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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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23 **ABSTRACT**

24 Animals perceive human activities as risky and generally respond with fear-induced proactive  
25 behaviors, to buffer the circadian patterns of lethal and nonlethal disturbances, such as diel  
26 migrations between risky places during safe nighttime and safer places during risky daytime.  
27 However, such responses potentially incur costs through movement or reduced foraging time,  
28 hence, individuals should adjust their tolerance when human activities are harmless, through  
29 habituation. Yet this is a challenging cognitive task when lethal and nonlethal risks co-occur,  
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  
32 (*Rupicapra rupicapra rupicapra*, 89 GPS-tracked individual-years) from/to trails in the French  
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  
38 migration in relation to distance to a trail was a consistent response by chamois (~85% of  
39 individuals) to avoid human disturbance during daytime, especially during the hiking and hunting  
40 periods. Such behavior unveiled a low tolerance of most chamois to human activities, although  
41 there was considerable inter-individual heterogeneity in diel migration. Chamois performed  
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,  
44 chamois which were most human-habituated during the hiking period remained more tolerant in  
45 the subsequent harvesting periods, which could increase their risk of being harvested. In contrast,

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**

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

56

### 57 **INTRODUCTION**

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

68 induced behavioral changes can cascade to population dynamic components (Frid & Dill, 2002;  
69 Lesmerises et al., 2017; Sawyer et al., 2017; Gaynor et al., 2018) and disrupt food web dynamic  
70 processes, such as herbivory, intra- and inter-specific competition and predator-prey interactions  
71 (Fahrig, 2007; Tuomainen & Candolin, 2011; Courbin et al., 2014; Gaynor et al., 2019; Guiden et  
72 al., 2019).

73 Nature-based tourism, defined as visitation to a natural destination for recreational  
74 harmless activities (e.g., hiking, skiing), has increased tremendously in the last decades  
75 (Newsome, 2014; Balmford et al., 2015). It creates nonlethal disturbances which can impact  
76 animal populations through multiple pathways (reviewed in Tablado & Jenni, 2017; Wolf et al.,  
77 2019), with animals often perceiving nonlethal human disturbances as a predation risk (Frid &  
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  
84 document (Say-Sallaz et al., 2019), especially when they affect behavior, are nonetheless  
85 receiving an increasing level of empirical support (Frid & Dill, 2002; Tablado & Jenni, 2017).  
86 Behavioral responses to fear can occur in the form of reactive responses, such as the well-studied  
87 flight response in reaction to humans (Stankowich, 2008; Blumstein, 2016), but also as proactive  
88 anti-predator behaviors (Valeix et al., 2009; Marchand et al., 2014; Basille et al., 2015; Creel,  
89 2018; Courbin et al., 2019; Gaynor et al., 2019). These proactive responses are more likely to  
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 long-  
93 term risk (Laundré et al., 2001; Laundré et al., 2010). Nature-based tourism, which typically  
94 occurs during daytime, in delimited areas and along trails, should therefore lead animals to adopt  
95 such proactive responses. Accordingly, changes in individual space use (e.g., Thiel et al., 2008;  
96 Lesmerises et al., 2018) and in day/night allocation of activities (e.g., Marchand et al., 2014;  
97 Pęksa & Ciach, 2018) have been unveiled in several herbivore species in response to hiking and  
98 backcountry skiing. Ultimately, in such contexts, including spatially-restricted and temporally  
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  
101 disturbance and stress-mediated costs associated with reactive behavior by using risky areas  
102 during the safer period (e.g. nighttime) and by moving away from the same spatially risky areas  
103 during risky times (e.g. daytime; Creel, 2018). The diel migration tactic was firstly  
104 conceptualized in aquatic systems as an anti-predator behavior (Iwasa, 1982; Alonzo et al., 2003).  
105 More recently, diel migration was quantified in response to natural predation (Courbin et al.,  
106 2019) and has been observed in response to hunting (Tolon et al., 2009; Bonnot et al., 2013;  
107 Marchand et al., 2014; Fortin et al., 2015) and nature-based tourism (Lesmerises et al., 2017).  
108 The occurrence and extent of diel migration may therefore be a meaningful metrics of proactive  
109 responses to highly predictable perceived risks in various ecological systems.

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.

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

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

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

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



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

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

190

## 191 **METHODS**

### 192 *Study area*

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

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

207 In addition to hunting, hiking and backcountry skiing are common recreational activities  
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  
210 hiking activities only (hunting forbidden), (ii) the hunting period (September to November) when  
211 hunting and moderate levels of hiking activities occurred, and (iii) the skiing period (January to  
212 March) when backcountry skiing and snowshoeing were the main sources of human disturbance  
213 (see details in Appendix S1). Human activities were heterogeneously distributed within the  
214 Reserve and hunting was prohibited in the Armenaz area (300 ha; Fig. 2). Thereby, the five  
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***

219 The trail network shaped the backbone of human activities within the Reserve and was  
220 considered as a good proxy of where human disturbances took place (see complete details in  
221 Appendix S1). We considered two trail networks, one for the hiking and hunting periods and one  
222 for the skiing period, because snow cover reshaped the trail network seasonally (Fig. 2). Using an  
223 independent GPS dataset collected on a large representative sample of hikers (n = 270 tracks in  
224 2014 and 2015), hunters (n = 223 tracks between 2014 and 2018), and skiers (n = 83 tracks in  
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

227 harvested less than 200 m away from a trail using the database of chamois harvesting sites since  
228 2006 (n = 1112, Appendix S1: Figure S6).

