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

Nicolas Courbin, Mathieu Garel, Pascal Marchand, Antoine Duparc, Lucie Debeffe, Luca Börger, Anne Loison

To cite this version:

Nicolas Courbin, Mathieu Garel, Pascal Marchand, Antoine Duparc, Lucie Debeffe, et al.. Interacting lethal and nonlethal human activities shape complex risk tolerance behaviors in a mountain herbivore. Ecological Applications, 2022, 32 (7), pp.e2640. 10.1002/eap.2640 . hal-03694845

HAL Id: hal-03694845
https://hal.inrae.fr/hal-03694845v1

Submitted on 27 Mar 2024

Running head: Human-induced tolerance adjustments

Title: **Interacting lethal and nonlethal human activities shape complex risk tolerance behaviors in a mountain herbivore**

Nicolas Courbin[1*], Mathieu Garel[2], Pascal Marchand[3], Antoine Duparc[1], Lucie Debeffe[4], Luca Börger[5], Anne Loison[1]

[1]Laboratoire d'Écologie Alpine (LECA), UMR 5553, Université Grenoble Alpes, Université Savoie Mont-Blanc, Centre National de la Recherche Scientifique (CNRS), Bâtiment Belledonne, 73376 Le Bourget-du-Lac, France.

[2]Office Français de la Biodiversité (OFB), Unité Ongulés Sauvages, 5 allée de Bethléem, Z.I. Mayencin, 38610 Gières, France.

[3]Office Français de la Biodiversité (OFB), Unité Ongulés Sauvages, Les Portes du Soleil, 147 avenue de Lodève, 34990 Juvignac, France.

[4]Comportement et Ecologie de la Faune Sauvage (CEFS), Université de Toulouse, Institut national de recherche pour l'agriculture, l'alimentation et l'environnement (INRAE), Castanet-Tolosan, France.

[5]Department of Biosciences, Swansea University, Singleton Park, Swansea, Wales SA2 8PP, UK.

* Corresponding author: ncourbin@gmail.com; nicolas.courbin@univ-savoie.fr

Open Research statement: data will be deposited in Figshare upon acceptance of the manuscript.

ABSTRACT

Animals perceive human activities as risky and generally respond with fear-induced proactive behaviors, to buffer the circadian patterns of lethal and nonlethal disturbances, such as diel migrations between risky places during safe nighttime and safer places during risky daytime. However, such responses potentially incur costs through movement or reduced foraging time, hence, individuals should adjust their tolerance when human activities are harmless, through habituation. Yet this is a challenging cognitive task when lethal and nonlethal risks co-occur, forming complex landscapes of fear. The consequences of this human-induced complexity have 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 Alps, in areas with co-occurring lethal (hunting) and nonlethal (hiking and skiing) disturbances, with different intensities across seasons. We developed a conceptual framework relying on the risk-disturbance hypothesis and habituation to predict tolerance adjustments of chamois under various disturbance contexts and across contrasted seasonal periods. Based on spatial and 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 individuals) to avoid human disturbance during daytime, especially during the hiking and hunting 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 shorter diel migrations in areas highly disturbed by hikers. Interestingly there was an increased 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 the subsequent harvesting periods, which could increase their risk of being harvested. In contrast, individuals less tolerant to hiking performed longer diel migrations when hunting risk increased, and compared to hiking, hunting exacerbated the threshold distance to trails triggering diel migrations. No carry-over effect of hunting beyond the hunting period was observed. In conclusion, complex human-induced landscapes of fear with co-occurring disturbances by nature-based tourism and hunting may shape unexpected patterns of tolerance to human activities, whereby animal tolerance could become potentially deleterious for individual survival.

KEYWORDS

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

INTRODUCTION

The direct effect of human exploitation on animal survival has led to anthropogenic defaunation with direct consequences for ecosystem functioning worldwide (Dirzo et al., 2014). However, 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 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 et al., 2014; Gaynor et al., 2018; Bonnot et al., 2020), reducing their movement range (Tucker et al., 2018) and altering their space use and access to food (Harris et al., 2014; Richard & Côté, 2016; Sawyer et al., 2017; Ciach & Pęksa, 2019). Similarly to the non-consumptive risk effects of predation (Lima, 1998; Preisser et al., 2005; Creel, 2018; Say-Sallaz et al., 2019), such human-induced 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 harmless activities (e.g., hiking, skiing), has increased tremendously in the last decades (Newsome, 2014; Balmford et al., 2015). It creates nonlethal disturbances which can impact animal populations through multiple pathways (reviewed in Tablado & Jenni, 2017; Wolf et al., 2019), with animals often perceiving nonlethal human disturbances as a predation risk (Frid & Dill, 2002; Gaynor et al., 2019). The risk-disturbance hypothesis stipulates that 'predation and nonlethal disturbance stimuli create similar trade-offs between avoiding perceived risk and other fitness-enhancing activities' (Frid & Dill, 2002). It formalizes that fear effect can have important cascading effects on individual behavior and demography (Brown et al., 1999; Laundré et al., 2001; Gaynor et al., 2019), and may even exceed those from direct predation or harvest effects (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 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 flight response in reaction to humans (Stankowich, 2008; Blumstein, 2016), but also as proactive 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 arise when animals face a spatiotemporally predictable risk (Creel, 2018; Kohl et al., 2018;

Courbin et al., 2019; Riotte-Lambert & Matthiopoulos, 2020), i.e. within predictable landscapes of fear, where the “landscape of fear” is defined as the spatial variation in the perception of long-term risk (Laundré et al., 2001; Laundré et al., 2010). Nature-based tourism, which typically occurs during daytime, in delimited areas and along trails, should therefore lead animals to adopt such proactive responses. Accordingly, changes in individual space use (e.g., Thiel et al., 2008; Lesmerises et al., 2018) and in day/night allocation of activities (e.g., Marchand et al., 2014; Pęksa & 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 predictable human disturbance, animals may perform movement tactics to decrease risk such as 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 during the safer period (e.g. nighttime) and by moving away from the same spatially risky areas 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). More recently, diel migration was quantified in response to natural predation (Courbin et al., 2019) and has been observed in response to hunting (Tolon et al., 2009; Bonnot et al., 2013; Marchand et al., 2014; Fortin et al., 2015) and nature-based tourism (Lesmerises et al., 2017). 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.

However, proactive responses to nature-based tourism may entail costs related to changes in movement, activity budget, energy expenditures and lost foraging opportunities (see reviews Frid & Dill, 2002; Tablado & Jenni, 2017). Spatial proactive responses that involve avoiding 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 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 stimulus. For example, animals may decrease their flight initiation distance (Stankowich, 2008; Reimers et al., 2010) and vigilance (Schuttler et al., 2017) in areas with high levels of human recreation. Animals may likewise increase their tolerance to repeated exposures to nonlethal anthropogenic stimuli through habituation, up to a certain level of disturbance intensity (Frid & Dill, 2002; Bejder et al., 2009; Geffroy et al., 2015; Blumstein, 2016; Fig. 1A). Habituation was originally defined in neuroscience in the seminal works of Thompson and Spencer (1966) and 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; e.g., Dehaudt et al., 2019) with a high degree of variability among individuals (Blumstein, 2016; Tablado & Jenni, 2017). Urbanization in birds is for example a severe case of increased tolerance to humans, potentially driven by habituation (Vincze et al., 2016; Geffroy et al., 2020). Yet identifying and measuring habituation in the field remains a challenging task (Bejder et al., 2009; Blumstein, 2016), especially in complex situations with multiple sources of risk and disturbance.

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 hunters and not with other recreationists, they would perceive an overall higher human disturbance level and increase their responsiveness to all human activities during the hunting period (Fig. 1C solid line). Outside the hunting period, animals may then either resume their basal tolerance level (solid line) or continue being wary of humans (Fig. 1C dotted line). Hunters may indeed trigger a carry-over effect inhibiting tolerance adjustments and habituation beyond 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; Gaynor et al., 2018). While there should be some benefits for individuals to tolerate and habituate to nonlethal risks, recent works have argued that, in contrast, the most tolerant and human-habituated individuals may lose their ability to respond to lethal risk (Geffroy et al., 2015). For instance, they may continue to relax their antipredator behavior even during the hunting period. Thus, undesirable tolerance to hunters may occur (Fig. 1C dashed line). Such mechanism may have deleterious consequences for animal populations coping with reintroduction of natural predators or experiencing short hunting periods (Geffroy et al., 2015, 2020).

