of most chamois to human activities, although there was considerable inter-individual heterogeneity in diel migration. Chamois performed 41 42 shorter diel migrations in areas highly disturbed by hikers. Interestingly there was an increased 43 tolerance among the most disturbed diel migrants, potentially through habituation. Crucially, chamois which were most human-habituated during the hiking period remained more tolerant in 44 the subsequent harvesting periods, which could increase their risk of being harvested. In contrast, 45

46 individuals less tolerant to hiking performed longer diel migrations when hunting risk increased,

47 and compared to hiking, hunting exacerbated the threshold distance to trails triggering diel

48 migrations. No carry-over effect of hunting beyond the hunting period was observed. In

49 conclusion, complex human-induced landscapes of fear with co-occurring disturbances by nature-

50 based tourism and hunting may shape unexpected patterns of tolerance to human activities,

51 whereby animal tolerance could become potentially deleterious for individual survival.

52

#### 53 **KEYWORDS**

behavioral plasticity; diel migration; French Alps, hunting; landscape of fear; nature-based
tourism; *Rupicapra rupicapra rupicapra*; trail network

56

#### 57 INTRODUCTION

The direct effect of human exploitation on animal survival has led to anthropogenic defaunation 58 with direct consequences for ecosystem functioning worldwide (Dirzo et al., 2014). However, 59 60 wildlife suffers also from the expansion of human activities in natural areas and from the resulting disturbance, defined as the deviation from the behavior an animal would have had 61 62 without human influences (Frid & Dill, 2002; Sih et al., 2010; Tuomainen & Candolin, 2011). Indeed, human activities can affect animals indirectly by increasing their nocturnality (Marchand 63 et al., 2014; Gaynor et al., 2018; Bonnot et al., 2020), reducing their movement range (Tucker et 64 al., 2018) and altering their space use and access to food (Harris et al., 2014; Richard & Côté, 65 2016; Sawyer et al., 2017; Ciach & Peksa, 2019). Similarly to the non-consumptive risk effects of 66 67 predation (Lima, 1998; Preisser et al., 2005; Creel, 2018; Say-Sallaz et al., 2019), such humaninduced behavioral changes can cascade to population dynamic components (Frid & Dill, 2002;
Lesmerises et al., 2017; Sawyer et al., 2017; Gaynor et al., 2018) and disrupt food web dynamic
processes, such as herbivory, intra- and inter-specific competition and predator-prey interactions
(Fahrig, 2007; Tuomainen & Candolin, 2011; Courbin et al., 2014; Gaynor et al., 2019; Guiden et
al., 2019).

Nature-based tourism, defined as visitation to a natural destination for recreational 73 harmless activities (e.g., hiking, skiing), has increased tremendously in the last decades 74 (Newsome, 2014; Balmford et al., 2015). It creates nonlethal disturbances which can impact 75 animal populations through multiple pathways (reviewed in Tablado & Jenni, 2017; Wolf et al., 76 2019), with animals often perceiving nonlethal human disturbances as a predation risk (Frid & 77 78 Dill, 2002; Gaynor et al., 2019). The risk-disturbance hypothesis stipulates that 'predation and 79 nonlethal disturbance stimuli create similar trade-offs between avoiding perceived risk and other 80 fitness-enhancing activities' (Frid & Dill, 2002). It formalizes that fear effect can have important 81 cascading effects on individual behavior and demography (Brown et al., 1999; Laundré et al., 82 2001; Gaynor et al., 2019), and may even exceed those from direct predation or harvest effects 83 (Creel & Christianson, 2008; Ciuti et al., 2012). Such fear effects, though far from being easy to document (Say-Sallaz et al., 2019), especially when they affect behavior, are nonetheless 84 85 receiving an increasing level of empirical support (Frid & Dill, 2002; Tablado & Jenni, 2017). Behavioral responses to fear can occur in the form of reactive responses, such as the well-studied 86 flight response in reaction to humans (Stankowich, 2008; Blumstein, 2016), but also as proactive 87 88 anti-predator behaviors (Valeix et al., 2009; Marchand et al., 2014; Basille et al., 2015; Creel, 2018; Courbin et al., 2019; Gaynor et al., 2019). These proactive responses are more likely to 89 90 arise when animals face a spatiotemporally predictable risk (Creel, 2018; Kohl et al., 2018;

91 Courbin et al., 2019; Riotte-Lambert & Matthiopoulos, 2020), i.e. within predictable landscapes 92 of fear, where the "landscape of fear" is defined as the spatial variation in the perception of longterm risk (Laundré et al., 2001; Laundré et al., 2010). Nature-based tourism, which typically 93 occurs during daytime, in delimited areas and along trails, should therefore lead animals to adopt 94 such proactive responses. Accordingly, changes in individual space use (e.g., Thiel et al., 2008; 95 Lesmerises et al., 2018) and in day/night allocation of activities (e.g., Marchand et al., 2014; 96 97 Peksa & Ciach, 2018) have been unveiled in several herbivore species in response to hiking and backcountry skiing. Ultimately, in such contexts, including spatially-restricted and temporally 98 99 predictable human disturbance, animals may perform movement tactics to decrease risk such as 100 diel migration (Courbin et al., 2019). This routine behavior allows animals to avoid the source of disturbance and stress-mediated costs associated with reactive behavior by using risky areas 101 during the safer period (e.g. nighttime) and by moving away from the same spatially risky areas 102 103 during risky times (e.g. daytime; Creel, 2018). The diel migration tactic was firstly conceptualized in aquatic systems as an anti-predator behavior (Iwasa, 1982; Alonzo et al., 2003). 104 More recently, diel migration was quantified in response to natural predation (Courbin et al., 105 2019) and has been observed in response to hunting (Tolon et al., 2009; Bonnot et al., 2013; 106 Marchand et al., 2014; Fortin et al., 2015) and nature-based tourism (Lesmerises et al., 2017). 107 108 The occurrence and extent of diel migration may therefore be a meaningful metrics of proactive responses to highly predictable perceived risks in various ecological systems. 109 110 However, proactive responses to nature-based tourism may entail costs related to changes 111 in movement, activity budget, energy expenditures and lost foraging opportunities (see reviews

112 Frid & Dill, 2002; Tablado & Jenni, 2017). Spatial proactive responses that involve avoiding

113 disturbed areas also prevent updates of the risk level assessment, a potential damaging situation.

