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Research Article

Hunting, but not outdoor recreation, modulates behavioural tolerance to human disturbance in Alpine marmots *Marmota marmota*

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Humans are often perceived as predators by free-living animals, and thus, even non-consumptive human activities such as outdoor recreation may trigger behavioural and physiological responses, often with negative consequences on individual fitness and population persistence. Nonetheless, there is growing evidence that wildlife can also have remarkable behavioural tolerance, but no clear picture has yet emerged regarding the mechanisms explaining different responses to humans. We investigated the effect of different types of human activity – hunting and outdoor recreation – on behavioural tolerance to humans in Alpine marmots *Marmota marmota*. Marmots were studied in areas with contrasting protection regimes and under different levels of outdoor recreation in northern Italy over three seasons (2021–2023). Flight initiation distance (i.e. the distance at which an animal escapes from an approaching person) was used as a proxy of tolerance to human disturbance and tested against levels of outdoor recreation and hunting using linear mixed modelling. Marmots were more sensitive to human disturbance in hunted as compared to protected areas, whereas we did not find evidence for changes in behavioural tolerance when exposed to varying levels of outdoor recreation. In turn, our study suggests that hunting, by reducing behavioural tolerance to humans, could exacerbate the negative effects of non-lethal human activities on wildlife. This has implications for conservation and management strategies aimed at promoting coexistence in human-altered landscapes.

Keywords: behavioural response, flight initiation distance, human disturbance, indirect effects, tolerance, wildlife

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Introduction

Human activity has expanded to almost every part of the world, rapidly altering environments and increasing the overlap between humans and wildlife (Soga and Gaston 2020). As highly efficient hunters, humans impact animal populations directly through harvesting (Darimont et al. 2015) but also indirectly through risk effects, inducing behavioural changes in risk-averse animals (Ciuti et al. 2012a, b, Palmer et al. 2023). Even non-lethal human activities such as outdoor recreation or ecotourism, can cause disturbance, that is, trigger physiological and/or behavioural responses such as stress or flight (Brown et al. 1999), with potential consequences on population dynamics, communities and ecosystem functioning (Carney and Sydeman 1999, Ripple and Beschta 2004, Coetzee and Chown 2016, Blumstein 2017, Suraci et al. 2019). Given the current expansion of outdoor recreational activities both in time and space, including within protected areas, unintended consequences of human disturbance are a growing conservation concern (Carney and Sydeman 1999, Coetzee and Chown 2016, Blumstein 2017).

Humans have historically killed and consumed many wild animals and hunted others for sport, and thus have left a legacy of fearfulness (Washburn and Lancaster 1968, Frid and Dill 2002). Consequently, humans are often perceived by wildlife as predators, which can result in trade-offs between avoiding a perceived risk and investing in other fitness-relevant behaviours, such as foraging, resting, mating or parental care (Lima and Bednekoff 1999, Frid and Dill 2002, Beale and Monaghan 2004, Clinchy et al. 2016). Yet, numerous studies conducted over the last decades have demonstrated that some individuals, populations and species exhibit remarkable behavioural tolerance – reduced responsiveness or absence of a behavioural response – to humans (Knight 2009, Samia et al. 2015, Blumstein et al. 2017). For example, in urban habitats where human density is high, but most wildlife is not persecuted (Markovchick-Nicholls et al. 2008), animals are often more tolerant to humans than rural congeners (Samia et al. 2015). This contrast has been documented across various taxa in birds (Cooke 1980, Møller 2008, van Dongen et al. 2015), mammals (Stillfried 2017, Uchida et al. 2019, Brooks et al. 2020), and, with few records, reptiles (Grolle et al. 2014). In human-dominated landscapes, behavioural tolerance seems to be a key factor facilitating coexistence (Samia et al. 2015), but may also yield adverse outcomes, for example, increased vulnerability to predation (Geffroy et al. 2015) or heightened risk of human–wildlife conflicts (Uchida et al. 2023). To effectively assess and possibly mitigate the negative effects of human disturbance, it is essential to identify the factors that help species reduce their fear of humans and understand how this varies among individuals, populations, species, and different contexts (Buckley 2004, Tablado and Jenni 2017, Uchida et al. 2023). Despite considerable conceptual advances towards unravelling determinants of wildlife behavioural responses to humans (Tablado and Jenni 2017, Lasky and Bombaci 2023, Čapkun-Huot et al. 2024), we are still lacking a clear picture, and empirical evidence is currently limited to a subset of species and contexts.

Recent work suggests that the observed variability in wildlife's behavioural tolerance to humans is related to multiple modulating factors (Tablado and Jenni 2017, Čapkun-Huot et al. 2024), including the type of human activity that animals are exposed to, and specifically whether it is harmful or benign to them (Lasky and Bombaci 2023, Palmer et al. 2023). Outdoor recreational activities can be consumptive or non-consumptive. The former include, for example, sports or subsidence hunting; the latter, outdoor recreation and ecotourism (Moll et al. 2021, Palmer et al. 2023, Uchida et al. 2023). Unlike consumptive uses, non-consumptive uses of wildlife do not intentionally negatively affect focal animals and are not depletive (Duffus and Dearden 1990, Knight 2009). Notably, non-consumptive activities can sometimes cause unintentional mortalities, such as road kills from ecotourists driving in protected areas (Gunther et al. 1998). Previous studies indicate that wild-living animals can adjust their behaviour to humans associated with the actual risk related to the type of human activity they experience (Ciuti et al. 2012a, b, Storch 2013, 2018). Consumptive uses of wildlife and hunting, in particular, have been linked to increased avoidance of humans in various species of mammals, birds and fish (Keuling et al. 2008, Stankowich 2008, Casas et al. 2009, Brøseth and Pedersen 2010, Klefoth et al. 2011, Ordiz et al. 2012, Fujioka 2020). For example, in hunted areas and/or during the hunting season animals often increase anti-predator behaviours such as vigilance, as seen in elk *Cervus elaphus* (Ciuti et al. 2012a, b) and black-tailed prairie dogs *Cynomys ludovicianus* (Pauli and Buskirk 2007). In prairie dogs, these behavioural alterations were associated with reduced time spent foraging and, consequently, lower body condition of surviving adults (Pauli and Buskirk 2007). Escaping from threats is a major anti-predator behaviour, and the distance at which an animal flees from an approaching person, referred to as flight initiation distance (FID), is a commonly used metric to assess behavioural tolerance to human disturbance (Ydenberg and Dill 1986, Blumstein 2003). FID is a suitable measure of behavioural tolerance because the decision when to flee is based on trade-offs between the costs of flight, including energetic costs and/or opportunity costs of interrupting current activities (e.g. foraging or resting), and the costs of mortality from predation, latter related to the perceived risk of an approaching predator (Lima and Dill 1990). For example, in hunted areas, roe deer *Capreolus capreolus* fled sooner from an approaching person as compared to roe deer in areas with no considerable hunting, with differences in FID ranging between about 10 and 45 m (De Boer et al. 2004). In contrast, a minority of studies found no behavioural effects of hunting; for example, Colman et al. (2001) found that hunting did not consistently affect flight response to an approaching person in a population of Svalbard reindeer *Rangifer tarandus platyrhynchus*.