Distinguishing nonlethal human stimuli and true predatory stimuli from hunters requires strong cognitive abilities that may outperform the capacities of hunted animals (Frid & Dill, 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 variation in the magnitude of risk (Liley & Creel, 2008). However, cues related to humans engaged in various lethal and nonlethal recreational activities may be more difficult for prey to interpret, especially if they co-occur in space and time and if animals have to constantly reassess the risk during daytime due to frequent human passage. Consequently, under some conditions (determined by the spatiotemporal variability of disturbance and the nature of activities), the human-induced landscape of fear may become too complex to decipher for animals. Given the increase of areas where nature-based tourism and hunting co-occur, the additive or multiplicative outcome of the diversification of recreation activities on animal behavior needs to be investigated in a comprehensive way (Geffroy et al., 2015). Accordingly, we aimed here to assess individual responsiveness to predictable circadian patterns of nature-based tourism in a human-induced 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 understand how hunting shapes animal tolerance to nature-based tourism and highlight potential maladaptive tolerant behavior. Our model species was chamois (*Rupicapra rupicapra rupicapra*), a particularly relevant species to delve into the complexity of animal responses to human lethal 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 vulnerable to the increase in outdoor recreation (Steven et al., 2011; Pęksa & Ciach, 2015). We benefited from a rare dataset combining a fine characterization of recreational activities (hiking, skiing and hunting) and intensity of human disturbances for three contrasted seasons (Appendix S1), together with an important long-term GPS monitoring for 89 chamois-years. Human 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 predicted the responses of chamois under alternative scenarios entailing the ability or inability of 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 tested for 1) existence of diel migration to buffer risk-disturbance during different periods. Given that individuals varied in their exposure to risk, we expected individual differences in tolerance to humans and further assessed 2) how individuals adjusted their diel migration to the risk-disturbance 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.

METHODS

Study area

The study took place in the National Game and Wildlife Reserve of Bauges Massif (hereafter ‘Reserve’), located in the northern French Alps (45°40’N, 6°23’E, Fig. 2) between 2014 and 2018. The Reserve covers 5200 ha of a mountain landscape with altitude varying from 900 to 2200 m. Landscape cover is a compound of forests (56%) dominated by beech (*Fagus sylvatica*) 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 et al., 2020). Biomass and quality of edible resources were generally low close to trails (see 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 (*Vulpes vulpes*), which may predate newborns. Chamois is the main hunted species within the Reserve (70% of the total number of ungulates harvested), with on average 104 chamois shot 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 within the Reserve. We delimited three periods associated with specific sources and levels of 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 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 (see details in Appendix S1). Human activities were heterogeneously distributed within the Reserve and hunting was prohibited in the Armenaz area (300 ha; Fig. 2). Thereby, the five sectors where chamois were trapped were characterized by various levels of environmental and anthropogenic disturbances (Fig. 2, Appendix S1: Figure S5).

Defining the human-induced landscape of fear

The trail network shaped the backbone of human activities within the Reserve and was considered as a good proxy of where human disturbances took place (see complete details in 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 independent GPS dataset collected on a large representative sample of hikers (n = 270 tracks in 2014 and 2015), hunters (n = 223 tracks between 2014 and 2018), and skiers (n = 83 tracks in 2015, Appendix S1), we found that hikers, hunters and skiers spent 97%, 61% and 81% of their 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 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 frequentation (Corradini et al., 2021). In addition, we determined the risk of encountering hunters by calculating the 95% utilization distribution (UD) of hunter GPS locations (n = 223 tracks, see above and Appendix S1). We mapped the risk of being harvested by estimating the 95% UD of 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 similar approach see Benoist et al., 2013) to account for the effect of vegetation structure and visibility on animal tolerance (see Appendix S3; Tablado & Jenni, 2017; Wolf et al., 2019).

GPS and activity data for chamois

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

Testing for diel migration of chamois

For each individual and time period, we tested for a cyclic variation in the distance to the closest trail (hereafter 'distance to a trail') used by chamois over a 24h-period, i.e., a diel migration representing the back-and-forth movement of chamois being away from trails during daytime and close to trails during nighttime. We fitted Lomb-Scargle periodogram (Ruf, 1999), a least-squares spectral analysis, based on the distance to a trail calculated from the GPS locations taken every 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 performed a diel migration when a significant peak occurred within a 20 to 28h window (Courbin et al., 2019). Significance of the highest peak, i.e., whether the timing of the displacement related to trails was different from a random expectation, was estimated by computing the probability of random peaks reaching or exceeding the observed peak (Ruf, 1999). Note that the schedule of GPS locations did not affect the periodogram shape (peak locations) and had an effect on the magnitude of the peak only (not its significance). After testing for the presence of a diel cycle for 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 diel migration.

Dynamic and determinants of diel migration tactics

Individual chamois most tolerant to human disturbance may relax their diel response, i.e. they may not perform diel migration or their diel cycle may not be necessarily the main cyclic response over the short-term. Hence, we refined the role of the diel cycle in chamois movement patterns to trails and assessed whether their diel cycle was the most important cycle over 48h. We refitted the periodogram within a 6 to 48h window for each chamois and tested the significance of the highest peak. Combining the results of the two periodograms (20-28h and 6-48h) for each 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 according to the randomization procedure, i.e., the highest significant peak occurred within a 20-28h window for both periodograms, 2) *minor-DM* tactic: the diel migration occurred, but was not 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, and 3) *no-DM* tactic: chamois did not perform diel migration, i.e., no significant peak was detected within a 20-28h window for both periodograms. We reclassified chamois significantly moving closer to trails during daytime than nighttime (diel migration in an opposite way, n = 3 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).

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 performed diel migration during the skiing period, see Results). An individual home range was computed as the 95% UD derived from its GPS locations during a given period and year using biased random bridges (Benhamou, 2011) on a 25-m resolution grid (Lmin = 15m, Tmax = twice 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 interval). We fitted a multinomial logistic model with a three-level response variable (main-DM, minor-DM, no-DM) for each period. Models included four covariates related to the human-induced landscape of fear estimated at the home range scale: the mean risk of encountering hikers, the mean risk of being harvested, the mean risk of encountering hunters and the mean risk of being seen by humans from trails (Appendices 1 and 3). For each covariate, we weighted the risk value of each pixel by its UD value before averaging the risk values within the individual home range. We tested for an effect of hunting on chamois tolerance to hikers during hiking and 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 but a significant effect of hunting or of the interaction will reveal a carry-over effect of hunting 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 (Blumstein, 2016; Tablado & Jenni, 2017) and body mass to get insights on potential costs of the different tactics. Individuals establishing their seasonal home range in areas with a high density 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 controlled for the mean distance to trails available within the home range. All continuous covariates were centered and scaled. Models did not include highly correlated variables (i.e. the ones for which $|r| > 0.6$) and had low multicollinearity with a condition index < 3.8 (Dormann et al., 2013) at each period (see model details in the Appendix S5). We had 53 chamois-years during the hiking period and 86 chamois-years during the hunting period.

Quantification and determinants of the spatial extent of diel migration

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 median daytime distance to trails over individual GPS locations for the given day (hereafter ‘daytime distance to a trail’) and the median distance to trails over individual GPS locations 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 relation to the nighttime distance to a trail (previous night; nonlinear relationship modeled with a natural spline with four degrees of freedom) and the diel migration tactic (categorical predictor with two levels: minor-DM and main-DM). We fitted linear mixed models with individual ID as random intercept to account for repeated measurements on the same individuals. Then, we tested for the effects of the risk-disturbance predictors within the seasonal home range (the mean risk of 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 framework (Fig. 1C), we assessed if the mean risk of being harvested shaped the extent of diel 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 period will reveal a carry-over effect of hunting on chamois tolerance to hikers (Fig. 1C dotted 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 to trails and the risk-disturbance predictors (see candidate models in Appendix S6: Tables S1 and S2). Models also included the effects of individual features (age, sex, body mass) and we controlled for the effect of the mean distance to trails available within the home range on diel 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 candidate models. None of the candidate models included highly correlated variables ($|r| > 0.6$) and had low multicollinearity with a condition index < 13 and a variance inflation factor < 2.2 (Dormann et al., 2013). We relied on data from 1165 chamois-days from 44 chamois-years for the hiking period, and 3088 chamois-days from 73 chamois-years for the hunting period.