Therefore, adjustments of animal tolerance to the level of nonlethal risk are expected to minimize 114 115 these costs (Enggist-Diiblin & Ingold, 2003; Sih, 2013; Samia et al., 2015) and allow coexistence with humans (Samia et al., 2015). An increased tolerance means a decreased reactiveness to a 116 stimulus. For example, animals may decrease their flight initiation distance (Stankowich, 2008; 117 Reimers et al., 2010) and vigilance (Schuttler et al., 2017) in areas with high levels of human 118 recreation. Animals may likewise increase their tolerance to repeated exposures to nonlethal 119 anthropogenic stimuli through habituation, up to a certain level of disturbance intensity (Frid & 120 Dill, 2002; Bejder et al., 2009; Geffroy et al., 2015; Blumstein, 2016; Fig. 1A). Habituation was 121 originally defined in neuroscience in the seminal works of Thompson and Spencer (1966) and 122 123 Groves and Thompson (1970), and recently reviewed in neuroscience by Rankin et al. (2009). It is a common and important response of animals to disturbance in the wild (Samia et al., 2015; 124 e.g., Dehaudt et al., 2019) with a high degree of variability among individuals (Blumstein, 2016; 125 Tablado & Jenni, 2017). Urbanization in birds is for example a severe case of increased tolerance 126 to humans, potentially driven by habituation (Vincze et al., 2016; Geffroy et al., 2020). Yet 127 identifying and measuring habituation in the field remains a challenging task (Bejder et al., 2009; 128 Blumstein, 2016), especially in complex situations with multiple sources of risk and disturbance. 129

For instance, the perception of nonlethal disturbance risk may be largely altered in ecosystems subject to an important diversification and intensification of nature-based tourism all year round, especially if co-occurring with hunting. In such cases, the presence of a human can have both lethal and nonlethal consequences. The key-question is then whether animals have the ability to assess the differences between humans performing different activities. If animals can distinguish hunters from other humans, they could specifically respond to hunting risk, while their tolerance to nonlethal disturbances would remain unchanged during the hunting period (Fig.

1B). Alternatively, if animals cannot distinguish that the lethal risk is only associated with 137 hunters and not with other recreationists, they would perceive an overall higher human 138 disturbance level and increase their responsiveness to all human activities during the hunting 139 period (Fig. 1C solid line). Outside the hunting period, animals may then either resume their 140 basal tolerance level (solid line) or continue being wary of humans (Fig. 1C dotted line). Hunters 141 may indeed trigger a carry-over effect inhibiting tolerance adjustments and habituation beyond 142 143 restricted hunting periods. The consequences of hunting on animal tolerance and habituation to other types of human activities may therefore be largely underestimated (Frid & Dill, 2002; 144 145 Gaynor et al., 2018). While there should be some benefits for individuals to tolerate and habituate 146 to nonlethal risks, recent works have argued that, in contrast, the most tolerant and humanhabituated individuals may lose their ability to respond to lethal risk (Geffroy et al., 2015). For 147 instance, they may continue to relax their antipredator behavior even during the hunting period. 148 Thus, undesirable tolerance to hunters may occur (Fig. 1C dashed line). Such mechanism may 149 have deleterious consequences for animal populations coping with reintroduction of natural 150 predators or experiencing short hunting periods (Geffroy et al., 2015, 2020). 151

152 Distinguishing nonlethal human stimuli and true predatory stimuli from hunters requires strong cognitive abilities that may outperform the capacities of hunted animals (Frid & Dill, 153 154 2002; Ciuti et al., 2012; Tablado & Jenni, 2017). Evidence show that ungulates have evolved high capacities to finely assess the predation risk posed by their natural predators, including 155 variation in the magnitude of risk (Liley & Creel, 2008). However, cues related to humans 156 engaged in various lethal and nonlethal recreational activities may be more difficult for prey to 157 interpret, especially if they co-occur in space and time and if animals have to constantly reassess 158 the risk during daytime due to frequent human passage. Consequently, under some conditions 159

(determined by the spatiotemporal variability of disturbance and the nature of activities), the 160 human-induced landscape of fear may become too complex to decipher for animals. Given the 161 increase of areas where nature-based tourism and hunting co-occur, the additive or multiplicative 162 outcome of the diversification of recreation activities on animal behavior needs to be investigated 163 in a comprehensive way (Geffroy et al., 2015). Accordingly, we aimed here to assess individual 164 responsiveness to predictable circadian patterns of nature-based tourism in a human-induced 165 166 landscape of fear, complicated by hunting seasonality (e.g., Ciuti et al., 2012). We posit that studying the seasonal dynamics of individual diel migration tactics should help us to better 167 168 understand how hunting shapes animal tolerance to nature-based tourism and highlight potential 169 maladaptive tolerant behavior. Our model species was chamois (Rupicapra rupicapra, a particularly relevant species to delve into the complexity of animal responses to human lethal 170 171 and nonlethal disturbances, as it faces nature-based tourism occurring all year round with an overlapping hunting period. Mountain ecosystems and associated fauna are particularly 172 vulnerable to the increase in outdoor recreation (Steven et al., 2011; Peksa & Ciach, 2015). We 173 benefited from a rare dataset combining a fine characterization of recreational activities (hiking, 174 skiing and hunting) and intensity of human disturbances for three contrasted seasons (Appendix 175 S1), together with an important long-term GPS monitoring for 89 chamois-years. Human 176 177 activities mostly occurred on a trail network that shaped a predictable daytime human-induced landscape of fear for chamois (Appendix S1). Within the framework outlined in Figure 1, we 178 predicted the responses of chamois under alternative scenarios entailing the ability or inability of 179 180 individuals to distinguish hunters from recreationists (Fig. 1B or C), the presence or absence of a carry-over effect of hunting and the persistent tolerant behavior to hunters (Fig. 1C). We then 181 tested for 1) existence of diel migration to buffer risk-disturbance during different periods. Given 182 that individuals varied in their exposure to risk, we expected individual differences in tolerance to 183

humans and further assessed 2) how individuals adjusted their diel migration to the riskdisturbance context. We studied the determinants of both the diel migration tactic in relation to trails and the spatial extent of diel migration at the individual level, during and outside the hunting period. We finally assessed which scenario was best supported by our empirical results and discussed the value of different diel migration tactics based on an assessment of proxies of their costs.

190

#### 191 METHODS

#### 192 *Study area*

The study took place in the National Game and Wildlife Reserve of Bauges Massif (hereafter 193 'Reserve'), located in the northern French Alps (45°40'N, 6°23'E, Fig. 2) between 2014 and 194 2018. The Reserve covers 5200 ha of a mountain landscape with altitude varying from 900 to 195 2200 m. Landscape cover is a compound of forests (56%) dominated by beech (Fagus sylvatica) 196 197 and fir (Abies alba), alpine grasslands (36%) and rocky areas (8%, Lopez 2001). Chamois feed in grasslands characterized by heterogeneous levels of biomass and quality of edible plants (Duparc 198 et al., 2020). Biomass and quality of edible resources were generally low close to trails (see 199 200 details in Appendix S2). Chamois had no natural predators in the study area, except for occasional non-resident wolves (Canis lupus), golden eagles (Aquila chrysaetos) and red foxes 201 (Vulpes vulpes), which may predate newborns. Chamois is the main hunted species within the 202 Reserve (70% of the total number of ungulates harvested), with on average 104 chamois shot 203 204 every year since 2006 over the 4900 ha area. Hunting was performed by small parties of 3 to 4

hunters. Mouflon (*Ovis gmelini musimon*, 20%), roe deer (*Capreolus capreolus*, 4%), wild boar
(*Sus scrofa*, 4%) and red deer (*Cervus elaphus*, 2%) are also hunted within the Reserve.