Repeated exposure to non-harmful human-related stimuli in outdoor recreational areas may allow species to lose fear and habituate to human presence (Blumstein 2016). Habituation can be defined as 'a waning of response to a repeated, neutral stimulus' (Whittaker and Knight 1998, p. 313). Habituation-like responses associated with exposure to non-consumptive types of human disturbance have been demonstrated in different species and taxa (Steidl and Anthony 2000, Reimers and Colman 2006, Thiel et al. 2007, Engelhardt and Weladji 2011, McGowan et al. 2014). In eastern grey squirrels *Sciurus carolinensis*, for instance, FID decreased with increasing exposure to non-lethal human activities, with mean raw FIDs being about 70% lower in high-activity areas as compared to low-activity areas (Engelhardt and Weladji 2011). Moreover, there seems to be generally increased tolerance to humans among wildlife populations that are more exposed to humans (Samia et al. 2015). However, not all species habituate (Blumstein 2016); some may even become sensitised, showing increased responsiveness to a neutral stimulus with repeated exposure (Blumstein 2016, Uchida and Blumstein 2021). Not least, understanding observed behavioural responses to humans can be challenging when populations are exposed to multiple types of human activities. For example, Colman et al. (2001) suggested that the unclear effect of hunting on reindeer's flight response to humans might have been due to interacting, habituation-like effects to outdoor recreational activities in the same area (Colman et al. 2001). However, few studies have explicitly investigated the combined effects of different types of human activities on wildlife's risk perception towards humans (Colman et al. 2001, Courbin et al. 2022, Mols et al. 2022), and it remains unclear how interacting consumptive and non-consumptive human activities shape risk-perception to humans.

Alpine marmots *Marmota marmota* are large, diurnal, and ground-dwelling rodents, inhabiting high-elevation alpine and subalpine grasslands in Europe (Cassola 2016). They are highly social and live in family groups of 2–20 individuals composed of a resident breeding pair, subdominant adults, yearlings and juveniles of the year (Barash 1989). Sociality allows marmots to cope with harsh alpine environments, characterised by a short growing season in summer for growth and reproduction and severe winters in which marmots survive hibernating together (Arnold 1990). Marmot habitats are often located in alpine pastures and meadows, and areas with many tourists, which may subject animals to high levels of human disturbance (Ingold et al. 1993), and, in some cases, may lead to conflicts with people due to burrowing activities in meadows and below buildings (FZ pers. comm. with locals on Seiser Alm, Autonomous Province of Bolzano, IT; https://www.provinz.bz.it/land-forstwirtschaft/fauna-jagd-fischerei/downloads/Piano_di_gestione_marmotta_-_Managementplan_Murmeltier_2022-26.pdf, accessed 22 August 2024). Alpine marmots have traditionally been hunted for their meat, fur and fat (latter used for medical purposes) all over Europe, which has led to local extirpation of entire populations (Armitage 2014). Since 1981, this species has been legally protected by the Bern Convention on the Conservation of European Wildlife and Natural Habitat (Annex III: protected fauna species), which restricts hunting to populations with a conservation status of least concern. In the IUCN red list of threatened species, the Alpine marmot is classified as least concern (Cassola 2016). To date, Alpine marmots are protected in parts of their distribution range and hunted in others. To our knowledge, few studies have so far investigated the effects of different types of human activities on FID in Alpine marmots. Notably, Neuhaus and Mainini (1998) have compared FIDs between Alpine marmots in highly frequented and remote areas, finding that in highly frequented areas, adult marmots fled at short distances of about 50 m, whereas mean FID was closer to 150 m in remote areas. However, with only 20 subjects, the sample size of this particular study was rather low. In contrast, no studies have yet investigated the effects of hunting on FID in Alpine marmots.

Here, we focus on the effect of two contrasting types of human activity – hunting and outdoor recreation – as well as their interaction on behavioural tolerance to humans, measured as FID to an approaching person, in Alpine marmots. We hypothesise that marmot's behavioural tolerance to humans will be shaped by the actual risk associated with the type of human activities that animals encounter. Based on previous studies in other species (Steidl and Anthony 2000, Reimers and Colman 2006, Thiel et al. 2007, Engelhardt and Weladji 2011, McGowan et al. 2014) we predict that marmots will be more sensitive to human disturbance (i.e. have larger FIDs) in hunted areas as compared to non-hunted areas. Further, we predict that in non-hunted areas, but not in hunted areas, sensitivity to human disturbance will decrease with increasing levels of outdoor recreation, due to habituation-like processes (Knight 2009, Samia et al. 2015, Blumstein 2016).