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

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).

RESULTS

Evidence for plastic diel migration

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 tests). This pattern was due to back-and-forth movements to trails between night and day with a 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-DM or a minor-DM, n = 76/89 chamois-years during the hunting period using a main-DM or a minor-DM, Appendix S4: Table S1). However, the diel spatial shift was highly variable between individuals (Appendix S4: Figures S1 and S2) and highly context-dependent. Indeed, the distance of diel migration varied with chamois nighttime location: the closer chamois were to a trail during nighttime, the further they were from a trail during the next day (Figs 3A, 3C). For example, chamois that were 50 m away from a trail at night (i.e., peak of the distribution) tended to perform large diel migration (see Results section Determinants of the spatial extent of diel migration). Importantly, the extent of the daytime movement away from a trail was highly constrained by the low availability of areas away from a trail (dotted lines in Figs 3A, 3C) with a median distance to a trail available within the home range of ~175 m (Appendix S4: Table S2). By contrast, such a diel migration did not occur during the skiing period (Figs 3E, 3F, Appendix S4: Table S1, Figure S3).

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%) had a low tolerance and performed diel migrations (main-DM and minor-DM tactics) during hiking and hunting periods, with the main-DM tactic being dominant (>50%; Fig. 4, Appendix 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 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 four chamois out of 10 performing a diel migration lived 400 m away from trails during the skiing period and the causal effect of trails on their diel migration pattern was thus questionable (Appendix S4: Figure S3).

Determinants of diel migration tactics

During the hiking period, the diel migration tactic was neither related to hiker attendance to trail 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 support a carry-over effect of hunting during this period (Fig. 1C dotted line). In contrast, during the hunting period, the patterns support that the diel migration tactic was largely driven by the human-induced landscape of fear. After controlling for inter-individual variation in the 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. ×4.1 between extreme values) and increasing risk of encountering hikers (i.e. ×4.4 between 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 (Fig. 1A) nor undesirable tolerance persistence in the choice of tactic during the hunting period (Fig. 1C dashed lined). Chamois had also higher probabilities of using a main-DM tactic than a minor-DM tactic when they used areas with a low mean risk of being seen and a low mean risk of encountering hunters (Appendix S5: Table S2, Figures S1A, S1B). However, these latter effects were weaker than the effects of risk of encountering hikers and of being harvested (the size effects were 1.5 to 2 times lower). During the hunting period, females were most likely to use a main-DM tactic, while no differences were observed for males (Appendix S5: Table S2, Figure S1C). The choice of tactic did not depend on body mass and age.

Determinants of the spatial extent of diel migration

The top-ranked model included an interaction between the distance to trails the previous night and either the mean risk of encountering hikers during the hiking period or the mean risk of being harvested during the hunting period (ΔAICc with the second best models > 4, Appendix S6: 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 within individual home ranges, chamois indeed moved a lesser distance away from trails at 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 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 hypothesis that diel migrants developed a greater tolerance to hiker disturbance when nature-based tourism increased, whereas they displayed a low tolerance at low levels of hiker disturbance (Fig. 1A). Daytime movements of chamois away from trails were not influenced by 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 period, chamois performed longer diel migrations with increasing mean risk of being harvested in areas with a low risk of encountering hikers, while they did not respond to hunting risk at high encounter risk with hikers (Fig. 6B, Appendix S6: Table S4). Hunting also exacerbated the threshold nighttime distance to trails triggering diel migrations in chamois (i.e., 300 m) in areas of low risk of encountering hikers. On average, when chamois were located at 50 m from a trail at night during the hunting period, they moved 166 m away the next day when the risk of being 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. This suggests that chamois tolerant to hikers also increased their tolerance to hunting during the harvesting period (Fig. 1C dashed line). The extent of diel migration was neither influenced by the tactic, the mean risk of being seen, nor individual characteristics during both periods (Appendix S6: Tables S3 and S4).

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).

DISCUSSION

Our study demonstrated how overlapping nature-based tourism and hunting shaped complex proactive responses and tolerance patterns to human activities for a large mountain herbivore species. Chamois were generally wary of humans: most individuals performed diel migration (i.e., back-and-forth movements further away from trails during daytime and closer to trails 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 period, unveiling additive risk effects. However, we found no carry-over effect of hunting beyond the hunting period. Importantly, chamois performed shorter diel migration in areas highly 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 hunting period could be maladaptative. Overall, we stress the importance to consider potential deleterious survival consequences of animal tolerance adjustments to disturbances in multi-use landscapes with complex human-induced landscapes of fear.

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

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

Diel migration was common in our population, but chamois shifted between diel migration tactics and adjusted the spatial extent of their diel migration to varying levels of human disturbances in a complex way (see details in the next sections). Overall, the seasonal increase in 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 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 at a broader scale. The inconsistent pattern of diel migration found during the skiing period was 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 home range > 450 m) compared to other periods (~175 m, Appendix S4: Table S2). Overall, chamois did not necessarily avoid winter areas frequented by humans. However, most trails were covered by snow during the skiing period, and in addition, chamois left the Alpine grasslands (where trails are located) to move to steeper slopes or at lower altitude (Appendix S4: Table S2).

While the movement of chamois away from trails during daytime was expected, the rationale behind chamois moving closer to trails in the nighttime remains a challenging question. 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 food resources for chamois with increasing distance from a trail during the summer (Appendix S2: Figure S2). Food quality is especially important for chamois (Duparc et al., 2020) but only slightly decreased for individuals getting closer to trails within the first 100 m from a trail (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) distance to a trail of chamois during the hiking and hunting periods (Appendix S2: Figure S2). 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 close to trails (<100 m) were not allocated to an important extent to foraging (e.g. resting, vigilance and moving). Interestingly, also Tatra chamois (*Rupicapra rupicapra tatrica*) experienced a decrease in the proportion of foraging in the daytime budget close to hiking trails (Pęksa & Ciach, 2018). Together, these results suggest more frequent vigilance events or relocation bouts interspersed with foraging activities closer to than away from trails. Overall, 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 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 context, as is the case for our chamois population (Garel et al., 2011). Another explanation not 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 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 information on the spatio-temporal variations in human disturbance, using odor cues. For many large ungulates, predator odors provide evidence of their recent passage and the likelihood of their future presence in the area (e.g., red deer, Kuijper et al., 2014; caribou *Rangifer tarandus caribou*, Latombe et al., 2014).

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 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. As expected within our theoretical framework, the effect of hunting on chamois response was additive to and stronger than hiking (Fig. 1C, solid black line). Our results supported previous findings, as for example in a French mouflon population that responded more strongly to hunting 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 showed higher vigilance and subsequent loss in feeding time compared to elk living outside hunting areas (Ciuti et al., 2012).

When the landscape of fear emerges from several co-occurring sources of anthropogenic risk with different degrees of lethality, prey abilities required to adjust the strength of their 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 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 hunting and hiking created a complex human-induced landscape of fear that impeded chamois to 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 from hunters, especially as they used the same trails during the hunting period and as hunters are 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, adjust the extent of their diel migration depending on their approximate assessment of the lethal 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.

A potentially maladaptive increased tolerance to nature-based tourism

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 availability and with individual changes in diel migration tactics between periods, indicates a potential habituation process in the most disturbed areas (Figs 1A and 1C). Studies that ignored the individual dynamics of animal responsiveness to human disturbance in the long-term, failed to clarify the mechanism underlying tolerance adjustments (Bejder et al., 2009; Blumstein, 2016). 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 abilities to adjust tolerance to human disturbance is a basic requirement for a habituation process to occur (Blumstein, 2016). However, we cannot formally ignore additional mechanisms such as differential selection among personality types or local adaptation for increased tolerance (Samia 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).

Regardless of the mechanisms, we found an undesirable outcome of the increased 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 risk (Fig. 1C, dashed black line). Such an increased tolerance to humans may be maladaptative in 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 predators (Geffroy et al., 2015; Blumstein, 2016). Such habituation transfer may have unfortunate conservation outcomes (Blumstein, 2016). Overall, our findings support a previous warning by Geffroy et al. (2015) to take outcomes of animal tolerance adjustments into account in ecological and conservation perspectives.

