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Combined effects of fine-scale intensity and spatial extent of exposure to outdoor recreation shape wildlife responses and tolerance to human activity

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ABSTRACT

Outdoor recreational activities and nature-based tourism are rapidly expanding, both in intensity and space. Even non-consumptive activities can have adverse effects by altering animal behaviour and physiology, but wildlife can also develop behavioural tolerance to humans and adjust to human activities. However, few general patterns have emerged, likely due to incomplete knowledge of the factors that modulate wildlife responses. For example, it remains unclear how fine-scale intensity and spatial extent of exposure to outdoor recreational activities influence disturbance effects on wildlife. Here, we investigated how the combined effects of current on-site visitor numbers, the extent of areas used by humans, such as around picnic areas, within animal's home ranges and the proximity of animals' activity centres to main recreational infrastructure, such as main hiking trails, affect behavioural and physiological responses to outdoor activity. We used Alpine marmots *Marmota marmota* in Stelvio National Park (central Italian Alps) as a case study. Marmots occupying territories with low human area use and with activity centres located farther from the main hiking trail in the study area increased anti-predator behaviours and decreased foraging during higher visitor presence. In contrast, marmots from territories with higher area use and/or activity centres closer to the main trail were more tolerant. Stress levels assessed through faecal cortisol metabolites (FCMs) mirrored this pattern, but high uncertainty around FCMs estimates suggests cautious interpretation. This case study demonstrates that wildlife responsiveness to outdoor activity can depend on multiple interacting factors, highlighting the importance of context-specific impact assessment and targeted mitigation strategies.

1. Introduction

Outdoor recreational activities and nature-based tourism are rapidly expanding, both in intensity and space (Balmford et al., 2015; Bell et al., 2007). While nature tourism can have important benefits for engaging individuals (e.g. by improving health and well-being [Coventry et al., 2021; Wolsko et al., 2019]), local economies (Winter et al., 2019; Blumstein et al., 2017), and conservation (e.g. by capitalising on tourist revenues or through enhancing environmental consciousness [Schild, 2019; Steven et al., 2013]), research over the last decades has also highlighted negative environmental effects and hazards to wildlife. Nature tourism includes consumptive (e.g. hunting or fishing) and non-consumptive activities (e.g. hiking, mountain biking or wildlife viewing) (Bell et al., 2007). Even non-consumptive activities, which are often assumed to be compatible with conservation, are increasingly considered a conservation concern because of disturbance effects (Blumstein

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et al., 2017; Coetzee and Chown, 2016; Larson et al., 2016).

Wildlife often perceives humans as a threat and responds with anti-predator behaviour, following similar economic principles as in encounters with non-human predators (Frid and Dill, 2002). These responses typically involve trade-offs between avoiding a perceived risk and engaging in other fitness-relevant behaviours (Frid and Dill, 2002; Lima and Bednekoff, 1999). In this context, non-lethal effects of human activity can be defined as adjustments in animal behaviour and/or physiology triggered by human presence, often with adverse outcomes for animals. Human activity can alter wildlife-habitat relationships (McGarigal et al., 1991; Mols et al., 2022), disrupt movement (Tucker et al., 2018), shift activity patterns (Gaynor et al., 2018), alter vigilance behaviours and foraging (Steidl and Powell, 2006), and induce physiological stress (Muehlenbein et al., 2012; Thiel et al., 2008). For example, a study investigating wildlife behavioural responses to over-snow vehicles in Yellowstone National Park recorded increased vigilance, movement and flight behaviour in elk *Cervus canadensis* and bison *Bison bison* (Borkowski et al., 2006). In Sika deer *Cervus nippon*, the presence of outdoor activities such as hiking was related to increased vigilance and reduced foraging (Tsunoda, 2021). Another study (Thiel et al., 2008) showed that capercaillie *Tetrao urogallus* avoided areas with high levels of winter sports activities in the ski season, and birds in areas with higher intensities of outdoor recreation had elevated levels of stress hormones as measured through faecal corticosterone metabolites (FCMs). Physiological stress in response to outdoor activity was also reported in a variety of other species, such as mountain hares *Lepus timidus* (Rehnus et al., 2014), African lions *Panthera leo* (Creel et al., 2013), Gentoo penguins *Pygoscelis papua* (Barbosa et al., 2013), or Barbary macaques *Macaca sylvanus* (Maréchal et al., 2016).