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

239

#### 240 *GPS and activity data for chamois*

241 Eighty-seven adult chamois (70 females and 17 males) were trapped during the 2014-2018  
242 summers using falling nets baited with artificial salt licks within grasslands at five sites (Fig. 2).

243 Individuals were weighed and their age at capture was determined by counting horn growth  
244 annuli (Schröder & von Elsner-Schack, 1985). Individuals were equipped with GPS collars  
245 (3300S Lotek Engineering Inc. or Vectronics GPS Plus-1C Store On Board) scheduled to record  
246 one location every 1h or 2h continuously, or every 4h interspersed with periods of 20-min  
247 interval recording during at least two consecutive days depending on periods and individuals.

248 Almost all individuals were monitored for only one year; the final dataset consisted of GPS tracks

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

256

### 257 *Testing for diel migration of chamois*

258 For each individual and time period, we tested for a cyclic variation in the distance to the closest  
259 trail (hereafter ‘distance to a trail’) used by chamois over a 24h-period, i.e., a diel migration  
260 representing the back-and-forth movement of chamois being away from trails during daytime and  
261 close to trails during nighttime. We fitted Lomb-Scargle periodogram (Ruf, 1999), a least-squares  
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  
264 a 20-min interval were subsampled at a regular 1h interval. We considered that a chamois  
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

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

274

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

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

292 We then tracked individual consistency and change among tactics between consecutive  
293 periods to assess the seasonal dynamics of individual diel migration tactics throughout the year.  
294 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  
296 disturbances within their home ranges during the hiking and hunting periods (only few chamois  
297 performed diel migration during the skiing period, see Results). An individual home range was  
298 computed as the 95% UD derived from its GPS locations during a given period and year using  
299 biased random bridges (Benhamou, 2011) on a 25-m resolution grid ( $L_{min} = 15m$ ,  $T_{max} =$  twice  
300 times the sampling rate and  $h_{min} = 100m$ ). We used locations recorded with a regular 1h, 2h or  
301 4h interval (here, locations taken with a 20-min interval were subsampled at a regular 4h  
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  
310 of encountering hikers (Fig. 1C dashed line). Hunting was not allowed during the hiking period  
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  
313 characteristics: age and sex of chamois to consider the effect of intrinsic differences on tolerance  
314 (Blumstein, 2016; Tablado & Jenni, 2017) and body mass to get insights on potential costs of the

315 different tactics. Individuals establishing their seasonal home range in areas with a high density  
316 of trails cannot move away from a trail without moving close to another trail, limiting the range  
317 of their diel migration and potentially confounding the drivers of diel migration. We thus  
318 controlled for the mean distance to trails available within the home range. All continuous  
319 covariates were centered and scaled. Models did not include highly correlated variables (i.e. the  
320 ones for which  $|r| > 0.6$ ) and had low multicollinearity with a condition index  $< 3.8$  (Dormann et  
321 al., 2013) at each period (see model details in the Appendix S5). We had 53 chamois-years during  
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  
326 tolerance to human disturbance. We defined diel migration extent as the difference between the  
327 median daytime distance to trails over individual GPS locations for the given day (hereafter  
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  
330 periods. For each period, we modeled the daytime distance to a trail (response variable) in  
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  
337 weighted by the UD value), as previously described. In accordance with our hypothetical



338 framework (Fig. 1C), we assessed if the mean risk of being harvested shaped the extent of diel  
339 migration in response to the mean risk of encountering hikers during hiking and hunting periods,  
340 with an interaction term. As previously, a significant effect of hunting risk during the hiking  
341 period will reveal a carry-over effect of hunting on chamois tolerance to hikers (Fig. 1C dotted  
342 line). We expected that chamois responses to trail frequentation and hunting risk should depend  
343 on their distance to trails at night. We thus tested for interactions between the nighttime distance  
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  
348 criterion corrected for finite sample size (AICc) was used to select the most parsimonious  
349 candidate models. None of the candidate models included highly correlated variables ( $|r| > 0.6$ )  
350 and had low multicollinearity with a condition index  $< 13$  and a variance inflation factor  $< 2.2$   
351 (Dormann et al., 2013). We relied on data from 1165 chamois-days from 44 chamois-years for  
352 the hiking period, and 3088 chamois-days from 73 chamois-years for the hunting period.

353

#### 354 *Assessing proxies of diel migration costs*

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

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

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

378

379 We performed all analyses using R software v.3.6.2 (R Development Core Team, 2019) and  
380 packages *lomb* for assessment of least-squares spectral analyses (Ruf, 1999), *riverplot* to plot the  
381 Sankey diagram (Weiner, 2017), *adehabitatHR* for home range and UD computation (Calenge,  
382 2006), *nnet* (Venables & Ripley, 2002) and *lme4* (Bates et al., 2015) for fitting multinomial