In addition to hunting, hiking and backcountry skiing are common recreational activities 207 208 within the Reserve. We delimited three periods associated with specific sources and levels of 209 human disturbances: (i) the hiking period (July and August) characterized by a high level of hiking activities only (hunting forbidden), (ii) the hunting period (September to November) when 210 211 hunting and moderate levels of hiking activities occurred, and (iii) the skiing period (January to March) when backcountry skiing and snowshoeing were the main sources of human disturbance 212 (see details in Appendix S1). Human activities were heterogeneously distributed within the 213 Reserve and hunting was prohibited in the Armenaz area (300 ha; Fig. 2). Thereby, the five 214 215 sectors where chamois were trapped were characterized by various levels of environmental and 216 anthropogenic disturbances (Fig. 2, Appendix S1: Figure S5).

217

#### 218 Defining the human-induced landscape of fear

The trail network shaped the backbone of human activities within the Reserve and was 219 considered as a good proxy of where human disturbances took place (see complete details in 220 221 Appendix S1). We considered two trail networks, one for the hiking and hunting periods and one for the skiing period, because snow cover reshaped the trail network seasonally (Fig. 2). Using an 222 independent GPS dataset collected on a large representative sample of hikers (n = 270 tracks in 223 2014 and 2015), hunters (n = 223 tracks between 2014 and 2018), and skiers (n = 83 tracks in 224 225 2015, Appendix S1), we found that hikers, hunters and skiers spent 97%, 61% and 81% of their 226 time on trails at daytime, respectively. We also determined that half of the chamois were

harvested less than 200 m away from a trail using the database of chamois harvesting sites since
2006 (n = 1112, Appendix S1: Figure S6).

We assessed spatial variation in the risk of encountering hikers or skiers along trails by 229 230 characterizing the relative intensity of use by hikers or skiers from Strava Global Heatmap (Strava, 2018; Appendix S1: Figure S1). Strava heatmap is a good proxy of relative human 231 frequentation (Corradini et al., 2021). In addition, we determined the risk of encountering hunters 232 by calculating the 95% utilization distribution (UD) of hunter GPS locations (n = 223 tracks, see 233 above and Appendix S1). We mapped the risk of being harvested by estimating the 95% UD of 234 235 chamois harvesting locations collected since 2006 (n = 1112, Appendix S1). Finally, we spatialized the risk of being seen by humans from a trail using a GIS viewshed analysis (for a 236 237 similar approach see Benoist et al., 2013) to account for the effect of vegetation structure and 238 visibility on animal tolerance (see Appendix S3; Tablado & Jenni, 2017; Wolf et al., 2019).

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#### 240 GPS and activity data for chamois

Eighty-seven adult chamois (70 females and 17 males) were trapped during the 2014-2018 241 summers using falling nets baited with artificial salt licks within grasslands at five sites (Fig. 2). 242 Individuals were weighed and their age at capture was determined by counting horn growth 243 annuli (Schröder & von Elsner-Schack, 1985). Individuals were equipped with GPS collars 244 (3300S Lotek Engineering Inc. or Vectronics GPS Plus-1C Store On Board) scheduled to record 245 one location every 1h or 2h continuously, or every 4h interspersed with periods of 20-min 246 interval recording during at least two consecutive days depending on periods and individuals. 247 248 Almost all individuals were monitored for only one year; the final dataset consisted of GPS tracks

for 55 chamois-years during the hiking period (48 females and 7 males), 89 chamois-years during the hunting period (71 females and 18 males), and 83 chamois-years during the skiing period (66 females and 17 males). Activity sensors on GPS collars continuously calculated activity as the difference in acceleration between two consecutive measurements taken every 0.25 sec along two axes, the forward/backward and sideways axes. From these measures the on-board data loggers derived and stored a standardized average activity value per-5 min interval, with values ranging between 0 (always inactive) and 255 (always highly active).

256

#### 257 Testing for diel migration of chamois

For each individual and time period, we tested for a cyclic variation in the distance to the closest 258 trail (hereafter 'distance to a trail') used by chamois over a 24h-period, i.e., a diel migration 259 representing the back-and-forth movement of chamois being away from trails during daytime and 260 close to trails during nighttime. We fitted Lomb-Scargle periodogram (Ruf, 1999), a least-squares 261 262 spectral analysis, based on the distance to a trail calculated from the GPS locations taken every 263 1h, 2h or 4h (during the skiing period only) depending on individuals. Here, locations taken with a 20-min interval were subsampled at a regular 1h interval. We considered that a chamois 264 265 performed a diel migration when a significant peak occurred within a 20 to 28h window (Courbin 266 et al., 2019). Significance of the highest peak, i.e., whether the timing of the displacement related 267 to trails was different from a random expectation, was estimated by computing the probability of 268 random peaks reaching or exceeding the observed peak (Ruf, 1999). Note that the schedule of 269 GPS locations did not affect the periodogram shape (peak locations) and had an effect on the 270 magnitude of the peak only (not its significance). After testing for the presence of a diel cycle for 271 each chamois, we studied how individuals adjusted their tolerance to the risk-disturbance context

by investigating both the changes in the diel migration tactics and the spatial extent of dielmigration.

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#### 275 Dynamic and determinants of diel migration tactics

Individual chamois most tolerant to human disturbance may relax their diel response, i.e. they 276 may not perform diel migration or their diel cycle may not be necessarily the main cyclic 277 response over the short-term. Hence, we refined the role of the diel cycle in chamois movement 278 patterns to trails and assessed whether their diel cycle was the most important cycle over 48h. We 279 refitted the periodogram within a 6 to 48h window for each chamois and tested the significance 280 of the highest peak. Combining the results of the two periodograms (20-28h and 6-48h) for each 281 282 individual, we determined three diel migration (DM) tactics based on the importance of the diel cycle: 1) main-DM tactic: the diel migration was the main cyclic response to trails for chamois 283 according to the randomization procedure, i.e., the highest significant peak occurred within a 20-284 285 28h window for both periodograms, 2) *minor-DM* tactic: the diel migration occurred, but was not 286 the main cyclic response to trails, i.e., the significant peak occurring for the 20-28h periodogram did not remain the highest significant peak within a 20-28h window for the 6-48h periodogram, 287 288 and 3) no-DM tactic: chamois did not perform diel migration, i.e., no significant peak was 289 detected within a 20-28h window for both periodograms. We reclassified chamois significantly 290 moving closer to trails during daytime than nighttime (diel migration in an opposite way, n = 3291 during hiking, 5 during hunting and 5 during skiing) as no-DM tactic (Appendix S4: Table S1).