During the hiking period, the majority of individuals performed a diel migration. 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 time of the year, disturbance by hikers occurs every day. This baseline disturbance level may be sufficient to trigger a systematic response from chamois. In other study areas, individuals may 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 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 influenced by human group size (Hamr, 1988). We thus encourage future studies to consider a 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 constraints (Bourgoin et al., 2008).

On the costs of diel migration

The costs of anti-predator responses (i.e., the risk effects) may have important consequences for population demography (Preisser et al., 2005) and should not be ignored (Creel et al., 2019; Say-Sallaz et al., 2019). However, there is still considerable debate regarding the demographic consequences of risk effects. For example, fervent debates have taken place concerning the fear effects of wolf (*Canis lupus)* on elk in the Greater Yellowstone Ecosystem between Creel et al. (2007), Creel et al. (2011), Middleton et al. (2013) and Kohl et al. (2018). Here, we found that a 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 energetic expenditures during hunting. However, no increase in proxies of daily energetic 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 & Dill, 1986; Frid & Dill, 2002). Detecting body mass effects across various sex, age and years would have required however very large sample sizes. Furthermore, risk-disturbance effects are not only limited to energetic loss but are also related to time, stress, reproduction and survival costs in large mammals (review in Say-Sallaz et al., 2019). Possibly compensatory responses may also occur in diel migrants. As an example, mouflon disturbed by hunters during daytime were more active and increased their use of favorable foraging resources the night following 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 strong and generalized behavioral response in animal populations. This is especially relevant in the Anthropocene context, where more and more animal populations will have to cope with complex human-induced landscapes of fear, combining both lethal risk and nature-based tourism.

ACKNOWLEDGMENTS

This study was funded by ANR grant Mov-It #16-CE02-0010 coordinated by Anne Loison, CNRS, Zone Atelier Alpes, a member of the ILTER-Europe network ZAA, and by ANR grant HUMANI #18-CE03-0009 coordinated by Clémence Perrin-Malterre. We gratefully acknowledge all participants for helping with the capture and marking of animals, for the recovery of GPS collars and for collecting GPS data on human activities: volunteers and professionals from the Office Français de la Biodiversité (formerly Office National de la Chasse et de la Faune Sauvage), the Office National des Forêts, the Groupement d'Intérêt Cynégétique des Bauges, the Parc Naturel Régional du massif des Bauges, the Observatoire Grande Faune et Habitats, and the laboratory Environnements DYnamiques TErritoires Montagnes. Thanks to Nadège Bonnot for revising the manuscript, and Sebastien Ibanez and the Mov-It group for our fruitful discussions.

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.

LITERATURE CITED

Alonzo, S.H., P.V. Switzer, and M. Mangel. 2003. Ecological games in space and time: The distribution and abundance of Antarctic krill and penguins. *Ecology* 84:1598-1607.

Balmford, A., J.M.H. Green, M. Anderson, J. Beresford, C. Huang, R. Naidoo, M. Walpole, and A. Manica. 2015. Walk on the wild side: estimating the global magnitude of visits to protected areas. *PLoS Biology* 13:e1002074.

Basille, M., D. Fortin, C. Dussault, G. Bastille-Rousseau, J.-P. Ouellet, and R. Courtois. 2015. Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology* 96:2622-2631.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48.

Barton, K. 2020. MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bejder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series* 395:177-185.

Benhamou, S. 2011. Dynamic Approach to Space and Habitat Use Based on Biased Random Bridges. *PLoS ONE* 6: e14592.

Benoist, S., M. Garel, J.-M. Cugnasse, and P. Blanchard. 2013. Human disturbances, habitat characteristics and social environment generate sex-specific responses in vigilance of mediterranean mouflon. *PLoS ONE* 8:e82960.

Benoit, L., A.J.M. Hewison, A. Coulon, L. Debeffe, D. Grémillet, D. Ducros, B. Cargnelutti, Y. Chaval, and N. Morellet. 2020. Accelerating across the landscape: the energetic costs of natal dispersal in a large herbivore. *Journal of Animal Ecology* 89:173-175.

Blumstein, D.T. 2016. Habituation and sensitization: new thoughts and old ideas. *Animal Behaviour* 120:255-262.

Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A.J.M. Hewison. 2013. Habitat use under predation risk: Hunting, roads and human dwellings influence the spatial behavior of roe deer. *European Journal of Wildlife Research* 59:185-193.

Bonnot, N., O. Couriot, A. Berger, F. Cagnacci, S. Ciuti, J.E. De Groeve, B. Gehr, M. Heurich, P. Kjellander, M. Kröschel, N. Morellet, L. Sönnichsen, and A.J.M. Hewison. 2020. Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. *Journal of Animal Ecology* 89:132-145.

Bourgoin, G., M. Garel, B. Van Moorter, D. Dubray, D. Maillard, E. Marty, and J.-M. Gaillard. 2008. Determinants of seasonal variation in activity patterns of mouflon. *Canadian Journal of Zoology* 86:1410-1418.

Brown, J.S., J.W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385-399.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516-519.

Ciach, M., and L. Pęksa. 2019. Human-induced environmental changes influence habitat use by an ungulate over the long-term. *Current Zoology* 65:129-137.

Ciuti, S., J.M. Northrup, T.B. Muhly, S. Simi, M. Musiani, J.A. Pitt, and M.S. Boyce. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE* 7:e50611.

Corradini, A., M. Randles, L. Pedrotti, E. van Loon, G. Passoni, V. Oberosler, F. Rovero, C. Tattoni, M. Ciolli, and F. Cagnacci. 2021. Effects of cumulated outdoor activity on wildlife habitat use. *Biological Conservation* 253:108818.

Courbin, N., D. Fortin, C. Dussault, and R. Courtois. 2014. Logging-induced changes in habitat network connectivity shape behavioral interactions in the wolf-caribou-moose system. *Ecological Monographs* 84:265-285.

Courbin, N., A. Besnard, C. Péron, C. Saraux, J. Fort, S. Perret, J. Tornos, and D. Grémillet. 2018. Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator. *Ecology Letters* 21:1043-1054.

Courbin, N., A.J. Loveridge, H. Fritz, D.W. Macdonald, R. Patin, M. Valeix, and S. Chamaillé-Jammes. 2019. Zebra diel migrations reduce encounter risk with lions at night. *Journal of Animal Ecology* 88:92-101.

Creel, S. 2018. The control of risk hypothesis: reactive vs. proactive antipredator response and stress-mediated vs. food-mediated costs of response. *Ecology Letters* 21:947-956.

Creel, S., D. Christianson, S. Liley, and J.A. Winnie Jr. 2007. Predation risk affects reproductive physiology and demography of elk. *Science* 315:960.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23:194-201.

Creel, S., D.A. Christianson, and J.A. Winnie Jr. 2011. A survey of the effects of wolf predation risk on pregnancy rates and calf recruitment in elk. *Ecological Applications* 21:2847-2853.

Creel, S., M. Becker, E. Dröge, J. M'soka, W. Matandiko, E. Rosenblatt, T. Mweetwa, H. Mwape, M. Vinks, B. Goodheart, J. Merkle, T. Mukula, D. Smit, C. Sanguinetti, C. Dart, D. Christianson, and P. Schuette. 2019. What explains variation in strength of behavioral responses to predation risk? A standardized test with large carnivore and ungulate guilds in three ecosystems. *Biological Conservation* 232:164-172.

Dehaudt, B., M. Nguyen, A. Vadlamudi, and D.T. Blumstein. 2019. Giant clams discriminate threats along a risk gradient and display varying habituation rates to different stimuli. *Ethology* 125:392-398.

Dirzo, R., H.S. Young, M. Galetti, G. Ceballos, N.J.B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345:401-406.

Dormann, C.F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J.R. Garcia Marquez, B. Gruber, B. Lafourcade, P.J. Leitao, T. Münkemüller, C. McClean, P.E. Osborne, B. Reineking, B. Schröder, A.K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27-46.

Duparc, A., M. Garel, P. Marchand, D. Dubray, D. Maillard, and A. Loison. 2020. Through the taste buds of a large herbivore: foodscape modeling contributes to an understanding of forage selection processes. *Oikos* 129:170-183.

Enggist-Dublin, P., and P. Ingold. 2003. Modelling the impact of different forms of wildlife harassment, exemplified by a quantitative comparison of the effects of hikers and paragliders on feeding and space use of chamois *Rupicapra rupicapra. Wildlife Biology* 9:37-45.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. *Functional Ecology* 21:1003-1015.