383 logistic regressions and linear mixed effect models, respectively, and *MuMin* for model selection  
384 (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  
389 trail during nighttime than during daytime (Figs 3A, 3C;  $P < 0.001$ , paired samples Wilcoxon  
390 tests). This pattern was due to back-and-forth movements to trails between night and day with a  
391 24-h periodicity at individual level, as shown by periodograms (Figs 3B, 3D, Appendix S4:  
392 Figure S4) for most individuals ( $n = 46/55$  chamois-years during the hiking period using a main-  
393 DM or a minor-DM,  $n = 76/89$  chamois-years during the hunting period using a main-DM or a  
394 minor-DM, Appendix S4: Table S1). However, the diel spatial shift was highly variable between  
395 individuals (Appendix S4: Figures S1 and S2) and highly context-dependent. Indeed, the distance  
396 of diel migration varied with chamois nighttime location: the closer chamois were to a trail  
397 during nighttime, the further they were from a trail during the next day (Figs 3A, 3C). For  
398 example, chamois that were 50 m away from a trail at night (i.e., peak of the distribution) tended  
399 to perform large diel migration (see Results section Determinants of the spatial extent of diel  
400 migration). Importantly, the extent of the daytime movement away from a trail was highly  
401 constrained by the low availability of areas away from a trail (dotted lines in Figs 3A, 3C) with a  
402 median distance to a trail available within the home range of  $\sim 175$  m (Appendix S4: Table S2).  
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  
406 level to human disturbances by switching between diel migration tactics (Fig. 4). Most (~85%)  
407 had a low tolerance and performed diel migrations (main-DM and minor-DM tactics) during  
408 hiking and hunting periods, with the main-DM tactic being dominant (>50%; Fig. 4, Appendix  
409 S4: Table S1). In addition, most chamois performing minor-DM during the hiking period  
410 switched to a main-DM tactic during the hunting period (Fig. 4). On the opposite, chamois were  
411 located further away from trails during the less disturbed skiing period (Fig. 3E, Appendix S4:  
412 Table S2) and adopted a no-DM tactic (Fig. 4, Appendix S4: Table S1). It has to be noted that  
413 four chamois out of 10 performing a diel migration lived 400 m away from trails during the  
414 skiing period and the causal effect of trails on their diel migration pattern was thus questionable  
415 (Appendix S4: Figure S3).

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  
420 characteristics (age, sex and body mass, Appendix S5: Table S1). Similarly, our results did not  
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-  
425 DM tactic over the other tactics rapidly increased with increasing risk of being harvested (i.e.  
426  $\times 4.1$  between extreme values) and increasing risk of encountering hikers (i.e.  $\times 4.4$  between  
427 extreme values), without significant interacting effects between both risks (Fig. 5, Appendix S5:

428 Table S2). Therefore, the data supported neither higher tolerance with increasing hiker attendance  
429 (Fig. 1A) nor undesirable tolerance persistence in the choice of tactic during the hunting period  
430 (Fig. 1C dashed lined). Chamois had also higher probabilities of using a main-DM tactic than a  
431 minor-DM tactic when they used areas with a low mean risk of being seen and a low mean risk of  
432 encountering hunters (Appendix S5: Table S2, Figures S1A, S1B). However, these latter effects  
433 were weaker than the effects of risk of encountering hikers and of being harvested (the size  
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*

439 The top-ranked model included an interaction between the distance to trails the previous night  
440 and either the mean risk of encountering hikers during the hiking period or the mean risk of being  
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  
443 short diel migrations (Appendix S6: Tables S3 and S4). After controlling for trail availability  
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  
446 the first 100 m from a trail at the previous nighttime (Figs 6A, 6B, Appendix S6: Tables S3 and  
447 S4). Moreover, diel migration behavior was triggered over a greater nighttime distance from trail  
448 at low than high encounter risk with hikers (Figs 6A, 6B). Overall, these findings support the  
449 hypothesis that diel migrants developed a greater tolerance to hiker disturbance when nature-  
450 based tourism increased, whereas they displayed a low tolerance at low levels of hiker

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

466

#### 467 *Costs of diel migration*

468 The diel migration behavior involved a higher daily distance travelled for chamois during the  
469 hunting period only, i.e., +370 m per 24h between main-DM and no-DM tactic (Appendix S7:  
470 Table S2, Figure S1). That represented > 33 additional kilometers travelled by diel migrant  
471 chamois over the three months of the harvesting period. Also, males travelled 453 m more than  
472 females each day during the hunting period (> 41 additional kilometers over the period), while  
473 they were less active than females during all periods (Appendix S7: Tables S2 and S3). Overall,

474 chamois had similar energy expenditure within a period independently of the diel migration tactic  
475 (Appendix S7: Table S3, Figure S1). Note that chamois increased their daytime and nighttime  
476 activity when located within the first 100 m from a trail, especially during the hiking and hunting  
477 periods (Appendix S8: Figure S1).