Material and methods

Study area

Marmots were studied in two areas in northern Italy, with varying intensities of outdoor recreation and different protection regimes – Stelvio National Park (Sondrio, 46°42′N, 10°57′E; hereafter PNS) and Seiser Alm (Autonomous Province of Bolzano, 46°54′N, 11°61′E; hereafter SE) over the summers 2021–2023 (Fig. 1 for a map of the study areas and locations of FID tests). PNS extends over about 100 ha at an altitude of 2178–2706 m a.s.l., whereas SE study area covers approximately 4100 ha at an altitude of 1680–2350 m a.s.l. Both areas are similar with respect to climatic and other environmental variables: both are characterised by boreal Alpine meadows and the typical temperature of the Alpine regions, ranging between −14°C in winter and 24.5°C in summer (https://it.weatherspark.com/); non-human predators of marmots – red fox *Vulpes vulpes* and golden eagle *Aquila chrysaetos* – are present in both areas; both areas are popular destinations for outdoor recreational activities. Thus, PNS and SE differ mainly with respect to the protection regime of the Alpine marmot. Marmots are protected in PNS, and hunting is not permitted in the area. In SE, marmot hunting

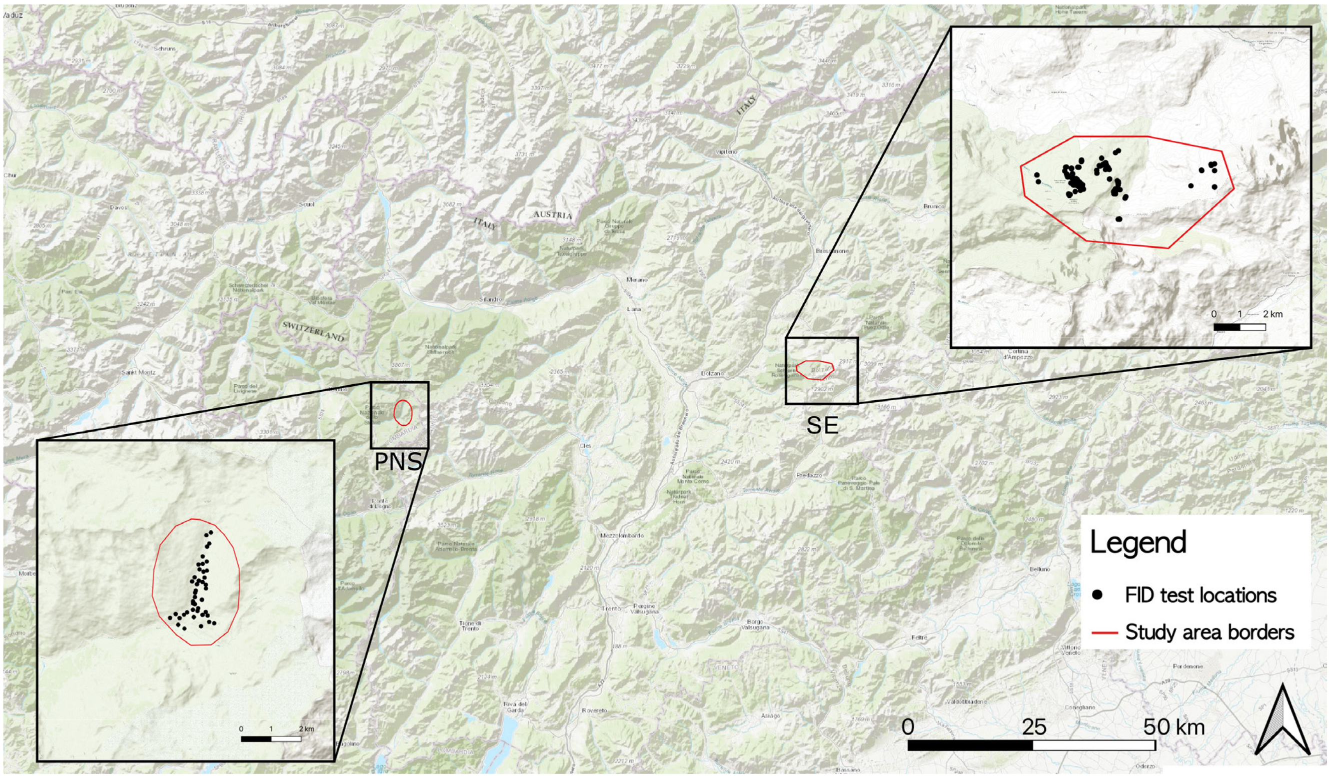

Figure 1. Map of the study areas in Italy, including Stelvio National Park (PNS) in Sondrio and Seiser Alm in the Autonomous Province of Bolzano (red outlines), and locations of FID tests (black points).

has been permitted since 2017, motivated by the desire of local hunters' associations to utilise the species in hunting activities and management purposes, i.e. conflict-mitigation with local farmers who face challenges due to marmots' burrowing activities in alpine pastures and below buildings. In SE, the hunting concept stipulates a maximum harvest of 5% of the spring population, which is to be primarily taken from reported conflict areas (for details, see https://www.provinz.bz.it/land-forstwirtschaft/fauna-jagd-fischerei/downloads/DLH_Nr._12459_Managementplan_Murmeltier_2022-26_(1).pdf, accessed 30 May 2024). In SE, marmot hunting season is open throughout September each year. Marmots are typically hunted by shooting from distances between 90 and 180 m, using a mix of staking and ambush techniques. For example, hunters may locate a marmot from a distance using binoculars or a scope and then move slowly and carefully to get within shooting range without alerting animals, possibly moving close to the ground or using terrain features for cover. Alternatively, hunters may identify an active burrow, pick a hidden spot within shooting range and wait for marmots to emerge. After a successful shot, hunters will walk into the area to retrieve the marmot.

Marmot captures

In both study areas, a subset of marmots was captured and individually marked using coloured ear tags and subcutaneous injection of a microchip. Additionally, physical measurements were taken (e.g. sex, age, or body mass) as part of a larger study investigating the abundance and behavioural ecology of local populations in PNS and SE. At both sites, marmots were captured in the spring, shortly after hibernation, using one- and two-door Tomahawk life-traps, baited with dandelion *Taraxacum officinalis*, following a well-established protocol (details in Giari et al. 2024). Captures were authorized by ISPRA (the Italian Institute for Environmental Protection and Research) for PNS and by decree of the Provincial Council, Autonomous Province of Bolzano (no. 8079/2022 and 8092/2023) for SE. Based on previous investigations on the same population in PNS, we can exclude effects of capture on escape response and behavioural tolerance to humans (Giari et al. 2024).