Fortin, D., J.A. Merkle, M. Sigaud, S.G. Cherry, S. Plante, A. Drolet, and M. Labrecque. 2015. Temporal dynamics in the foraging decisions of large herbivores. *Animal Production Science* 55:376-383.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:11.

Garel, M., J.-M. Gaillard, J.-M. Jullien, D. Dubray, D. Maillard, and A. Loison. 2011. Population abundance and early spring conditions determine variation in body mass of juvenile chamois. *Journal of Mammalogy* 92:1112-1117.

Gaynor, K.M., C.E. Hojnowski, N.H. Carter, and J.S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360:1232-1235.

Gaynor, K.M., J.S. Brown, A.D. Middleton, M.E. Power, and J.S. Brashares. 2019. Landscapes of fear: spatial patterns of risk perception and response. *Trends in Ecology and Evolution* 34:355-368.

Geffroy, B., D.S.M. Samia, E. Bessa, and D.T. Blumstein. 2015. How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology and Evolution* 30:755-765.

Geffroy, B., B. Sadoul, B.J. Putman, O. Berger-Tal, L.Z. Garamszegi, A.P. Møller, and D.T. Blumstein. 2020. Evolutionary dynamics in the Anthropocene: life history and intensity of human contact shape antipredator responses. *PLoS Biology* 18:e3000818.

Goumas, M., V.E. Lee, N.J. Boogert, L.A. Kelley, and A. Thornton. 2020. The role of animal cognition in human-wildlife interactions. *Frontiers in Psychology* 11:589978.

Groves, P.M., and R.F. Thompson. 1970. Habituation: a dual-process theory. *Psychological Review* 77:419-450.

Guiden, P.W., S.L. Bartel, N.W. Byer, A.A. Shipley, and J.L. Orrock. 2019. Predator-prey interactions in the Anthropocene: reconciling multiple aspects of novelty. *Trends in Ecology and Evolution* 34:616-627.

Hamr, J. 1988. Disturbance behaviour of chamois in an Alpine tourist area of Austria. *Mountain Research and Development* 8:65-73.

Harris, G., R.M. Nielson, T. Rinaldi, and T. Lohuis. 2014. Effects of winter recreation on northern ungulates with focus on moose (*Alces alces*) and snowmobiles. *European Journal of Wildlife Research* 60:45-58.

Hays, G.C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503:163-170.

Iwasa, Y. 1982. Vertical migration of zooplankton: A game between predator and prey. *American Naturalist* 120:171-180.

Kohl, M.T., D.R. Stahler, M.C. Metz, J.D. Forester, M.J. Kauffman, N. Varley, P.J. White, D.W. Smith, and D.R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* 88:638-652.

Kuijper, D.P.J., M. Verwijmeren, M. Churski, A. Zbyryt, K. Schmidt, B. Jędrzejewska, and C. Smit. 2014. What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE* 9:e84607.

Latombe, G., D. Fortin, and L. Parrott. 2014. Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology* 83:185-198.

Laundré, J.W., L. Hernández, and K.B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79:1401-1409.

Laundré, J.W., L. Hernández, and W.J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *Open Ecology Journal* 3:1-7.

Lesmerises, F., C.J. Johnson, and M.-H. St-Laurent. 2017. Refuge or predation risk? Alternate ways to perceive hiker disturbance based on maternal state of female caribou. *Ecology and Evolution* 7:845-854.

Lesmerises, F., F. Déry, C.J. Johnson, and M.-H. St-Laurent. 2018. Spatiotemporal response of mountain caribou to the intensity of backcountry skiing. *Biological Conservation* 217:149-156.

Liley, S., and S. Creel. 2008. What best explains vigilance in elk: characteristics of prey, predators, or the environment? *Behavioral Ecology* 19:245-254.

Lima, S.L. 1998. Nonlethal effects in the ecology of predator-prey interactions–What are the ecological effects of anti-predator decision-making? *BioScience* 48:25-34.

Loison, A., J.-M. Jullien, and P. Menaut. 1999. Subpopulation structure and dispersal in two populations of chamois. *Journal of Mammalogy* 80:620-632.

Loison, A., G. Darmon, S. Cassar, J.-M. Jullien, and D. Maillard. 2008. Age-and sex-specific settlement patterns of chamois (*Rupicapra rupicapra*) offspring. *Canadian Journal of Zoology* 86:588-593.

Lopez, J.F. 2001. *Inventaire systématique de la flore et de la végétation du Massif des Bauges*. Technical Report, Parc Naturel Régional du Massif des Bagues, Le Châtelard, France.

Marchand, P., M. Garel, G. Bourgoin, D. Dubray, D. Maillard, and A. Loison. 2014. Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area. *Biological Conservation* 177:1-11.

Marchand, P., M. Garel, N. Morellet, L. Benoit, Y. Chaval, C. Itty, E. Petit, B. Cargnelutti, A.J.M. Hewison, and A. Loison. 2021. A standardized biologging approach to infer parturition: an application in large herbivores across the hider-follower continuum. *Methods in Ecology and Evolution* 12:1017-1030.

Middleton, A.D., M.J. Kauffman, D.E. McWhirter, M.D. Jimenez, R.C. Cook, J.G. Cook, S.E. Albeke, H. Sawyer, and P.J. White. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters* 16:1023-1030.

Newsome, D. 2014. Appropriate policy development and research needs in response to adventure racing in protected areas. *Biological Conservation* 171:259-269.

Pęksa, L., and M. Ciach. 2015. Negative effects of mass tourism on high mountain fauna: the case of the Tatra chamois *Rupicapra rupicapra tatrica*. *Oryx* 49:500-505.

Pęksa, L., and M. Ciach. 2018. Daytime activity budget of an alpine ungulate (Tatra chamois *Rupicapra rupicapra tatrica*): influence of herd size, sex, weather and human disturbance. *Mammal Research* 63:443-453.

Preisser, E.L., D.I. Bolnick, and M.F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501-509.

R Development Core Team. 2019. *R: A language and environment for statistical computing*. Version 3.6.2. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Rankin, C.H., T. Abrams, R.J. Barry, S. Bhatnagar, D. Clayton, J. Colombo, G. Coppola, M.A. Geyer, D.L. Glanzman, S. Marsland, F. McSweeney, D.A. Wilson, C.-F. Wu, and R.F. Thompson. 2009. Habituation revisited: an updated and revisited description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory* 92:135-138.

Reimers, E., K.H. Røed, Ø Flaget, E. and Lurås. 2010. Habituation responses in wild reindeer exposed to recreational activities. *Rangifer* 30:45-59.

Richard, J.H., and S.D. Côté. 2016. Space use analyses suggest avoidance of a ski area by mountain goats. *Journal of Wildlife Management* 80:387-395.

Riotte-Lambert, L., and J. Matthiopoulos. 2020. Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology and Evolution* 35:163-174.

Ruf, T. 1999. The Lomb-Scargle periodogram in biological rhythm research: Analysis of incomplete and unequally spaced time-series. *Biological Rhythm Research* 30:178-201.

Samia, D.S.M., S. Nakagawa, F. Nomura, T.F. Rangel, and D.T. Blumstein. 2015. Increased tolerance to humans among disturbed wildlife. *Nature Communications* 6:8877.

Sawyer, H., N.M. Korfanta, R.M. Nielson, K.L. Monteith, and D. Strickland. 2017. Mule deer and energy development – Long-term trends of habituation and abundance. *Global Change Biology* 23:4521-4529.

Say-Sallaz, E., S. Chamaillé-Jammes, H. Fritz, and M. Valeix. 2019. Non-consumptive effects of predation in large terrestrial mammals: Mapping our knowledge and revealing the tip of the iceberg. *Biological Conservation* 235:36-52.

Schröder, W., and I. Von Elsner-Schak. 1985. Correct age determination in chamois. In *The biology and management of mountain ungulates*, edited by S. Lovari, 65-70. London: Croom Helm.

Schuttler, S.G., A.W. Parsons, T.D. Forrester, M.C. Baker, W.J. McShea, R. Costello, and R. Kays. 2017. Deer on the lookout: how hunting, hiking and coyotes affect white-tailed deer vigilance. *Journal of Zoology* 301:320-327.

Sih, A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Animal Behaviour* 85:1077-1088.