478

## 479 **DISCUSSION**

480 Our study demonstrated how overlapping nature-based tourism and hunting shaped complex  
481 proactive responses and tolerance patterns to human activities for a large mountain herbivore  
482 species. Chamois were generally wary of humans: most individuals performed diel migration  
483 (i.e., back-and-forth movements further away from trails during daytime and closer to trails  
484 during nighttime) in response to the landscape of fear imposed by recreational activities,  
485 especially during hiking and hunting periods. Diel migration was increased during the hunting  
486 period, unveiling additive risk effects. However, we found no carry-over effect of hunting beyond  
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  
489 for the most disturbed diel migrants. Yet, the persistence of such tolerance to humans during the  
490 hunting period could be maladaptive. 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*

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

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



519 increased occurrence of the diel cycle at the individual level. However, home ranges overlapped  
520 within and among periods (Appendix S4: Figure S5), which indicated that local changes in  
521 disturbances affected short-term movement tactics (i.e. the diel migration) rather than space use  
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  
524 availability of distance of chamois to trails (median distance of chamois to trails within their  
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  
532 on vegetation surveys indicate an inconsistent pattern in increased or decreased abundance of  
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  
537 quality of food resources in areas between the median daytime (~140 m) and nighttime (~100 m)  
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  
540 all the times during the hiking and hunting periods (Appendix S8). This suggests that activities  
541 close to trails (<100 m) were not allocated to an important extent to foraging (e.g. resting,

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

559

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

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

565 tourism, as we hypothesized (Fig. 1C, solid colored line). Chamois were more likely to perform  
566 diel migrations with increasing risks of being harvested and encountering hikers. Those living in  
567 areas with few hikers made diel migrations with an increasing extent as hunting risk increased.  
568 As expected within our theoretical framework, the effect of hunting on chamois response was  
569 additive to and stronger than hiking (Fig. 1C, solid black line). Our results supported previous  
570 findings, as for example in a French mouflon population that responded more strongly to hunting  
571 than tourism, simultaneously altering their activity, movements and habitat use (Marchand et al.,  
572 2014). Likewise, elk (*Cervus elaphus*) coping with cumulative hunting and hiking activities  
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  
578 responses to lethal and nonlethal human activities (Frid & Dill, 2002). Yet, ungulates are capable  
579 of assessing a complex set of factors that affect the need for and utility of antipredator responses  
580 when faced with natural predators (Liley & Creel, 2008). Here, we found that the mixture of  
581 hunting and hiking created a complex human-induced landscape of fear that impeded chamois to  
582 adequately adjust their tolerance level to hikers, at least during the hunting period (the tolerance  
583 pattern in Fig. 1B was not supported). Chamois may not be able to distinguish accurately hikers  
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  
586 foremost establish a diel migration to avoid a lethal risk during the hunting period, and then,  
587 adjust the extent of their diel migration depending on their approximate assessment of the lethal

588 nature of the risk. Hunting activities, even sporadic, may therefore indirectly strengthen the  
589 consequences of nature-based tourism for ungulate populations (see also Marchand et al., 2014).  
590 This may lead to critical constraints on foraging and space use for species inhabiting mountain  
591 ecosystems. In fact, mountain animals may suffer from the diversification and intensification of  
592 nature-based tourism in the last decades (Pęksa & Ciach, 2015), especially where hunting  
593 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  
597 and hunting periods. This increased tolerance to nature-based tourism, under equal trail  
598 availability and with individual changes in diel migration tactics between periods, indicates a  
599 potential habituation process in the most disturbed areas (Figs 1A and 1C). Studies that ignored  
600 the individual dynamics of animal responsiveness to human disturbance in the long-term, failed  
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  
603 individual ungulates between periods with contrasting landscapes of fear. Such individual  
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  
608 experience and behavioral decision-making processes (Sih et al., 2011; Goumas et al., 2020).

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  
611 disturbance, the most tolerant chamois did not increase their responsiveness to increasing hunting  
612 risk (Fig. 1C, dashed black line). Such an increased tolerance to humans may be maladaptive in  
613 a hunting context, with individuals being exposed to a greater lethal risk. One possible  
614 explanation is the habituation transfer from a harmless human disturbance to human or natural  
615 predators (Geffroy et al., 2015; Blumstein, 2016). Such habituation transfer may have unfortunate  
616 conservation outcomes (Blumstein, 2016). Overall, our findings support a previous warning by  
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  
621 human frequentation, but the spatial extent of the diel migration away from a trail did. At this  
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  
625 proactive response. Likewise, female caribou moved away from trails during the day in the  
626 Gaspésie National Park (QC, Canada) depending on direct human encounters or recent human  
627 activities (Lesmerises et al., 2017, 2018). Avoidance response of mountain ungulates is also  
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  
630 on real-time human presence, whilst also accounting for natural predators and thermoregulatory  
631 constraints (Bourgoin et al., 2008).

632

633 *On the costs of diel migration*

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

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

656

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669

## 670 **AUTHOR'S CONTRIBUTION**

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

675

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920 Figure legends.

921

922 Figure 1. Conceptual schemes representing the expected tolerance adjustments of animals to  
923 human activities. (A) Animals should respond to nonlethal human disturbance with higher  
924 intensity as the disturbance level increases. Individuals experiencing an intermediate level of  
925 nonlethal disturbances are then expected to increase their tolerance (decreased responsiveness) to  
926 disturbances through habituation. (B) In a context including hunting, animals able to distinguish  
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  
933 due to carry-over effects of hunters outside the hunting period (dotted line), and 2) tolerant and  
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).