We then tracked individual consistency and change among tactics between consecutive periods to assess the seasonal dynamics of individual diel migration tactics throughout the year. We summarized the results with a Sankey diagram (Weiner, 2017).

295 Finally, we assessed how the diel migration tactic of chamois was influenced by human disturbances within their home ranges during the hiking and hunting periods (only few chamois 296 performed diel migration during the skiing period, see Results). An individual home range was 297 computed as the 95% UD derived from its GPS locations during a given period and year using 298 299 biased random bridges (Benhamou, 2011) on a 25-m resolution grid (Lmin = 15m, Tmax = twice 300 times the sampling rate and hmin = 100m). We used locations recorded with a regular 1h, 2h or 4h interval (here, locations taken with a 20-min interval were subsampled at a regular 4h 301 302 interval). We fitted a multinomial logistic model with a three-level response variable (main-DM, 303 minor-DM, no-DM) for each period. Models included four covariates related to the human-304 induced landscape of fear estimated at the home range scale: the mean risk of encountering 305 hikers, the mean risk of being harvested, the mean risk of encountering hunters and the mean risk 306 of being seen by humans from trails (Appendices 1 and 3). For each covariate, we weighted the 307 risk value of each pixel by its UD value before averaging the risk values within the individual 308 home range. We tested for an effect of hunting on chamois tolerance to hikers during hiking and 309 hunting periods with an interaction between the mean risk of being harvested and the mean risk of encountering hikers (Fig. 1C dashed line). Hunting was not allowed during the hiking period 310 311 but a significant effect of hunting or of the interaction will reveal a carry-over effect of hunting 312 on chamois tolerance to nonlethal activities (Fig. 1C dotted line). We also added three individual characteristics: age and sex of chamois to consider the effect of intrinsic differences on tolerance 313 (Blumstein, 2016; Tablado & Jenni, 2017) and body mass to get insights on potential costs of the 314

different tactics. Individuals establishing their seasonal home range in areas with a high density 315 316 of trails cannot move away from a trail without moving close to another trail, limiting the range of their diel migration and potentially confounding the drivers of diel migration. We thus 317 controlled for the mean distance to trails available within the home range. All continuous 318 319 covariates were centered and scaled. Models did not include highly correlated variables (i.e. the ones for which  $|\mathbf{r}| > 0.6$ ) and had low multicollinearity with a condition index < 3.8 (Dormann et 320 al., 2013) at each period (see model details in the Appendix S5). We had 53 chamois-years during 321 322 the hiking period and 86 chamois-years during the hunting period.

323

#### 324 Quantification and determinants of the spatial extent of diel migration

325 We quantified the spatial extent of diel migration that can translate varying levels of chamois tolerance to human disturbance. We defined diel migration extent as the difference between the 326 median daytime distance to trails over individual GPS locations for the given day (hereafter 327 328 'daytime distance to a trail') and the median distance to trails over individual GPS locations 329 during the preceding night (hereafter 'nighttime distance to a trail') during the hiking and hunting periods. For each period, we modeled the daytime distance to a trail (response variable) in 330 331 relation to the nighttime distance to a trail (previous night; nonlinear relationship modeled with a 332 natural spline with four degrees of freedom) and the diel migration tactic (categorical predictor 333 with two levels: minor-DM and main-DM). We fitted linear mixed models with individual ID as 334 random intercept to account for repeated measurements on the same individuals. Then, we tested 335 for the effects of the risk-disturbance predictors within the seasonal home range (the mean risk of 336 encountering hikers and hunters, of being harvested and of being seen by humans from trail, all weighted by the UD value), as previously described. In accordance with our hypothetical 337

framework (Fig. 1C), we assessed if the mean risk of being harvested shaped the extent of diel 338 339 migration in response to the mean risk of encountering hikers during hiking and hunting periods, with an interaction term. As previously, a significant effect of hunting risk during the hiking 340 period will reveal a carry-over effect of hunting on chamois tolerance to hikers (Fig. 1C dotted 341 342 line). We expected that chamois responses to trail frequentation and hunting risk should depend on their distance to trails at night. We thus tested for interactions between the nighttime distance 343 344 to trails and the risk-disturbance predictors (see candidate models in Appendix S6: Tables S1 and 345 S2). Models also included the effects of individual features (age, sex, body mass) and we 346 controlled for the effect of the mean distance to trails available within the home range on diel 347 migration extent. All continuous predictors were centered and scaled. Akaike's information criterion corrected for finite sample size (AICc) was used to select the most parsimonious 348 349 candidate models. None of the candidate models included highly correlated variables  $(|\mathbf{r}| > 0.6)$ and had low multicollinearity with a condition index < 13 and a variance inflation factor < 2.2350 (Dormann et al., 2013). We relied on data from 1165 chamois-days from 44 chamois-years for 351 the hiking period, and 3088 chamois-days from 73 chamois-years for the hunting period. 352

353

#### 354 Assessing proxies of diel migration costs

First, we calculated for each chamois and each period the cumulative daily topographic distance travelled between consecutive GPS locations collected with a 20-min interval. We considered only days when GPS recorded all the 72 possible locations. We relied on data from 42, 76 and 14 chamois-years during the hiking, hunting and skiing periods, respectively (more details on data availability in Appendix S7: Table S1). Topographic distance was calculated based on a digital elevation model with a 1-m resolution (Institut National de l'Information Géographique et

Forestière) and by rediscretizing chamois path in regular 1-m steps. For hiking and hunting periods, we tested for differences in the daily distance travelled (response variable) between diel migration tactics (three-level categorical predictor) using a linear mixed model. We included individual ID as random intercept to account for non-independence of daily distances within an individual and controlled for the sex and age of chamois.

Second, we estimated the mean daily energy expenditure of chamois for each period. We 366 computed an index of daily activity Activity index =  $\sqrt{X^2 + Y^2}$ , with X and Y the standardized 367 average activity at each 5-min interval along the forward/backward and sideways, respectively 368 (Marchand et al., 2021). The activity index is strongly correlated to the dynamic body 369 acceleration metric (Benoit et al., 2020), which is a reliable index of energy expenditure in 370 371 animals (Wilson et al., 2020). We calculated the mean activity index for each day of each 372 chamois recording at least 284/288 activity data (96% of the full dataset). We relied on data from 39, 82 and 78 chamois-years during the hiking, hunting and skiing periods, respectively (more 373 details on data availability in Appendix S7: Table S1). For the hiking and hunting periods, we 374 assessed the differences in the daily activity (response variable) between diel migration tactics 375 (three-level categorical predictor) using a linear mixed model with individual ID as random 376 377 intercept and controlling for sex and age by including them as fixed effects.