Sih, A., J. Stamps, L.H. Yang, R. McElreath, and M. Ramenofsky. 2010. Behavior as a key component of integrative biology in a human-altered world. *Integrative and Comparative Biology* 50:934-944.

Sih, A., M.C.O. Ferrari, and D.J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications* 4:367-387.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation* 141:2159-2173.

Steven, R., C. Pickering, and J.G. Castley. 2011. A review of the impacts of nature based recreation on birds. *Journal of Environmental Management* 92:2287-2294.

Strava. 2018. Strava Global Heatmap. Retrieved April, 2020 from strava.co m/heatmap.

Tablado, Z., and L. Jenni. 2017. Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews* 92:216-233.

Thiel, D., S. Jenni-Eiermann, V. Braunisch, R. Palme, and L. Jenni. 2008. Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. *Journal of Applied Ecology* 45:845-853.

Thompson, R.F., and W.A. Spencer. 1966. Habituation: a model phenomenon for the study of neuronal substrates of behavior. *Psychological Review* 73:16-43.

Tolon, V., S. Dray, A. Loison, A. Zeileis, C. Fischer, and E. Baubet. 2009. Responding to spatial and temporal variations in predation risk: Space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology* 87:1129-1137.

Tucker, M.A., et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359:466-469.

Tuomainen, U., and U. Candolin. 2011. Behavioural responses to human-induced environmental change. *Biological Reviews* 86:640-657.

Valeix, M., A.J. Loveridge, S. Chamaillé-Jammes, Z. Davidson, F. Murindagomo, H. Fritz, and D.W. Macdonald. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* 90:23-30.

Venables, W.N., and B.D. Ripley. 2002. *Modern Applied Statistics with S. Fourth Edition*. New York: Springer.

Vincze, E., S. Papp, B. Preiszner, G. Seress, V. Bókony, and A. Liker. 2016. Habituation to human disturbance is faster in urban than rural house sparrows. *Behavioral Ecology* 27:1304-1313.

Weiner, J. 2017. Riverplot: Sankey or ribbonplots. R package version 0.6. https://CRAN.R-project.org/package=riverplot

Wilson, R.P., L. Börger, M.D. Holton, D.M. Scantlebury, A. Gómez-Laich, F. Quintana, F. Rosell, P.M. Graf, H. Williams, R. Gunner, L. Hopkins, N. Marks, N.R. Geraldi, C.M. Duarte, R. Scott, M.S. Strano, H. Robotka, C. Eizaguirre, A. Fahlman, E.L.C. Shepard. 2020. Estimates for energy expenditure in free-living animals using acceleration proxies: a reappraisal. *Journal of Animal Ecology* 89:161-172.

Wolf, I.D., D.B. Croft, and R.J. Green. 2019. Nature conservation and nature-based tourism: a paradox? *Environments* 6:104.

Ydenberg, R.C., and L.M. Dill. 1986. The economics of fleeing from predators. *Advances in the Study of Behavior* 16:229-249.

Figure legends.

Figure 1. Conceptual schemes representing the expected tolerance adjustments of animals to human activities. (A) Animals should respond to nonlethal human disturbance with higher intensity as the disturbance level increases. Individuals experiencing an intermediate level of nonlethal disturbances are then expected to increase their tolerance (decreased responsiveness) to disturbances through habituation. (B) In a context including hunting, animals able to distinguish hunters from other humans would keep a constant response to nonlethal disturbances at the basal level, expected along with habituation effects, and would be intolerant to hunters. (C) When animals cannot distinguish hunters from other recreationists, they would perceive a high global disturbance level and sharply decrease their tolerance during the hunting period independently of their initial tolerance level, and then revert back to their basal tolerance level (solid line). Two 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 habituated animals may not perceive a sufficient significant increase in risk and maintain high tolerance to nature-based tourists and hunters during the hunting period (dashed line).

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 trails of GPS locations of an individual at a given day or night) of chamois during the three periods between 2014 and 2018, weighted by the number of locations per individual and number of individuals. Daytime and nighttime distributions significantly ($P < 0.001$; paired samples Wilcoxon test) differed during the hiking and hunting periods. We showed, for each period, the distribution of distances to a trail available within the seasonal chamois home ranges (dotted line), weighted by the home range surface per individual and the number of individuals. To 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 distance to trails was 1652 m during the skiing period and we only show data < 700 m (72%) for clarity. (B, D, F) Periodograms of the distance to a trail time-series for 55, 89 and 83 chamois-years within the 20 to 28h-period window during the hiking, hunting and skiing periods, respectively. Each dotted line represents the periodogram for one individual chamois. The maximum value of each periodogram is indicated by a triangle pointing up if significant ($P < 0.05$) or pointing down if non-significant ($P \geq 0.05$). Periodograms were labeled *a posteriori*.

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.

Figure 6. Predicted daytime distance to trails of chamois in relation to the distance to trails during the previous night, and (A) the risk of encountering hikers during the hiking period, and (B) both the risk of encountering hikers and the risk of being harvested during the hunting period. The 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 distance to a trail and the gray line, with daytime movement away from a trail when above the 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 response for a female chamois performing a main-DM tactic and fixed all other continuous predictors at their mean values. Low, average and high risk correspond to the 10th percentile, mean and 90th percentile, respectively. Shadow areas represent the 95% confidence interval. Daytime and nighttime distances to trails are truncated at 400 m, and 93% and 94% of data are shown in A and B, respectively.