936

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

943

944 Figure 3. (A, C, E) Distribution of daytime and nighttime locations (i.e., the median distance to  
945 trails of GPS locations of an individual at a given day or night) of chamois during the three  
946 periods between 2014 and 2018, weighted by the number of locations per individual and number  
947 of individuals. Daytime and nighttime distributions significantly ( $P < 0.001$ ; paired samples  
948 Wilcoxon test) differed during the hiking and hunting periods. We showed, for each period, the  
949 distribution of distances to a trail available within the seasonal chamois home ranges (dotted  
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  
952 the hiking ( $n = 46/55$  chamois-years) and hunting ( $n = 76/89$  chamois-years) period. Maximum  
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 chamois-  
955 years within the 20 to 28h-period window during the hiking, hunting and skiing periods,  
956 respectively. Each dotted line represents the periodogram for one individual chamois. The  
957 maximum value of each periodogram is indicated by a triangle pointing up if significant ( $P <$   
958  $0.05$ ) or pointing down if non-significant ( $P \geq 0.05$ ). Periodograms were labeled *a posteriori*.

959

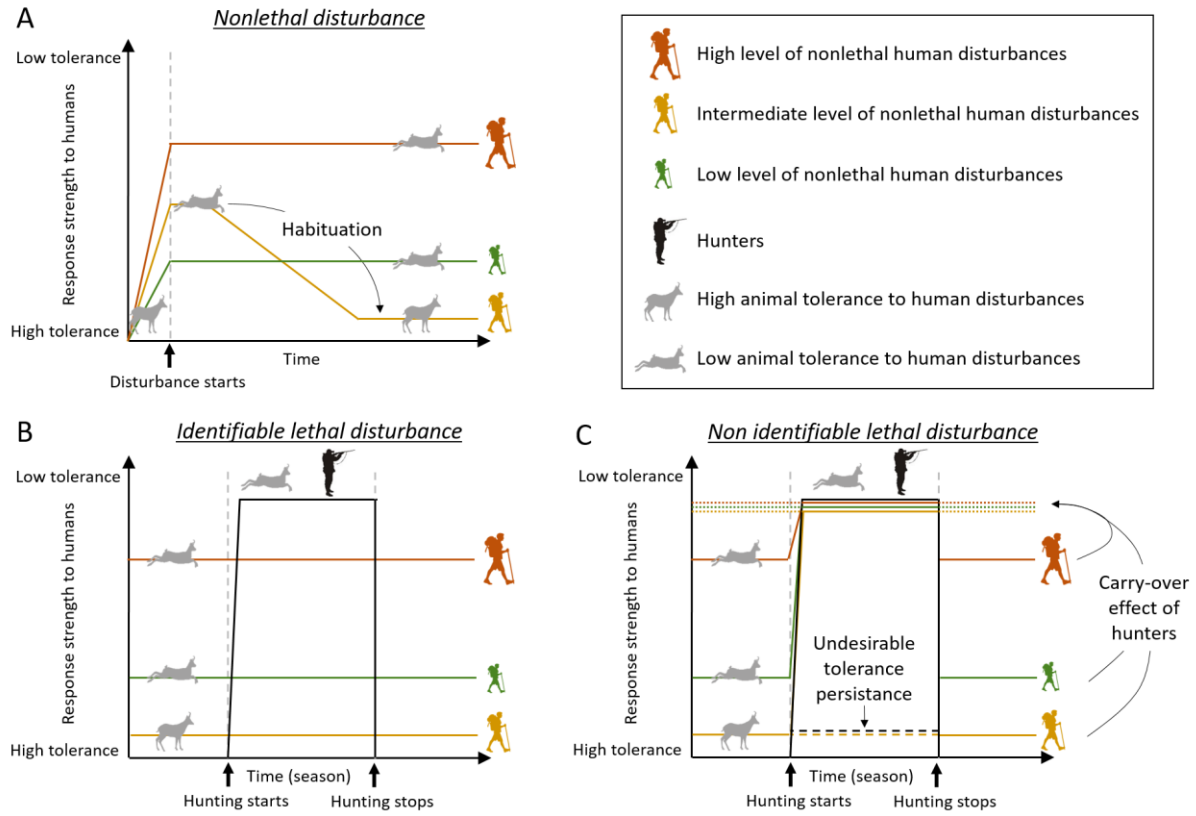
960 Figure 4. Dynamics of individual diel migration tactics between consecutive periods. Links  
961 represent individuals and sum to 100% between two periods. We followed 13, 44 and 83  
962 individuals between consecutive skiing and hiking periods, hiking and hunting periods, and  
963 hunting and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