378

We performed all analyses using R software v.3.6.2 (R Development Core Team, 2019) and
packages *lomb* for assessment of least-squares spectral analyses (Ruf, 1999), *riverplot* to plot the
Sankey diagram (Weiner, 2017), *adehabitatHR* for home range and UD computation (Calenge,
2006), *nnet* (Venables & Ripley, 2002) and *lme4* (Bates et al., 2015) for fitting multinomial

logistic regressions and linear mixed effect models, respectively, and *MuMIn* for model selection
(Barton, 2020).

385

#### 386 **RESULTS**

#### 387 Evidence for plastic diel migration

388 During the hiking and hunting periods, chamois were on average located significantly closer to a trail during nighttime than during daytime (Figs 3A, 3C; P<0.001, paired samples Wilcoxon 389 tests). This pattern was due to back-and-forth movements to trails between night and day with a 390 391 24-h periodicity at individual level, as shown by periodograms (Figs 3B, 3D, Appendix S4: Figure S4) for most individuals (n = 46/55 chamois-years during the hiking period using a main-392 DM or a minor-DM, n = 76/89 chamois-years during the hunting period using a main-DM or a 393 minor-DM, Appendix S4: Table S1). However, the diel spatial shift was highly variable between 394 individuals (Appendix S4: Figures S1 and S2) and highly context-dependent. Indeed, the distance 395 of diel migration varied with chamois nighttime location: the closer chamois were to a trail 396 during nighttime, the further they were from a trail during the next day (Figs 3A, 3C). For 397 example, chamois that were 50 m away from a trail at night (i.e., peak of the distribution) tended 398 to perform large diel migration (see Results section Determinants of the spatial extent of diel 399 migration). Importantly, the extent of the daytime movement away from a trail was highly 400 constrained by the low availability of areas away from a trail (dotted lines in Figs 3A, 3C) with a 401 median distance to a trail available within the home range of  $\sim 175$  m (Appendix S4: Table S2). 402 403 By contrast, such a diel migration did not occur during the skiing period (Figs 3E, 3F, Appendix 404 S4: Table S1, Figure S3).

405 Among the different periods, chamois thus showed evidence of adjusting their tolerance level to human disturbances by switching between diel migration tactics (Fig. 4). Most (~85%) 406 had a low tolerance and performed diel migrations (main-DM and minor-DM tactics) during 407 hiking and hunting periods, with the main-DM tactic being dominant (>50%; Fig. 4, Appendix 408 409 S4: Table S1). In addition, most chamois performing minor-DM during the hiking period switched to a main-DM tactic during the hunting period (Fig. 4). On the opposite, chamois were 410 411 located further away from trails during the less disturbed skiing period (Fig. 3E, Appendix S4: Table S2) and adopted a no-DM tactic (Fig. 4, Appendix S4: Table S1). It has to be noted that 412 four chamois out of 10 performing a diel migration lived 400 m away from trails during the 413 414 skiing period and the causal effect of trails on their diel migration pattern was thus questionable (Appendix S4: Figure S3). 415

416

#### 417 Determinants of diel migration tactics

418 During the hiking period, the diel migration tactic was neither related to hiker attendance to trail 419 networks and mean risk of being seen within individual home ranges, nor to individual characteristics (age, sex and body mass, Appendix S5: Table S1). Similarly, our results did not 420 421 support a carry-over effect of hunting during this period (Fig. 1C dotted line). In contrast, during 422 the hunting period, the patterns support that the diel migration tactic was largely driven by the 423 human-induced landscape of fear. After controlling for inter-individual variation in the 424 availability of trail networks within seasonal home ranges, the likelihood of displaying a main-DM tactic over the other tactics rapidly increased with increasing risk of being harvested (i.e. 425 426 ×4.1 between extreme values) and increasing risk of encountering hikers (i.e. ×4.4 between 427 extreme values), without significant interacting effects between both risks (Fig. 5, Appendix S5:

Table S2). Therefore, the data supported neither higher tolerance with increasing hiker attendance 428 (Fig. 1A) nor undesirable tolerance persistence in the choice of tactic during the hunting period 429 (Fig. 1C dashed lined). Chamois had also higher probabilities of using a main-DM tactic than a 430 minor-DM tactic when they used areas with a low mean risk of being seen and a low mean risk of 431 encountering hunters (Appendix S5: Table S2, Figures S1A, S1B). However, these latter effects 432 were weaker than the effects of risk of encountering hikers and of being harvested (the size 433 434 effects were 1.5 to 2 times lower). During the hunting period, females were most likely to use a 435 main-DM tactic, while no differences were observed for males (Appendix S5: Table S2, Figure 436 S1C). The choice of tactic did not depend on body mass and age.

437

#### 438 Determinants of the spatial extent of diel migration

The top-ranked model included an interaction between the distance to trails the previous night 439 and either the mean risk of encountering hikers during the hiking period or the mean risk of being 440 441 harvested during the hunting period ( $\Delta AICc$  with the second best models > 4, Appendix S6: 442 Tables S1 and S2). During both periods, chamois with home ranges located closest to trails made short diel migrations (Appendix S6: Tables S3 and S4). After controlling for trail availability 443 444 within individual home ranges, chamois indeed moved a lesser distance away from trails at 445 daytime when the risk of encountering hikers increased, especially when they were located within the first 100 m from a trail at the previous nighttime (Figs 6A, 6B, Appendix S6: Tables S3 and 446 447 S4). Moreover, diel migration behavior was triggered over a greater nighttime distance from trail at low than high encounter risk with hikers (Figs 6A, 6B). Overall, these findings support the 448 449 hypothesis that diel migrants developed a greater tolerance to hiker disturbance when naturebased tourism increased, whereas they displayed a low tolerance at low levels of hiker 450

disturbance (Fig. 1A). Daytime movements of chamois away from trails were not influenced by 451 452 the hunting risk during the hiking period (Appendix S6: Table S3) and there was no support for a carry-over effect of hunting outside the hunting period (Fig. 1C dotted line). During the hunting 453 period, chamois performed longer diel migrations with increasing mean risk of being harvested in 454 areas with a low risk of encountering hikers, while they did not respond to hunting risk at high 455 encounter risk with hikers (Fig. 6B, Appendix S6: Table S4). Hunting also exacerbated the 456 threshold nighttime distance to trails triggering diel migrations in chamois (i.e., 300 m) in areas 457 of low risk of encountering hikers. On average, when chamois were located at 50 m from a trail 458 459 at night during the hunting period, they moved 166 m away the next day when the risk of being 460 harvested was high and the encounter risk with hikers was low, 102 m when both risks were low, and only 50 m when the risk of encountering hikers was high independently of the hunting risk. 461 This suggests that chamois tolerant to hikers also increased their tolerance to hunting during the 462 harvesting period (Fig. 1C dashed line). The extent of diel migration was neither influenced by 463 the tactic, the mean risk of being seen, nor individual characteristics during both periods 464 (Appendix S6: Tables S3 and S4). 465