Flight initiation distance tests

FID tests followed a standardised protocol involving two trained investigators, one being the walker who approached the marmot and one being the observer, who remained at the starting positions and observed the behaviour of the focal marmot, noting when it fled from the approaching walker. Once we spotted a marmot to test from a distance, we moved to a position where the selected animal could be approached on flat terrain as much as possible and without ditches or other features in the terrain on the way where the walker might temporarily disappear from the marmot's view. When several animals available for testing were present, priority was given to the best visible individual (i.e. not obstructed by another marmot or environmental features) or the one that could be approached most unhindered (i.e. on a flat route without obstacles, as described above). We typically repositioned at distances far enough to not disturb the marmot (average starting distance: 125 ± 50 m; measured using a laser range finder); if our positioning caused a reaction, the test was aborted, and a new focal marmot was selected elsewhere. Because finding flat terrain was not always possible in the mountainous field site, sometimes we approached the marmot from slightly above or below. Anticipating that approaching from above could be perceived as more threatening by animals, we recorded the angle of approach for consideration during data analysis. Before starting an FID test, we noted down if the selected animal was marked and, if so, its identity. During the FID test, the walker approached the focal subject at a constant pace of about 0.5 m s^{-1}, while the observer remained at the starting position and observed the focal subject's behaviour using a 20–60× spotting scope. The observer communicated (by means of a walkie-talkie) to the walker the moment at which the animal flew, and the latter marked his/her position with a flag, thereby indicating the FID. We defined a flight as the focal animal moving at least one body length from its original position (in most cases, the animals fled, initiating a run over longer distances) or disappearing directly into a burrow. The walker reached the focal animal's initial position, identifying the escape burrow to which it fled (marmots typically flee into a burrow when faced with a threat; Armitage 2014), with the assistance of the observer, who also tracked the focal subject's movements during the test. The walker measured starting distance (i.e. the distance from the walker's initial position and the point where the animal first fled), FID, and distance from the focal subject's initial position to the escape burrow through the use of a laser rangefinder (Swarovski laser guide 8 × 30, in m). Finally, the observer recorded the following information, since they too may explain variation in FID: number of conspecifics within 5 m of the focal animals at the start of the FID test (all observers were trained to estimate distances in the field from various viewpoints), occurrence of conspecific alarm calls during the approach, age class of the focal animal (one-year-old; subadult or adult), marmot behaviour at the start of the FID test (rest; forage; other; for an ethogram see Supporting information) and the date. Over the entire study period, 18 different walkers (10 in PNS and 10 in SE, with some participating in both areas) and 15 different observers (8 in SE and 9 in PNS, with some participating in both areas) were involved in conducting behavioural tests (all were well-trained before collecting data). In PNS, FID tests were conducted over most of the entire marmot active period of marmots (June–October), typically in sessions of four to six field days per month). In SE marmots were tested in late summer only, outside of hunting season (August) and during hunting season (September). To prevent pseudo-replication, each marked animal was tested only once per session (i.e. once per month). For unmarked animals, only a limited number of distinguishable individuals were tested per area per session. For example, within a given area per session, one adult and one yearling – easily distinguishable by body size – were selected for testing.

Quantification of levels of outdoor recreation and hunting

Levels of outdoor recreation (Cumulative Outdoor activity Index, hereafter COI) were derived from the STRAVA heatmap (www.strava.com/maps/global-heatmap) following the procedure from Corradini et al. (2021). STRAVA is a digital platform in which public users worldwide can track and upload their activity data; the STAVA heatmap displays aggregated user activity data as colour-coded, where brighter tones indicate areas with higher activity levels. Specifically, for this study, only on-foot activities (running, hiking, and walking), which were the predominant types of activities, were displayed at a zoom level of 13 (for a resolution of 20 m). Note that there may be variations in the prevalence of other activities involving vehicle use or paragliding across different areas, which are not covered in this analysis. The derived COI, which ranges from 0 to 1, was extracted in December 2023, and because it represents the preceding 12 months of data, it depicts relative intensity of use of trails during the year 2023 based on publicly available user uploads. Importantly, STRAVA data has been shown to be representative of outdoor activity levels, both spatially (Corradini et al. 2021, Venter et al. 2023) and temporally, with yearly estimates of activity being highly correlated (Thorsen et al. 2022, Supporting information). The COI corresponding to each FID test was derived using the 'raster' R package (Hijmans et al. 2015) as the 95th percentile pixel value from the COI raster file in a 95 m buffer around the main burrow located in the area of the FID test, which we assumed was the centre of a marmot groups' territory. The buffer size of 95 m was chosen in a previous analysis based on the highest correlation coefficient between the 95th percentile pixel values from COI within known home ranges of marked individuals (unpublished data) and different 95th percentile pixel values in different buffer sizes (40–110 m) around the main burrow. Results indicated the highest correlation (0.97) for a buffer size of 95 m, which corresponds to an area of approximately 2.84 ha (the average home range territory of Alpine marmot is 2.5 (± 0.53) ha [Perrin and Berre 1993]).