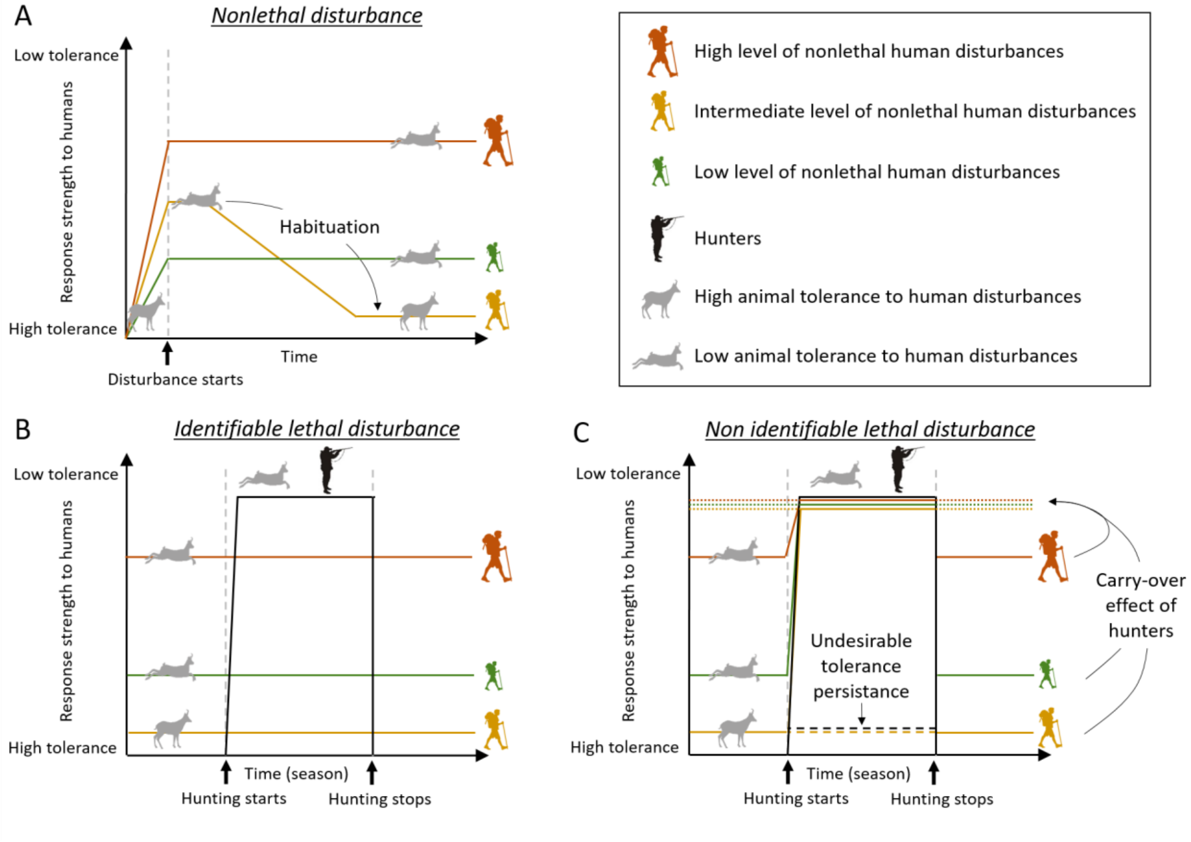
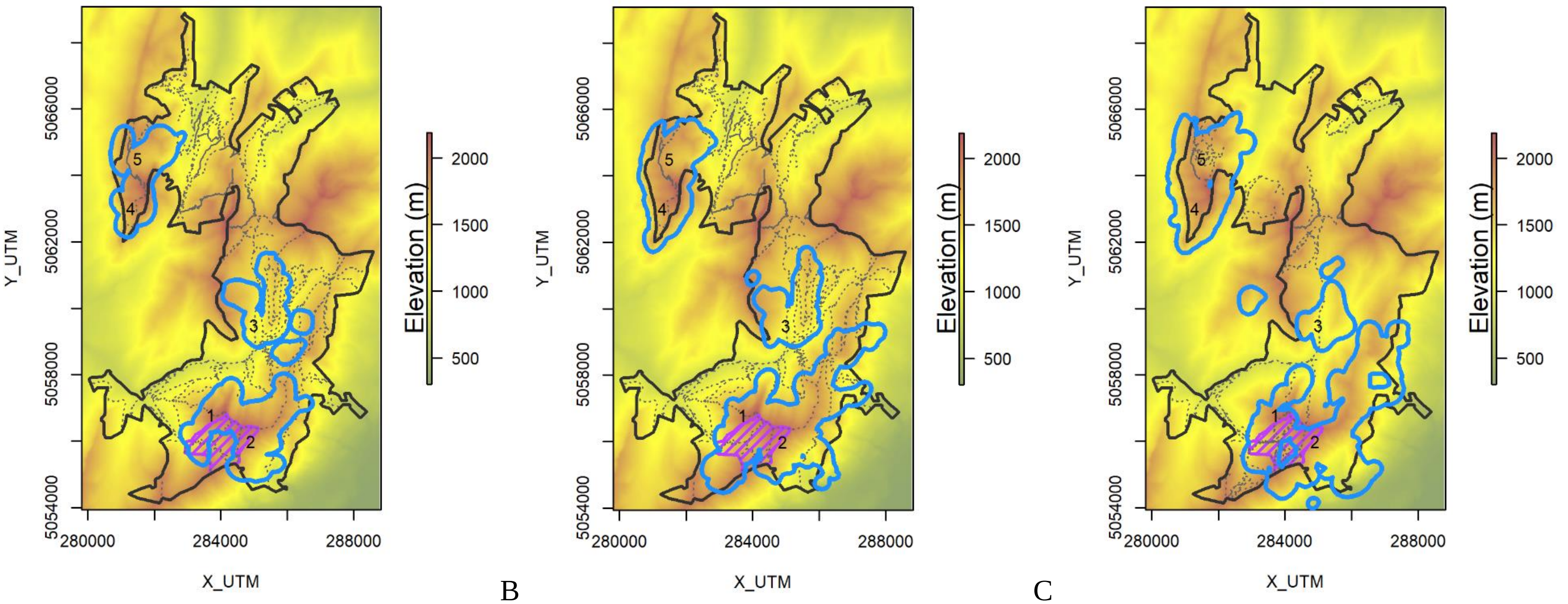

A
Nonlethal disturbance
Low tolerance
Response strength to humans
High tolerance
Habituation
Time
Disturbance starts
High level of nonlethal human disturbances
Intermediate level of nonlethal human disturbances
Low level of nonlethal human disturbances
Hunters
High animal tolerance to human disturbances
Low animal tolerance to human disturbances
B
Identifiable lethal disturbance
Low tolerance
Response strength to humans
High tolerance
Time (season)
Hunting starts
Hunting stops
C
Non identifiable lethal disturbance
Low tolerance
Response strength to humans
High tolerance
Undesirable tolerance persistance
Carry-over effect of hunters
Time (season)
Hunting starts
Hunting stops

Figure 1.


Y_UTM
5066000
5062000
5058000
5054000
280000
284000
288000
X_UTM
Elevation (m)
2000
1500
1000
500
1
2
3
4
5

A

B

C

Figure 2.

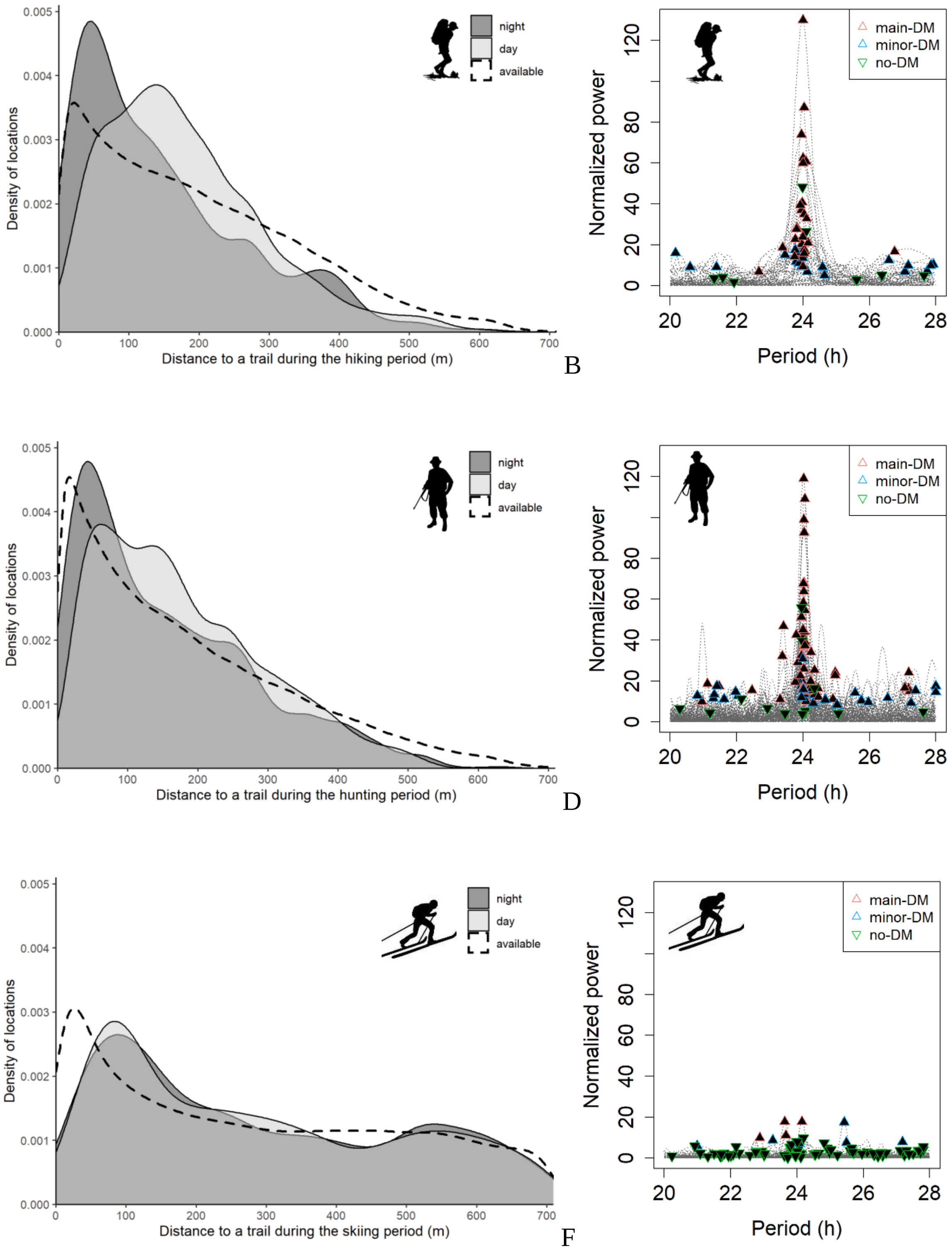

A
Density of locations
Distance to a trail during the hiking period (m)
night
day
available
B
Normalized power
Period (h)
main-DM
minor-DM
no-DM
C
Density of locations
Distance to a trail during the hunting period (m)
night
day
available
D
Normalized power
Period (h)
main-DM
minor-DM
no-DM
E
Density of locations
Distance to a trail during the skiing period (m)
night
day
available
F
Normalized power
Period (h)
main-DM
minor-DM
no-DM

Figure 3.