466

#### 467 Costs of diel migration

The diel migration behavior involved a higher daily distance travelled for chamois during the hunting period only, i.e., +370 m per 24h between main-DM and no-DM tactic (Appendix S7: Table S2, Figure S1). That represented > 33 additional kilometers travelled by diel migrant chamois over the three months of the harvesting period. Also, males travelled 453 m more than females each day during the hunting period (> 41 additional kilometers over the period), while they were less active than females during all periods (Appendix S7: Tables S2 and S3). Overall, chamois had similar energy expenditure within a period independently of the diel migration tactic
(Appendix S7: Table S3, Figure S1). Note that chamois increased their daytime and nighttime
activity when located within the first 100 m from a trail, especially during the hiking and hunting
periods (Appendix S8: Figure S1).

478

#### 479 **DISCUSSION**

Our study demonstrated how overlapping nature-based tourism and hunting shaped complex 480 proactive responses and tolerance patterns to human activities for a large mountain herbivore 481 species. Chamois were generally wary of humans: most individuals performed diel migration 482 (i.e., back-and-forth movements further away from trails during daytime and closer to trails 483 484 during nighttime) in response to the landscape of fear imposed by recreational activities, especially during hiking and hunting periods. Diel migration was increased during the hunting 485 period, unveiling additive risk effects. However, we found no carry-over effect of hunting beyond 486 487 the hunting period. Importantly, chamois performed shorter diel migration in areas highly 488 disturbed by hikers. Such behavior revealed increased tolerance to nonlethal human disturbance for the most disturbed diel migrants. Yet, the persistence of such tolerance to humans during the 489 490 hunting period could be maladaptative. Overall, we stress the importance to consider potential 491 deleterious survival consequences of animal tolerance adjustments to disturbances in multi-use 492 landscapes with complex human-induced landscapes of fear.

493

494 Diel migration: a common and plastic proactive response to spatiotemporally predictable
495 human activities

In agreement with the risk-disturbance hypothesis (Frid & Dill, 2002), most (~85%) chamois 496 performed a diel migration with back-and-forth movements to trails over a 24h cycle during the 497 hiking and hunting periods. Diel migrants were close to trails during nighttime (when humans are 498 absent) and moved towards areas at a median distance of  $\sim 140$  m away from a trail during 499 daytime (when human used trails). Importantly, this is a very relevant distance as the median 500 distance to a trail available within the home range was only ~175 m. This allowed chamois to 501 502 decrease their perceived risk associated with hikers and hunters, occurring nearly exclusively on or in the close proximity of trails. The avoidance of humans is largely demonstrated for chamois 503 in many study areas in the Alps (Hamr, 1988), for other mountain ungulates elsewhere 504 505 (Marchand et al., 2014; Peksa & Ciach, 2015; Richard & Côté, 2016), and ungulates in general (Stankowich, 2008). However, our results show the advantage of using diel statistics as proxies of 506 spatial adjustments to the variation in the landscape of fear associated with hiking and 507 backcountry skiing (Lesmerises et al., 2017, 2018). The emergence of diel migration requires a 508 strong spatiotemporal predictability of risk (Hays, 2003; Courbin et al., 2019). This is an inherent 509 property of human-induced landscape of fear, exacerbated in protected areas where humans 510 should comply with hiking on established trails (this study Appendix S1; Lesmerises et al., 2018). 511 Our findings concur with the general idea that environmental predictability has a major influence 512 513 on animal movements (Courbin et al., 2018; Gaynor et al., 2018; Riotte-Lambert & Matthiopoulos, 2020). 514

515 Diel migration was common in our population, but chamois shifted between diel 516 migration tactics and adjusted the spatial extent of their diel migration to varying levels of human 517 disturbances in a complex way (see details in the next sections). Overall, the seasonal increase in 518 human attendance and perceived risk from the skiing period to the hunting period triggered an

increased occurrence of the diel cycle at the individual level. However, home ranges overlapped 519 520 within and among periods (Appendix S4: Figure S5), which indicated that local changes in disturbances affected short-term movement tactics (i.e. the diel migration) rather than space use 521 522 at a broader scale. The inconsistent pattern of diel migration found during the skiing period was 523 likely induced by the lower trail frequentation (Appendix S1) and the general increasing in availability of distance of chamois to trails (median distance of chamois to trails within their 524 525 home range > 450 m) compared to other periods (~175 m, Appendix S4: Table S2). Overall, 526 chamois did not necessarily avoid winter areas frequented by humans. However, most trails were 527 covered by snow during the skiing period, and in addition, chamois left the Alpine grasslands 528 (where trails are located) to move to steeper slopes or at lower altitude (Appendix S4: Table S2).

529 While the movement of chamois away from trails during daytime was expected, the 530 rationale behind chamois moving closer to trails in the nighttime remains a challenging question. 531 One reason may be related to the distribution of food resources. In our study area, models based on vegetation surveys indicate an inconsistent pattern in increased or decreased abundance of 532 533 food resources for chamois with increasing distance from a trail during the summer (Appendix 534 S2: Figure S2). Food quality is especially important for chamois (Duparc et al., 2020) but only 535 slightly decreased for individuals getting closer to trails within the first 100 m from a trail 536 (Appendix S2: Figure S2). Thus overall in the study area we observed similar quantity and quality of food resources in areas between the median daytime (~140 m) and nighttime (~100 m) 537 538 distance to a trail of chamois during the hiking and hunting periods (Appendix S2: Figure S2). 539 Moreover, chamois were more active at day than night, and within the first 100 m from a trail at all the times during the hiking and hunting periods (Appendix S8). This suggests that activities 540 close to trails (<100 m) were not allocated to an important extent to foraging (e.g. resting, 541