We considered both long- and short-term effects of hunting on marmot FID by investigating differences between non-hunted and hunted areas (long-term effects) and, in hunted areas, by distinguishing between hunted areas outside of and during hunting season (short-term effects). Thus, hunting was considered as a factor with three levels (non-hunted, hunted-out-season, hunted-in-season). In PNS, hunting was not permitted, and all FID tests were classified as 'non-hunted', whereas hunting occurred in most areas in SE. In SE, we measured hunting based on detailed hunting data provided by the Office for Wildlife Management, Autonomous Province of Bolzano, specifying each marmot killed, along with the date and exact location. For each FID test, we considered all killings within a 95 m buffer around the main burrow, which we assumed to be the average territory size (above). Then, we used Kernel Density Estimation (KDE) to create an individual heatmap of hunting mortalities for each FID test, considering 1) all kills in the years prior to the respective FID test, starting from the onset of hunting activities in the area in 2017, and 2) all kills in the same year and previous to the FID test. Hunting was considered as 'hunted-out-season' if the KDE of hunting intensity at the location of the FID test was larger than zero for 1) but not 2) and considered as 'hunted-in-season' if the KDR of hunting intensity was larger than zero for 1) and 2). Thus, we defined the start of the hunting season based on when hunting activities in a respective area began rather than the legal start on the first of September.

Statistical analysis

All analyses and COI data extraction were conducted with the software R 4.3.1 (www.r-project.org) through RStudio (Posit Team 2023). To investigate whether variation in FID was explained by hunting and intensity of outdoor recreation in marmots' habitats, we adopted a linear mixed modelling approach with restricted maximum likelihood (REML) estimation using the R package 'glmmTMB' (Brooks et al. 2017). FID was square-root transformed, to meet distributional assumptions. The global model (sensu Burnham and Anderson 2002) included FID as response variable, with hunting (factor with three levels: non-hunted, hunted-out-season, hunted-in-season) in interaction with intensity of outdoor recreation in marmots' habitat (numeric variable with theoretical possible values ranging from 0: no-outdoor recreation, to 1: comparably highest level of outdoor recreation within the study region) as target explanatory variable, along with covariates that were deemed potentially associated with FID based on existing literature and ecological considerations. Covariates included starting distance (numeric variable in m), distance to the escape burrow (i.e. closest refuge; numeric variable in m), angle of approach (factor with three levels: horizontal, slightly descending, slightly ascending), number of conspecifics within 5 m of the focal subject (factor with two levels: conspecifics present, no conspecifics present), occurrence of conspecific alarm calls (factor with two levels: conspecific alarm call, no conspecific alarm call), individual age class (factor with two levels: yearling, subadult or adult), capture status (factor with two levels: captured, not-captured), marmot behaviour at the start of the FID test (factor with three levels: foraging, resting, other activity) day of the year (numeric variable) and study area (factor with two levels: PNS, SE). Day of the year was fitted as a linear effect, based on the hypothesis that, after emerging from hibernation, marmots may gradually become more accustomed to people over the course of the summer. Burrow distance was log-transformed to address the right-skewed distribution of data. Walker ID (factor with 18 levels) and year (numeric variable with three levels: 2021, 2022, 2023) were included as a random intercept to account for grouping in the data due to repeated measures of the same walker and within a given year. Animal ID was only available for a subset of animals, which had been captured and marked previously. Thus, this variable was not included in the global model. However, preliminary analysis indicated that animal ID was not influential when comparing two full additive models with and without animal ID using analysis of variance (ANOVA) and based on a subset of the data including marked animals only (for details, see Supporting information). Multi-collinearity was tested through the variance inflation factor (VIF) in the 'car' R package (Fox and Weisberg 2019) in a full additive model excluding the interaction between hunting and COI. The Variance Inflation Factor (VIF) indicated collinearity between the study area and hunting variables (VIF > 5). This was unsurprising because hunting was not permitted in PNS, and in SE just a small subset of FID tests was conducted in non-hunted areas (7 out of 184). Thus, we excluded the study area from the global model. With all other VIF values below 3, collinearity was considered inconsequential. To simplify the model structure, we applied a variable selection with the *buildglmmTMB* function, which, starting from the largest converging model, performs a stepwise elimination of terms based on the likelihood ratio test (Matuschek et al. 2017). Model assumptions and adequacy were assessed through residual diagnostics in the 'DHARMa' R package (Hartig 2022). Contrasts between factor variables with multiple levels, such as hunting, were assessed by pairwise comparison, adjusted by Tukey's honest-significant-difference procedure with *glht* function in the 'multcomp' R package (Hothorn et al. 2008). Finally, we visualised marginal effects with the 'visreg' R package (Breheny and Burchett 2017).

Results

A total of 594 FID tests (417 in non-hunted and 177 in hunted areas outside and during hunting season) were conducted between 2021 and 2023. The mean intensity of outdoor recreation within marmot habitats, derived from STRAVA data, averaged 0.27 (SD ± 0.11) in non-hunted areas and 0.06 (SD ± 0.08) in hunted areas, on a scale of 0 to 1. Model diagnostics indicated no major violations of model assumptions.

FID was best explained by start distance, log-transformed burrow distance, marmot behaviour at the time of observation (Table 1, Fig. 2a–c), and hunting (Table 1, Fig. 3a). Exposure to outdoor recreation, including its interaction with hunting, was not retained in the selected model (Fig. 3b). Hunting was related to decreased tolerance to human approach, with higher expected FIDs in hunted areas than in non-hunted areas, both during and outside of marmot hunting season, with mean marginal predicted FIDs of 47 (± 3.3) m in non-hunted areas, 56 (± 12.0) m in hunted areas outside the active hunting season, and 64 (± 16.2) m in hunted areas during the active hunting season. Notably, the post-hoc test revealed no evidence of a difference in expected FID in hunted areas during and outside of active hunting season.

Besides hunting, parameter estimates from our selected model revealed evidence for a positive relationship between start distance and logarithmic burrow distance on square-root

Table 1. Estimates of the model selected to explain variation in square-root transformed flight initiation distance in two marmot populations between 2021 and 2023. The table reports, for each parameter: estimate of regression coefficient, lower (LCL) and upper (UCL) 95% confidence limit, and p-value. Contrasts between hunting regimes, years, and behaviour, other than comparisons to the reference level, were determined using post-hoc pairwise comparisons adjusted by Tukey's honest significant difference procedure. Predictors whose confidence intervals do not include zero are in bold. Random effects include information on residual variance (σ^2), variance attributed to the random intercept ($\tau_{00\ year}$), Intraclass Correlation Coefficient (ICC; i.e. the proportion of total variance explained by the random effect year), and number groups (N_{year}), as well as conditional and marginal R^2.