964

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

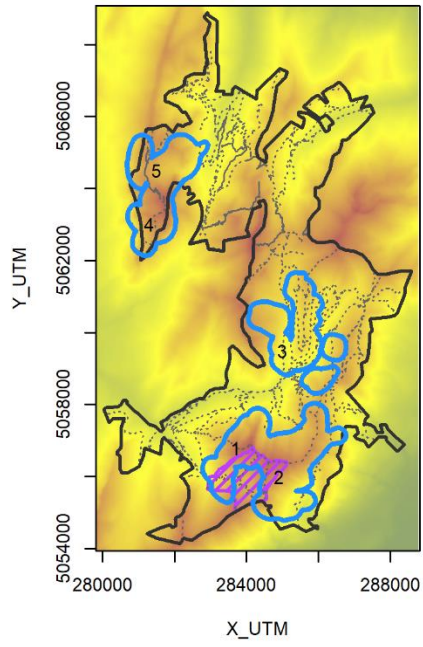
969

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

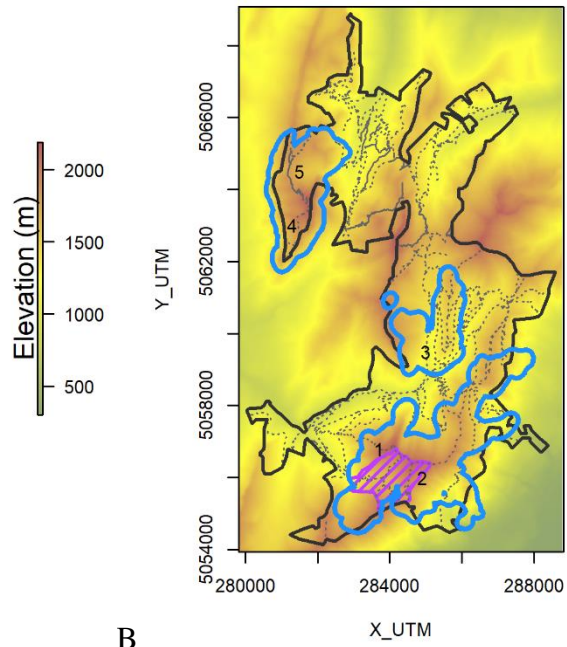


983

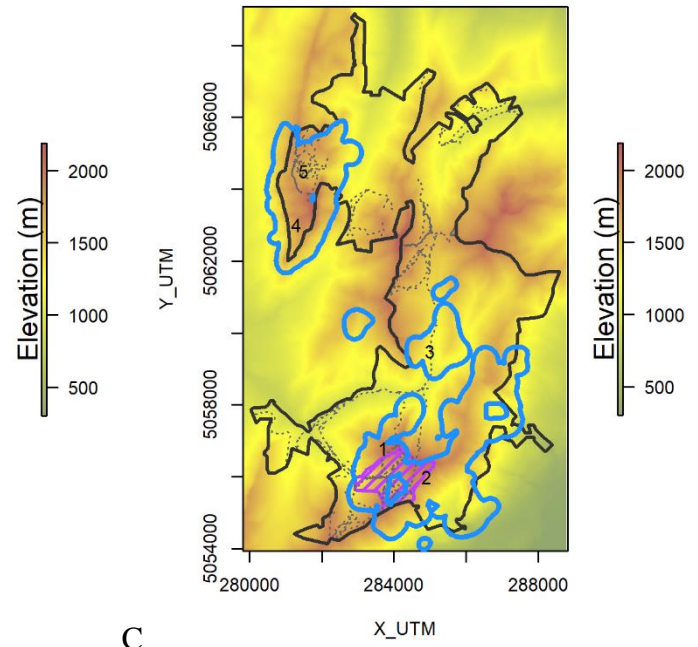
984 Figure 1.