542 vigilance and moving). Interestingly, also Tatra chamois (*Rupicapra rupicapra tatrica*) 543 experienced a decrease in the proportion of foraging in the daytime budget close to hiking trails (Peksa & Ciach, 2018). Together, these results suggest more frequent vigilance events or 544 relocation bouts interspersed with foraging activities closer to than away from trails. Overall, 545 546 chamois using diel migration did not have higher food opportunities at night and perceived increased risk all the time close to trails. Finally, chamois might need to forage on a sufficient 547 548 surface (area) to avoid resource depletion, and could move near trails to forage during nighttime, when the risk was lowest. Such a behavior would be strengthened in a density-dependence 549 550 context, as is the case for our chamois population (Garel et al., 2011). Another explanation not 551 related to food is the combined effects of the long-term competition for space depending on local density and the high spatial fidelity of female chamois keeping the same home ranges from year 552 553 to year (Loison et al., 1999, 2008). Accordingly, we found a higher propensity of diel migration for female chamois. Chamois could also move near to a trail at night to keep up-to-date 554 information on the spatio-temporal variations in human disturbance, using odor cues. For many 555 large ungulates, predator odors provide evidence of their recent passage and the likelihood of 556 their future presence in the area (e.g., red deer, Kuijper et al., 2014; caribou Rangifer tarandus 557 caribou, Latombe et al., 2014). 558

559

#### 560 Hunting strengthens chamois diel migration to trails

We found a strong negative hunting effect on chamois tolerance that was limited to the hunting period, i.e., without carry-over effects during the hiking period (Fig. 1C, the pattern of dotted colored lines was not supported). During the hunting period, the diel migration pattern was stronger compared to other periods, and hunting risk shaped chamois response to nature-based

tourism, as we hypothesized (Fig. 1C, solid colored line). Chamois were more likely to perform 565 566 diel migrations with increasing risks of being harvested and encountering hikers. Those living in areas with few hikers made diel migrations with an increasing extent as hunting risk increased. 567 As expected within our theoretical framework, the effect of hunting on chamois response was 568 additive to and stronger than hiking (Fig. 1C, solid black line). Our results supported previous 569 findings, as for example in a French mouflon population that responded more strongly to hunting 570 571 than tourism, simultaneously altering their activity, movements and habitat use (Marchand et al., 2014). Likewise, elk (Cervus elaphus) coping with cumulative hunting and hiking activities 572 573 showed higher vigilance and subsequent loss in feeding time compared to elk living outside 574 hunting areas (Ciuti et al., 2012).

575 When the landscape of fear emerges from several co-occurring sources of anthropogenic 576 risk with different degrees of lethality, prey abilities required to adjust the strength of their 577 response to different risks are probably rapidly exceeded. Hence, prey may maintain similar responses to lethal and nonlethal human activities (Frid & Dill, 2002). Yet, ungulates are capable 578 579 of assessing a complex set of factors that affect the need for and utility of antipredator responses when faced with natural predators (Liley & Creel, 2008). Here, we found that the mixture of 580 hunting and hiking created a complex human-induced landscape of fear that impeded chamois to 581 582 adequately adjust their tolerance level to hikers, at least during the hunting period (the tolerance pattern in Fig. 1B was not supported). Chamois may not be able to distinguish accurately hikers 583 584 from hunters, especially as they used the same trails during the hunting period and as hunters are 585 in small parties (usually less than 4), without hunting dogs. Consequently, chamois may first and foremost establish a diel migration to avoid a lethal risk during the hunting period, and then, 586 adjust the extent of their diel migration depending on their approximate assessment of the lethal 587

nature of the risk. Hunting activities, even sporadic, may therefore indirectly strengthen the
consequences of nature-based tourism for ungulate populations (see also Marchand et al., 2014).
This may lead to critical constraints on foraging and space use for species inhabiting mountain
ecosystems. In fact, mountain animals may suffer from the diversification and intensification of
nature-based tourism in the last decades (Pęksa & Ciach, 2015), especially where hunting
overlaps with nature-based activities.

594

#### 595 A potentially maladaptive increased tolerance to nature-based tourism

596 Chamois performed shorter diel migration in areas highly disturbed by hikers during both hiking and hunting periods. This increased tolerance to nature-based tourism, under equal trail 597 availability and with individual changes in diel migration tactics between periods, indicates a 598 potential habituation process in the most disturbed areas (Figs 1A and 1C). Studies that ignored 599 the individual dynamics of animal responsiveness to human disturbance in the long-term, failed 600 601 to clarify the mechanism underlying tolerance adjustments (Bejder et al., 2009; Blumstein, 2016). 602 Importantly, our results provide a rare demonstration of plastic diel migration for the same individual ungulates between periods with contrasting landscapes of fear. Such individual 603 604 abilities to adjust tolerance to human disturbance is a basic requirement for a habituation process 605 to occur (Blumstein, 2016). However, we cannot formally ignore additional mechanisms such as 606 differential selection among personality types or local adaptation for increased tolerance (Samia 607 et al., 2015; Blumstein, 2016). Individuals may also vary in their perception of cues, previous experience and behavioral decision-making processes (Sih et al., 2011; Goumas et al., 2020). 608

609 Regardless of the mechanisms, we found an undesirable outcome of the increased 610 tolerance to hiking during the hunting period. Contrary to individuals living in areas of low disturbance, the most tolerant chamois did not increase their responsiveness to increasing hunting 611 risk (Fig. 1C, dashed black line). Such an increased tolerance to humans may be maladaptative in 612 613 a hunting context, with individuals being exposed to a greater lethal risk. One possible explanation is the habituation transfer from a harmless human disturbance to human or natural 614 predators (Geffroy et al., 2015; Blumstein, 2016). Such habituation transfer may have unfortunate 615 conservation outcomes (Blumstein, 2016). Overall, our findings support a previous warning by 616 617 Geffroy et al. (2015) to take outcomes of animal tolerance adjustments into account in ecological 618 and conservation perspectives.

619 During the hiking period, the majority of individuals performed a diel migration. 620 Interestingly, the likelihood to perform a diel migration did not depend on the actual level of human frequentation, but the spatial extent of the diel migration away from a trail did. At this 621 622 time of the year, disturbance by hikers occurs every day. This baseline disturbance level may be 623 sufficient to trigger a systematic response from chamois. In other study areas, individuals may 624 adjust their diel response to immediate cues of human presence, relying more on a reactive than proactive response. Likewise, female caribou moved away from trails during the day in the 625 626 Gaspésie National Park (QC, Canada) depending on direct human encounters or recent human activities (Lesmerises et al., 2017, 2018). Avoidance response of mountain ungulates is also 627 628 influenced by human group size (Hamr, 1988). We thus encourage future studies to consider a 629 more dynamic framework and assess the variation in the importance of the diel cycle depending on real-time human presence, whilst also accounting for natural predators and thermoregulatory 630 constraints (Bourgoin et al., 2008). 631