Predictors	Estimate	LCL – UCL	p-value
(Intercept)	3.63	2.748–4.521	**< 0.001**
Start distance	**0.02**	**0.020–0.026**	**< 0.001**
Burrow distance + 0. 05 [log]	**0.3**	**0.237–0.440**	**< 0.001**
Hunting regime [non-hunted – hunted-out-season]	**0.65**	**0.229–1.079**	**0.003**
Hunting regime [non-hunted – hunted-in-season]	**1.17**	**0.703–1.644**	**< 0.001**
Contrast hunting regime [hunted-out-season – hunted-in-season]	0.52	−0.147–1.186	0.154
Behaviour [rest – other]	**0.85**	**0.284–1.408**	**0.003**
Behaviour [rest – forage]	**0.89**	**0.241–1.529**	**0.007**
Contrast behaviour [forage – other]	0.0	−0.447–0.525	0.981
Random effects			
σ^2	3.48		
$\tau_{00\ year}$	0.29		
ICC	0.08		
N_{year}	3		
Observations	594		
Marginal R^2/Conditional R^2	0.360/0.410		

transformed values of FID. Further, behaviour affected FID, where animals that were resting at the start of the observation tolerated a closer approach of a person before fleeing, as compared to active animals (i.e. those foraging or engaged in other activities).

Discussion

As expected, the occurrence of hunting was associated with longer FIDs in response to an approaching person, indicating that marmots were less tolerant to humans in hunted areas compared to non-hunted areas. Contrary to our initial hypothesis, we found no effect of outdoor recreation intensity on marmot FID. The intensity of outdoor recreation also did not change the effect of hunting on FID. Besides hunting, FID was explained by the covariates starting distance, burrow distance (i.e. distance to refuge), and marmot behaviour at the start of the test, aligning with findings of previous investigations (Giari et al. 2024).

While habituation-like processes to non-lethal human disturbance have previously been studied in the genus *Marmota* (Neuhaus and Mainini 1998, Griffin et al. 2007, Uchida and Blumstein 2021), to our knowledge, this research is the first

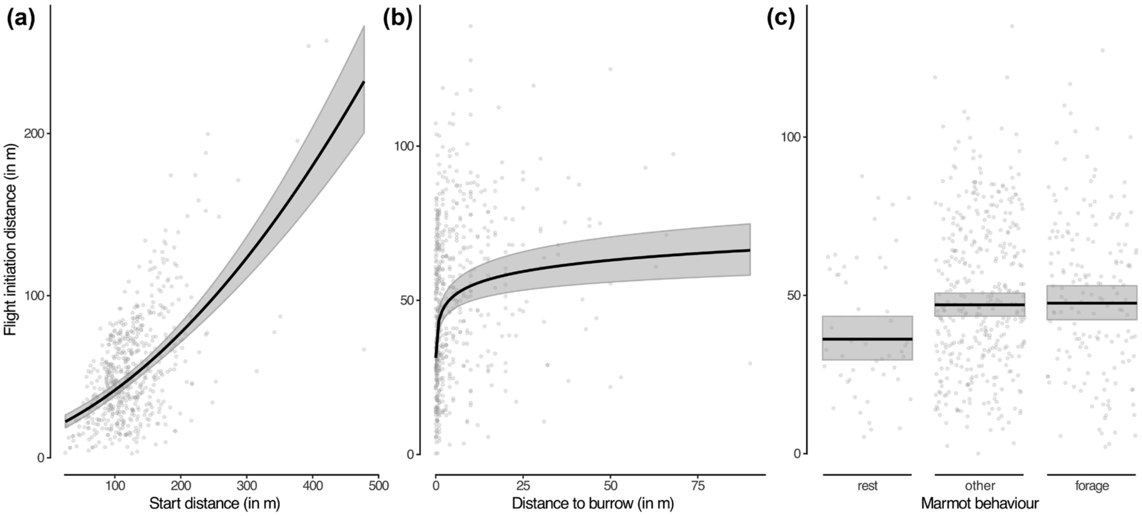

Figure 2. Marginal effects of (a) start distance, (b) burrow distance, and (c) marmot behaviour (c) on flight initiation distance (FID, in m) in Alpine marmots in northern Italy (Stelvio National Park and Seiser Alm) between 2021 and 2023. Grey shaded areas represent 95% confidence intervals. Partial residuals in light grey.

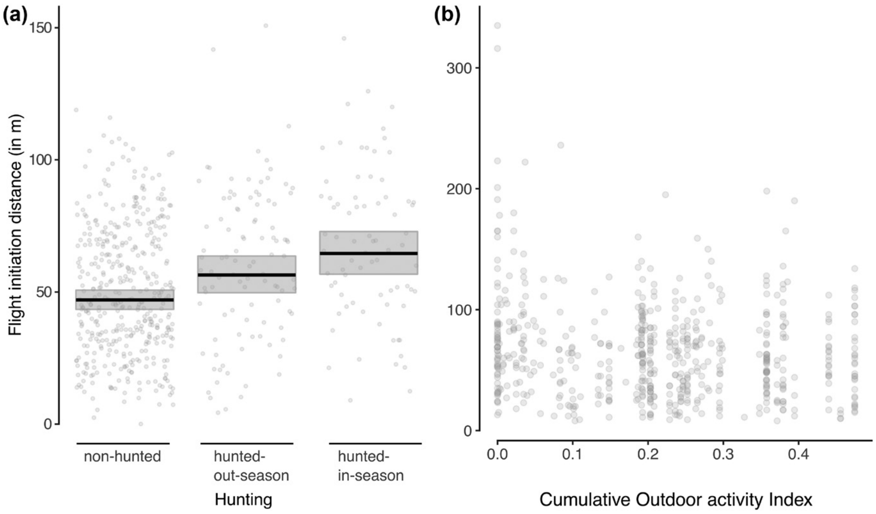

Figure 3. Marginal effects of (a) hunting regime (non-hunted, hunted-out-season [i.e. hunted areas outside of active hunting season], hunted-in-season [i.e. hunted areas during active hunting season]) on flight initiation distance (FID, in m) in Alpine marmots. Grey shaded areas represent 95% confidence intervals. Partial residuals in light grey. Distribution of raw FID (b) related to the Cumulative Outdoor activity Index (i.e. intensity of outdoor recreational activity) in marmots.