985 A

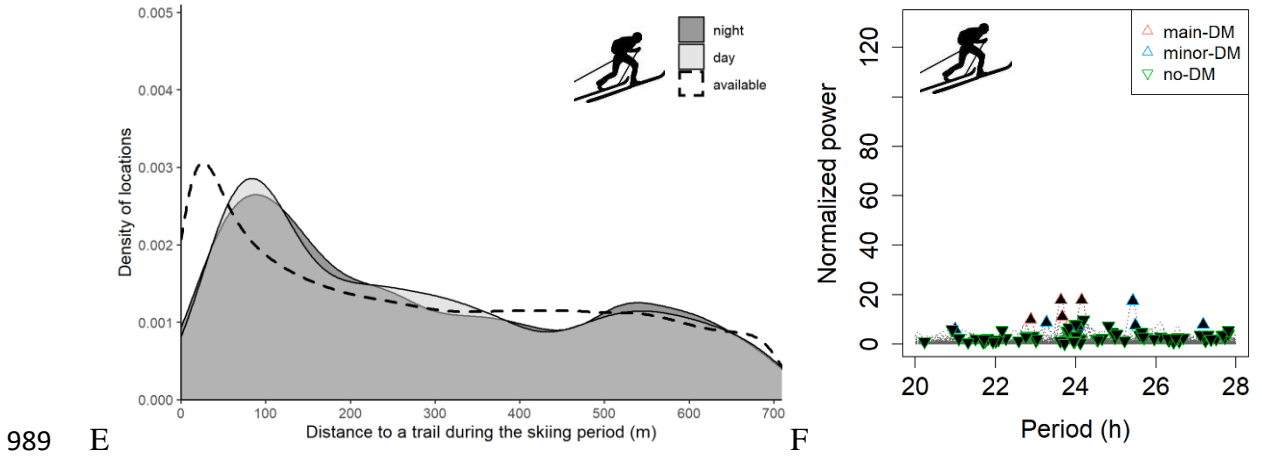
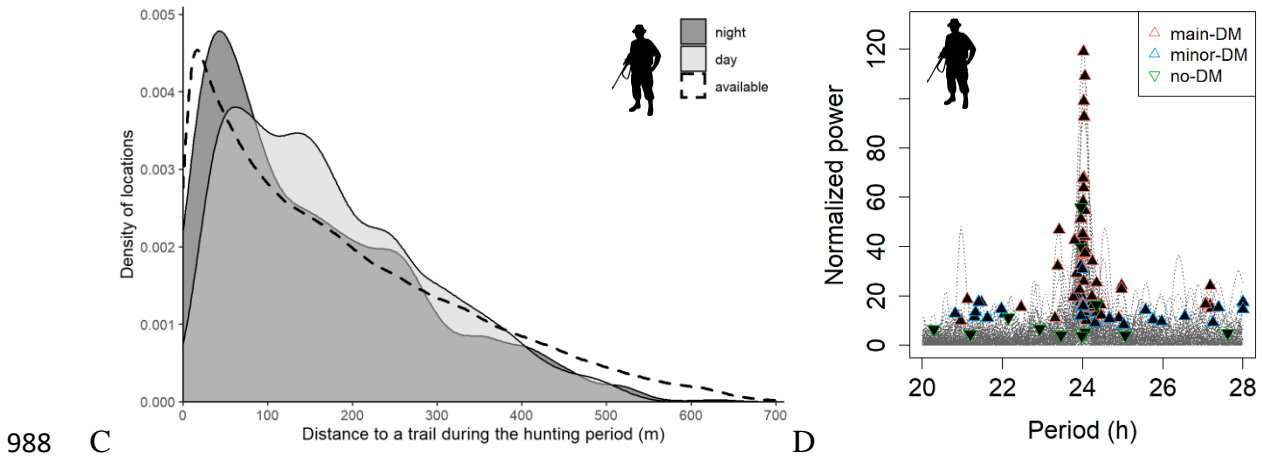
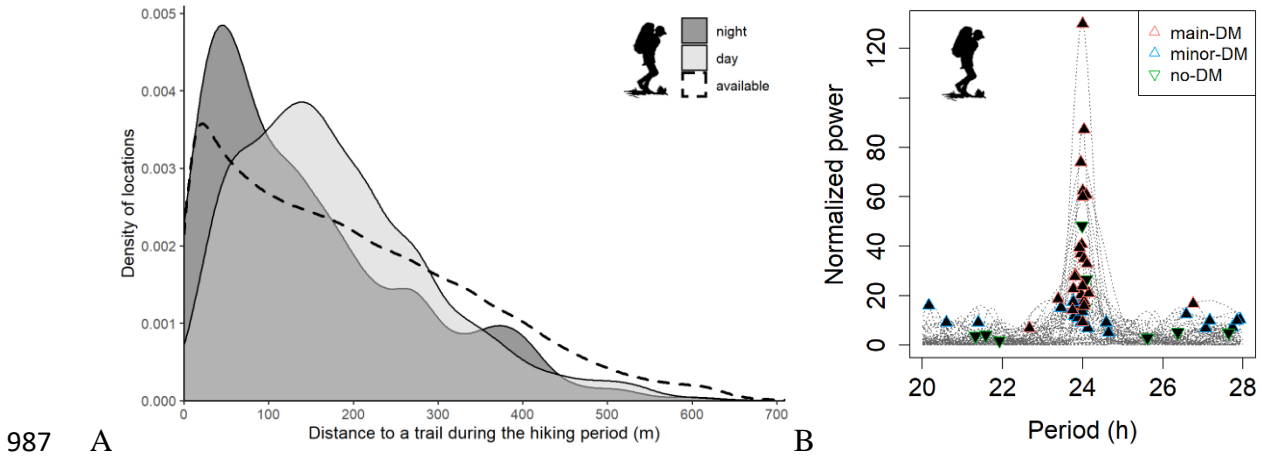