## 633 On the costs of diel migration

632

The costs of anti-predator responses (i.e., the risk effects) may have important consequences for 634 population demography (Preisser et al., 2005) and should not be ignored (Creel et al., 2019; Say-635 Sallaz et al., 2019). However, there is still considerable debate regarding the demographic 636 consequences of risk effects. For example, fervent debates have taken place concerning the fear 637 effects of wolf (*Canis lupus*) on elk in the Greater Yellowstone Ecosystem between Creel et al. 638 (2007), Creel et al. (2011), Middleton et al. (2013) and Kohl et al. (2018). Here, we found that a 639 640 diel migration involves an increase in distance traveled of 33 km over areas with an average slope of 39° during the three months of hunting. Diel migration is thus expected to result in additional 641 energetic expenditures during hunting. However, no increase in proxies of daily energetic 642 643 expenditure was observed within each period. There was no relationship with diel migration and body mass either, contrary to what is expected under the risk-disturbance hypothesis (Ydenberg 644 & Dill, 1986; Frid & Dill, 2002). Detecting body mass effects across various sex, age and years 645 would have required however very large sample sizes. Furthermore, risk-disturbance effects are 646 not only limited to energetic loss but are also related to time, stress, reproduction and survival 647 costs in large mammals (review in Say-Sallaz et al., 2019). Possibly compensatory responses may 648 also occur in diel migrants. As an example, mouflon disturbed by hunters during daytime were 649 650 more active and increased their use of favorable foraging resources the night following 651 disturbance (Marchand et al., 2014). Overall, it will be necessary to better assess costs and compensatory benefits to decipher the potential demographic consequences of diel migration, a 652 strong and generalized behavioral response in animal populations. This is especially relevant in 653

the Anthropocene context, where more and more animal populations will have to cope withcomplex human-induced landscapes of fear, combining both lethal risk and nature-based tourism.

656

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#### 670 AUTHOR'S CONTRIBUTION

NC, AL, AD and MG developed the ideas. MG, NC and AD led the collection of the data. NC
conducted statistical analyses with inputs of MG, PM, LB and AL. NC wrote the first draft of the
manuscript. AL, MG and PM led the project on chamois and human interactions. All authors
discussed the analyses and results and revised the manuscript.

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920 Figure legends.

921

Figure 1. Conceptual schemes representing the expected tolerance adjustments of animals to 922 human activities. (A) Animals should respond to nonlethal human disturbance with higher 923 intensity as the disturbance level increases. Individuals experiencing an intermediate level of 924 nonlethal disturbances are then expected to increase their tolerance (decreased responsiveness) to 925 disturbances through habituation. (B) In a context including hunting, animals able to distinguish 926 927 hunters from other humans would keep a constant response to nonlethal disturbances at the basal 928 level, expected along with habituation effects, and would be intolerant to hunters. (C) When 929 animals cannot distinguish hunters from other recreationists, they would perceive a high global 930 disturbance level and sharply decrease their tolerance during the hunting period independently of 931 their initial tolerance level, and then revert back to their basal tolerance level (solid line). Two 932 alternative effects may occur: 1) animals may maintain low tolerance to nonlethal disturbances due to carry-over effects of hunters outside the hunting period (dotted line), and 2) tolerant and 933 934 habituated animals may not perceive a sufficient significant increase in risk and maintain high 935 tolerance to nature-based tourists and hunters during the hunting period (dashed line).

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Figure 2. Study area delineated by the National Game and Wildlife Reserve of Bauges Massif
(solid black line). The trail network (dotted gray line), the areas used by chamois (overlap of
individual home ranges [95% UD], solid blue line) and the area where hunting is forbidden
(purple hatched zone) are shown for the (A) hiking, (B) hunting and (C) skiing periods. Chamois
were trapped within Pécloz (1), Armenaz (2), Coutarse (3), Pleuven (4) and Charbonnet (5)
sectors.

Figure 3. (A, C, E) Distribution of daytime and nighttime locations (i.e., the median distance to 944 trails of GPS locations of an individual at a given day or night) of chamois during the three 945 periods between 2014 and 2018, weighted by the number of locations per individual and number 946 of individuals. Daytime and nighttime distributions significantly (P < 0.001; paired samples 947 Wilcoxon test) differed during the hiking and hunting periods. We showed, for each period, the 948 distribution of distances to a trail available within the seasonal chamois home ranges (dotted 949 950 line), weighted by the home range surface per individual and the number of individuals. To 951 correctly show the diel spatial shift, we only represent chamois performing a diel migration for the hiking (n = 46/55 chamois-years) and hunting (n = 76/89 chamois-years) period. Maximum 952 953 distance to trails was 1652 m during the skiing period and we only show data < 700 m (72%) for 954 clarity. (B, D, F) Periodograms of the distance to a trail time-series for 55, 89 and 83 chamoisyears within the 20 to 28h-period window during the hiking, hunting and skiing periods, 955 respectively. Each dotted line represents the periodogram for one individual chamois. The 956 957 maximum value of each periodogram is indicated by a triangle pointing up if significant (P <0.05) or pointing down if non-significant ( $P \ge 0.05$ ). Periodograms were labeled *a posteriori*. 958

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Figure 4. Dynamics of individual diel migration tactics between consecutive periods. Links
represent individuals and sum to 100% between two periods. We followed 13, 44 and 83
individuals between consecutive skiing and hiking periods, hiking and hunting periods, and
hunting and skiing periods, respectively.

Figure 5. Probabilities of diel migration tactics for chamois in relation to (A) the risk of
encountering hikers and (B) the risk of being harvested during the hunting period between 2014
and 2018 in the northern French Alps, as predicted by a multinomial logit model. Shadow areas
represent the 95% confidence interval.

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Figure 6. Predicted daytime distance to trails of chamois in relation to the distance to trails during 970 the previous night, and (A) the risk of encountering hikers during the hiking period, and (B) both 971 the risk of encountering hikers and the risk of being harvested during the hunting period. The 972 973 solid gray line represents a hypothetical situation in absence of diel migration. The spatial extent of diel migration is depicted in the figure as the vertical distance between the predicted daytime 974 distance to a trail and the gray line, with daytime movement away from a trail when above the 975 976 gray line and daytime movement towards a trail when under the gray line. Most raw data were located above the grey line as indicated by their distribution along each axis. We modeled the 977 response for a female chamois performing a main-DM tactic and fixed all other continuous 978 predictors at their mean values. Low, average and high risk correspond to the 10<sup>th</sup> percentile, 979 mean and 90<sup>th</sup> percentile, respectively. Shadow areas represent the 95% confidence interval. 980 Daytime and nighttime distances to trails are truncated at 400 m, and 93% and 94% of data are 981 shown in A and B, respectively. 982









986 Figure 2.







992 Figure 4.



994 Figure 5.



996 Figure 6.