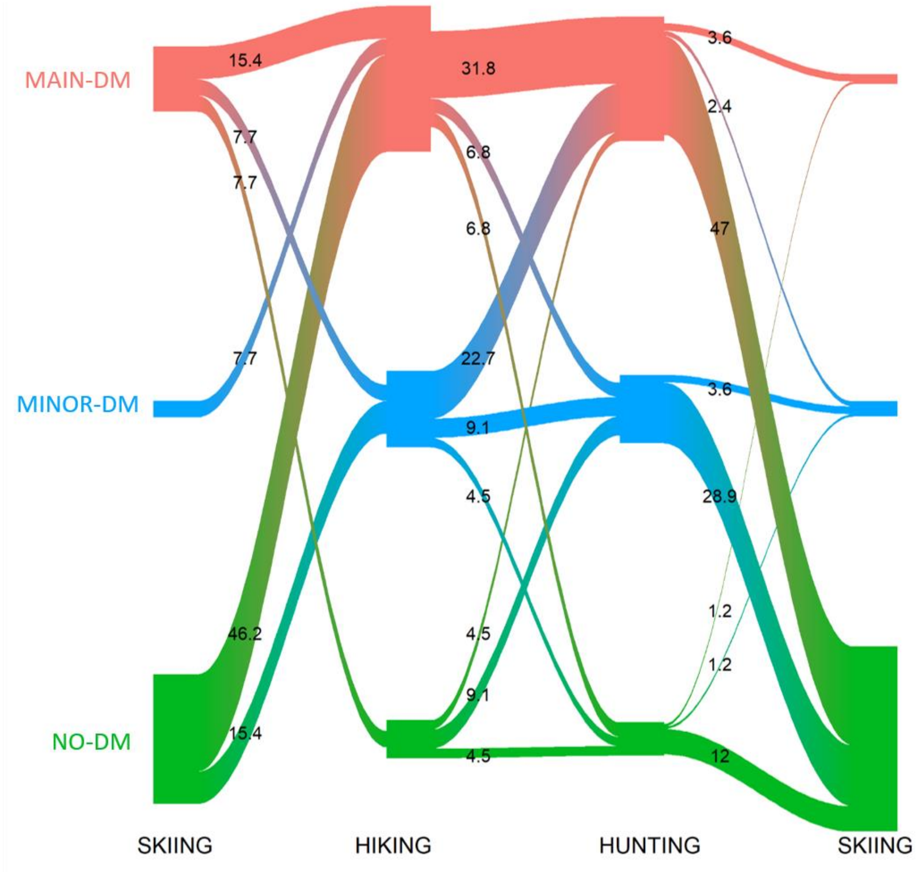

MAIN-DM
MINOR-DM
NO-DM
15.4
7.7
7.7
7.7
46.2
15.4
31.8
6.8
6.8
22.7
9.1
4.5
4.5
9.1
4.5
3.6
2.4
47
3.6
28.9
1.2
1.2
12
SKIING
HIKING
HUNTING
SKIING

Figure 4.

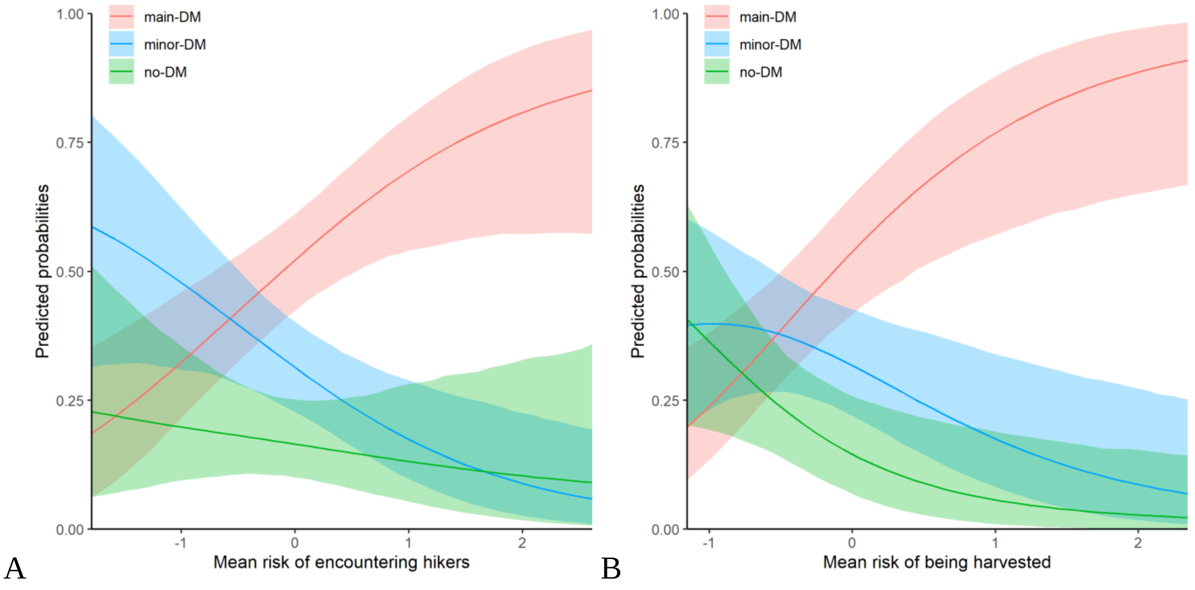
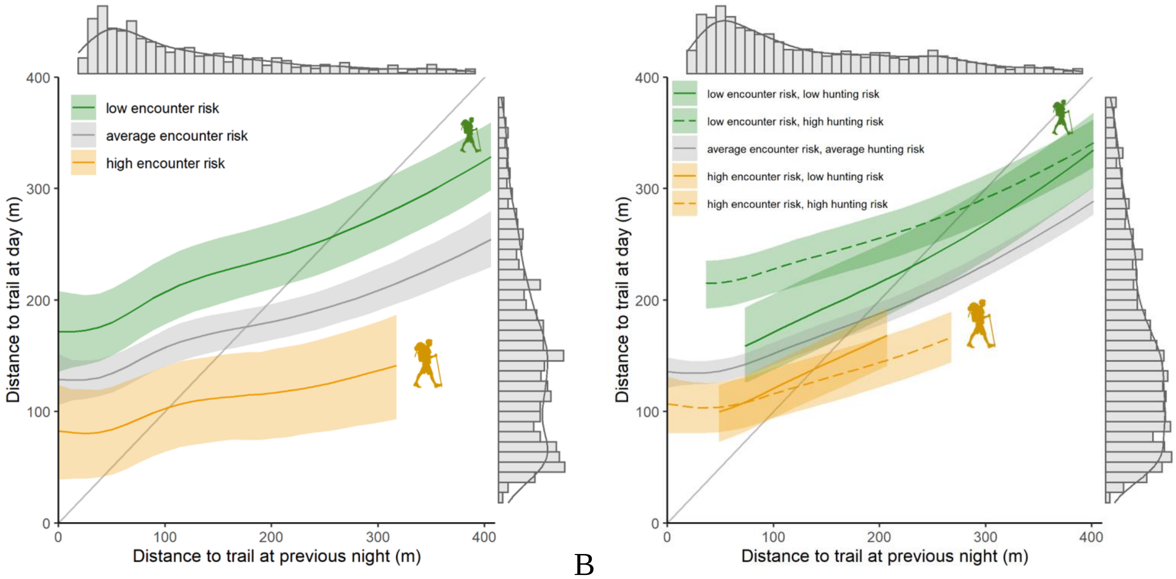

A
1.00
0.75
0.50
0.25
0.00
Predicted probabilities
main-DM
minor-DM
no-DM
-1
0
1
2
Mean risk of encountering hikers
B
1.00
0.75
0.50
0.25
0.00
Predicted probabilities
main-DM
minor-DM
no-DM
-1
0
1
2
Mean risk of being harvested

Figure 5.


400
300
200
100
0
Distance to trail at day (m)
0
100
200
300
400
Distance to trail at previous night (m)
low encounter risk
average encounter risk
high encounter risk
low encounter risk, low hunting risk
low encounter risk, high hunting risk
average encounter risk, average hunting risk
high encounter risk, low hunting risk
high encounter risk, high hunting risk

A B

Figure 6.