to examine the combined effects of outdoor recreation and hunting, as well as the isolated impact of hunting on behavioural tolerance to humans in a marmot. Our finding that marmots exhibit lower tolerance to humans in hunted areas compared to non-hunted areas is consistent with results in various other species and taxa, mostly ungulates and birds, that associated hunting with increased risk-perception, measured as FID, towards humans (Colman et al. 2001, Stankowich 2008, Tarakini et al. 2014, Sreekar et al. 2015). Thus, our results contribute to a growing body of research suggesting that humans are not always perceived as predators, but that previous experiences with certain types of human activities, and in particular whether these are benign or harmful to animals, is an important factor in shaping risk-perception of wildlife towards humans.

Behavioural tolerance to human disturbance has been suggested as an important factor that facilitates coexistence in human-shaped landscapes and more tolerant populations often do better in areas with human activities (Samia et al. 2015). However, and importantly, there can be negative outcomes of increased tolerance, such as increased vulnerability to predation by non-human predators (Geffroy et al. 2015) or heightened potential of human–wildlife conflict with more tolerant animals (Uchida et al. 2024). Thus, tolerance can be closely linked to an animal's success in coping in human-dominated environments. Alpine marmots frequently use human-modified landscapes, such as alpine pastures, and habitats used for human recreation (Bätzing 2002). During the current FID tests, marmots were approached by a person walking calmly and at a steady pace, similar to that of a typical hiker in the area. The person did not wear hunting gear or sneak up on the animals, as would be typical in a marmot hunt. Thus, our results suggest that marmots generalised the aversive experience of being hunted to humans in general, likely due to cue overlap between hunters and outdoor recreationists (Kays et al. 2017, Smith et al. 2021). Only a few species seem able to distinguish between risky and non-risky humans (e.g. African elephants *Loxodonta africana africana* [Goldenberg et al. 2018] or American crows *Corvus brachyrhynchos* [Cornell et al. 2012]). Marmots, too, can make fine discriminations about people; yellow-bellied marmots differentiate a human with and without a camera, but carrying a camera does not affect FID (Uchida et al. 2023). Generalized responses may lead to costly over-responses to non-risky humans and, in this way, exacerbate the negative effects of human disturbance (Paton et al. 2017, Smith et al. 2021). In hunted areas, fleeing early from people in general, not just hunters, may negatively affect fitness as marmots not only invest viable energy during flight but also lose important opportunities to forage, rest, mate or invest in other fitness-related activities during the short alpine summer. Specifically, opportunity costs should not be underestimated, as we observed that marmots typically retreated into a burrow following flight, and not rarely did it take them as much as 30 min or longer to resume their activities (FZ, CG pers. obs.). Other studies have shown that marmots are acutely sensitive to risk and rewards when making decisions about when to leave their burrows (Blumstein and Pelletier 2005, Rhoades and Blumstein 2007).

In hunted areas, FIDs were longer, averaging 9 and 17 m (outside and during hunting season) than in non-hunted areas. This is a considerable difference. For instance, considering that marmots run at about 3 m s^{-1} (Blumstein et al. 2004), in hunted areas, this gives hunters 3–5 s less time to point and shoot before a marmot disappears, which could be the difference between being shot and successfully escaping. As another example, considering a marmot territory that borders a hiking trail, an FID that is higher by 9–17 m would considerably decrease the area of the territory in which marmots can move without being majorly disturbed by people moving on the trail. It is also important to note that in our study area, hunting was limited to one month per year with a maximum harvest rate of 5%. In areas with more intense hunting – both in duration or harvest rate – the impact on FID could be significantly greater. While we show that hunting is a driver of fear responses to humans in Alpine marmot, further studies associating FID to fitness-related parameters such as body mass, survival and reproductive success are needed to clarify if, and at what intensities, hunting incurs biologically relevant consequences on individual fitness and population-level processes (Gill et al. 2001, Blumstein et al. 2023). Additionally, also considering the alert distance, i.e. the distance at which an animal first responds to an approaching threat, could further clarify potential fitness effect because, even before the flight, animals interrupt their current activities during alert behaviour (Uchida et al. 2019).

In hunted areas, marmots consistently fled earlier from an approaching person both during and outside of hunting season. Thus, marmots did not adjust their antipredator behaviour to temporally varying predation risk, despite being predictable (i.e. in the hunted area, hunting was restricted to the month of September each year). In contrast, other species have demonstrated remarkable abilities to do so and, in this way, optimize the trade-off between reducing predation risk and investment in other fitness-related behaviours (Keuling et al. 2008, Lone et al. 2015, Laursen et al. 2016). Male red deer *Cervus elaphus*, for example, were observed to shift habitat from areas with good forage but less cover (i.e. higher risk of being detected and killed by a human hunter) just at the onset of hunting season (Lone et al. 2015). Presumably, the deer used sensory cues (e.g. the sound of gunshots or increased human and/or dog activity off-trail) to recognize the start of hunting season, or they could have relied on an inner clock and regularity of hunting season (Lone et al. 2015). A possible explanation for a lack of dynamic behavioural response to hunting in marmots is that they were not able to identify the onset of hunting season (despite cues such as the presence of gunshots and the regularity in timing of the hunting season). Alternatively, behavioural plasticity to respond to cues about hunting may be limited in Alpine marmots (DeWitt et al. 1998, Snell-Rood 2013), possibly related to low genetic variability in this species (Auld et al. 2010, Gossmann et al. 2019).