B



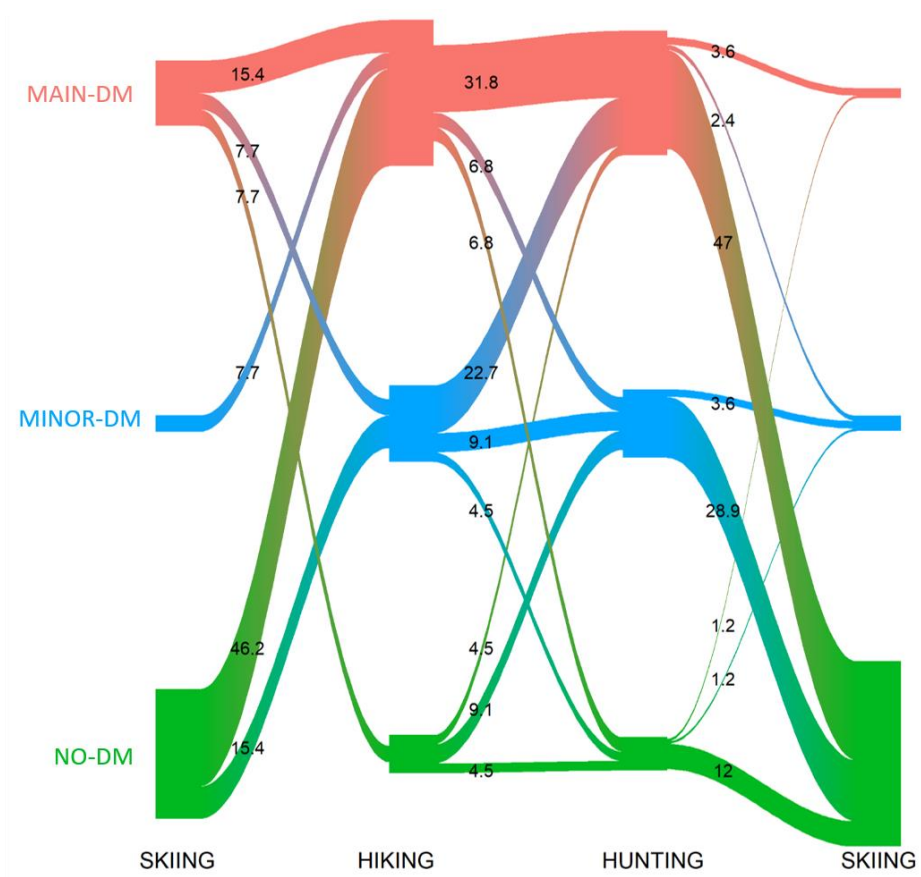
C

986 Figure 2.



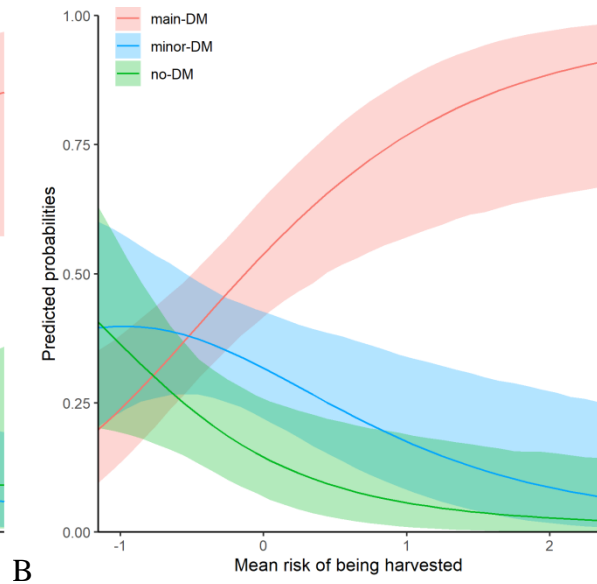
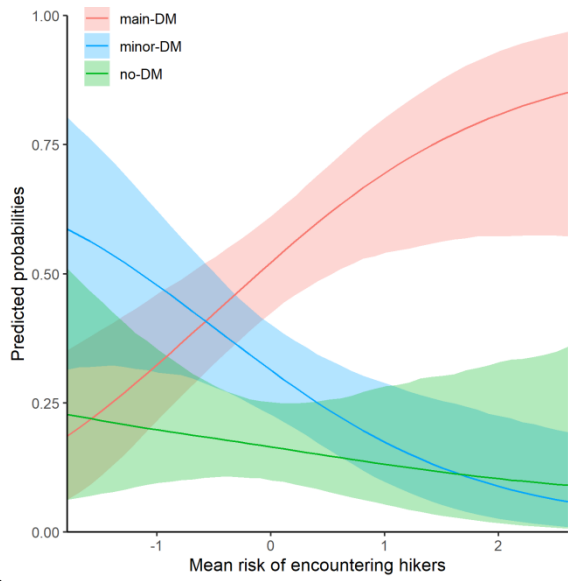
990 Figure 3.





991

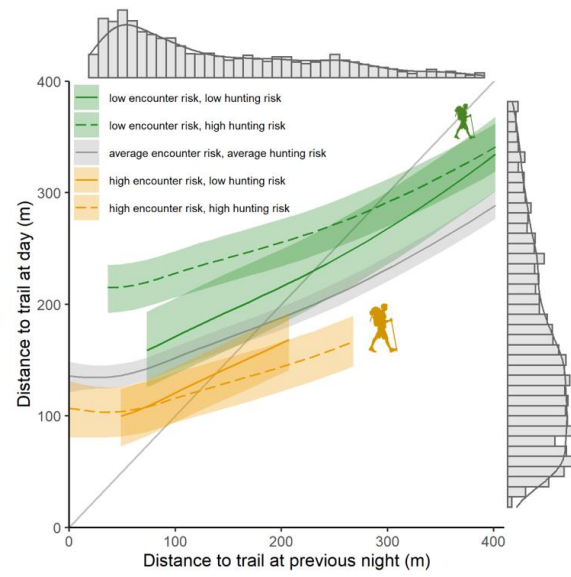
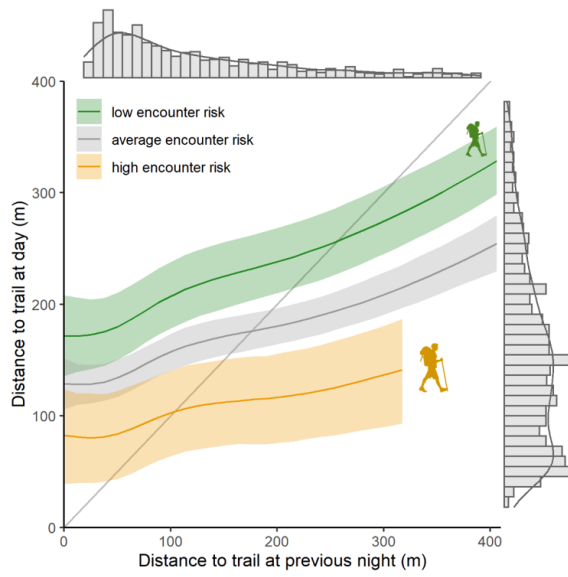
992 Figure 4.



993 A

B

994 Figure 5.



995 A

B

996 Figure 6.