Rather than being attributed to behavioural plasticity, the observed consistently longer FIDs of marmots in hunted as compared to non-hunted areas could also be explained by selection (Blumstein et al. 2017). Marmots are typically shot from distances ranging between 90 and 180 m (FZ, pers. comm. with local hunters), which overlaps with the average raw FID of 75 m (SD ± 50 m). Therefore, if hunters fail to approach an animal stealthily or conceal themselves from movements or sounds while waiting or pointing, they may trigger flight in targeted animals, potentially leading to the selective killing of bolder, more tolerant individuals. Similar effects were documented by Ciuti et al. (2012b), who found that harvested elk *Cervus elaphus* had exhibited bolder behavioural traits before and during hunting season, including higher movement rates and greater use of open areas, as compared to survivors, thus making them easier targets for hunters. In the long term, this shifted the personality profiles of the population to less bold individuals (Ciuti et al. 2012b). Additional studies investigating the inter-individual stability of behavioural traits, such as FID, are needed to substantiate such a mechanism in marmots.

Contrary to our initial hypothesis, we did not detect an effect of intensity of outdoor recreation on marmot FID, neither directly nor as an interaction with hunting. This may seem surprising, given that Alpine marmots are known to habituate to humans and even may be attracted to humans, as evidenced by anecdotal reports from tourist hotspots like the Grossglockner Mountain in Austria, where marmots commonly approach people for handouts. Yet, our result aligns with previous findings of Giari et al. (2024), who investigated the effects of capture and handling on Alpine marmot FID and found that the level of outdoor recreation did not emerge as a significant variable that explained variation in FID. Several other studies have assessed the effects of outdoor recreation on marmot FID with inconsistent results. In golden marmots, *Marmota caudata aurea* adult animals showed greater FID along roads, which suggests sensitization-like effects with increasing exposure to human activity (Zaman et al. 2019). A study on Himalayan marmots *Marmota himalayana* documented longer FIDs in highly disturbed marmots (i.e. marmots in areas with higher levels of human activity such as close to a village) as compared to undisturbed marmots but did not find significant difference in FID between highly disturbed animals as compared to animals that experience low levels of human disturbance (Guo et al. 2022). Similarly, Neuhaus and Mainini (1998) showed that marmots in remote areas had longer FIDs than marmots in highly frequented areas. The latter two studies, when considered alongside our findings regarding marmots' response to hunting, once more suggest that marmot behavioural plasticity may not be highly dynamic. In our study areas, levels of outdoor recreation may not have differed widely enough to trigger behavioural shifts; although our dataset included animals experiencing very low levels of human disturbance near their territories, our study areas were generally frequented by people, and no naïve animals were tested. Consequently, it might be that all the marmots we tested were similarly habituated to humans. This theory is further supported by a study on Olympic marmots *Marmota olympus*, which found lower flight initiation distances (FIDs) in marmots heavily exposed to humans compared to naïve marmots (Griffin et al. 2007). In such areas where tame marmots are found (i.e. Grossglockner Mountain in Austria), food-conditioning may play an important role in increasing habituation-like processes (Blumstein 2016) but did not occur in our study areas. We encourage further studies to explore FID in relation to outdoor recreation and hunting across different geographical regions to strengthen the reliability of findings and to assess potential geographical variability in FID for this species.

Individuals may differ from each other in how they respond to challenges and threats in their environments (Sih et al. 2013). In yellow-bellied marmots *Marmota flaviventer*, FID decreased in highly disturbed areas over a long-term period of 15 years yet exhibited significant individual variability (Uchida and Blumstein 2021). Contrary to the general population trend, some individuals had consistently longer FIDs, suggesting that they had sensitised to repeated human approaches. In our current study, we have limited data that permits us to study such individual effects. We encourage future studies on marked individuals, with repeated testing of the same individuals studied in areas with higher variation in levels of outdoor recreation, possibly including mostly undisturbed areas, to unravel population level and individual responses to human disturbance.

Alternatively, it is possible that we did not detect an effect of recreational outdoor activity because our metric, the COI, did not fully capture it at the local level, although the index was shown to be representative of the intensity of outdoor activities elsewhere (Corradini et al. 2021, Venter et al. 2023, Bolas et al. 2025). Moreover, in our study areas, activities related to meadow management and livestock keeping were present but not captured by the COI. Nevertheless, since the intensity of these working outdoor activities appeared to be much lower than that of nature-based tourism (FZ pers. obs.), we would not expect major biases. It is also possible that the overall intensity of human activity within marmot habitats is not the only critical factor; spatial overlap between human activities and the marmot's core areas within a territory might also be relevant. Detailed data on habitat use are needed to investigate this alternative explanation further**.** Importantly, while FID is an accurate measure of fear and susceptibility to human disturbance, FID is not a proxy of the entire range of disturbance effects (Ward and Cupal 1979, Gill et al. 2001). To comprehensively understand if different levels of outdoor recreation create different levels of disturbance, further investigations should additionally monitor other anti-predator behavioural responses, such as vigilance or measures of physiological stress, and test the fitness implication of behavioural changes.

Overall, our study suggests that hunting, but not the intensity of outdoor recreation, modulates behavioural tolerance to human disturbance in Alpine marmots. Thus, our findings add to a growing body of research suggesting that humans may not be generally perceived as predators and cause disturbance of wildlife, but that particularly consumptive activities such as hunting can cause and strengthen anti-predator responses to humans. We highlight that hunting can have non-lethal effects on wildlife populations. Specifically, by decreasing behavioural tolerance to humans in general, hunting may exacerbate negative disturbance effects of non-consumptive human activities in natural habitats. Particularly in natural areas that must balance conservation efforts with providing outdoor recreational opportunities, such non-lethal effects of hunting may be undesirable (Gaynor et al. 2021). By leading to lower behavioural tolerance, hunting could also affect the visibility of the iconic species Alpine marmot, potentially conflicting with public and economic interests in wildlife viewing (Knight 2009, Uchida et al. 2023). Ultimately, observing wild animals in their natural habitat can foster emotional engagement and encourage conservation behaviour (Hughes 2013, McIntosch and Wright 2017), thereby contributing to conservation efforts.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4mw6m90nt (Zenth et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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