By altering behaviour and inducing physiological stress, non-consumptive outdoor recreational activities can have negative outcomes for wildlife individuals, populations and communities. Anti-predator behaviour can have considerable energetic costs, for example, when prey flees from a predator at high speed, as well as opportunity costs if it diverts time from other fitness-related behaviour such as foraging, mating or parental care (Houston et al., 2012; Lima and Dill, 1990; Ydenberg and Dill, 1986). In California sea lions *Zalophus californianus*, high levels of human activity were linked to lower reproductive rates and, more long-term, reduced population growth rates (French et al., 2011). Increased adrenocortical activity (i.e. ‘stress’) is an adaptive response that helps organisms to cope with environmental challenges and to regain homeostasis after a stressful event (Sapolsky et al., 2000). However, chronic stress, for example, induced through a high frequency of human encounters, can have deleterious effects by impairing immune function (Dhabhar, 2014), growth or reproduction (Banerjee et al., 2024), thus ultimately compromising fitness (McEwen, 1998). In yellow-eyed penguins *Megadyptes antipodes*, for instance, birds in sites with unregulated, intensive tourism had higher baseline stress levels, lower fledging weights of chicks and overall lower breeding success as compared to non-touristic areas (Ellenberg et al., 2007). Yet, behavioural effects of human disturbance do not always translate into fitness or population consequences (Gill et al., 2001). Moreover, human activity in wildlife use areas does not even always cause a disturbance (Geffroy et al., 2017; Tablado and Jenni, 2017).

Whether recreational activities disturb wildlife can depend on multiple factors, including the characteristics of the activities (e.g. type, number of visitors, frequency, time and predictability of visitation), intrinsic attributes of the animals (e.g. sex, age class, body condition or species), and the spatiotemporal context of encounters with humans (e.g. time of the year or habitat characteristics) (Steidl and Powell, 2006; see Tablado and Jenni, 2017 for a review). For example, populations and species can have different threshold distances to human activity at which they start to respond behaviourally and/or physiologically (Dertien et al., 2021). In bottlenose dolphins *Tursiops* sp. in Shark Bay (Australia), dolphin-watching did not negatively affect populations when only one tour operator was active. However, the average dolphin abundance experienced a sudden drop when the number of tour operators increased to two (Bejder et al., 2006). Wildlife can also develop behavioural tolerance (i.e. low or absence of behavioural and/or physiological response) to human presence. Mechanistically, tolerance often results from habituation (Čapkun-Huot et al., 2024), which is a form of non-associative learning, where animals progressively reduce behavioural responses to a repeated or continuous stimulus that has no adverse consequences (Bejder et al., 2009). Habituation-like processes were documented in areas with frequent non-consumptive outdoor recreational activities in various species (e.g. Schuttler et al., 2017; Sytsma et al., 2022; Viblanc et al., 2012; Romero and Wikelski, 2002). Habituation may reduce negative effects of nature tourism (Higham and Shelton, 2011), but not all species habituate (Blumstein, 2016). Additionally, there can be considerable individual variation in behavioural responses to humans (Arlettaz et al., 2015; Uchida and Blumstein, 2021). Thus, few general patterns have emerged, and we lack knowledge not only on the isolated factors influencing wildlife responses to human presence, but also on the combined effects of multiple factors (Tablado and Jenni, 2017). For example, there is limited knowledge on the role of combined effects of fine-scale intensity and spatial context of exposure to outdoor activity in shaping disturbance effects. This is critical, because characteristics of exposure, such as number of visitors or proximity of out outdoor activities to animal use areas, may not only determine the severity of impacts, but may also drive learning processes such as habituation, that require specific intensity or frequency of exposure to a stimulus (Čapkun-Huot et al., 2024; Bejder et al., 2009).

We present a case study investigating how multiple interacting factors characterising intensity and spatial exposure to outdoor activity shape behavioural and physiological responses, and tolerance, in a population of Alpine marmots *Marmota marmota* within the Stelvio National Park (central Italian Alps) in 2022 and 2023. Alpine marmots are large, hibernating rodents that inhabit alpine grasslands at altitudes between 800 and 3000 m above sea level. They live in family groups of 2–20 individuals, occupying territories with an average size of about 2 ha (Perrin et al., 1993). The activity centre is typically around the winter burrow, which marmots also use for hibernation (Arnold, 1999). Their small, stable territories with an easily recognisable activity centre make marmots an ideal study system for our purpose, allowing us to trace animals' exposure to outdoor activity on a fine spatial scale much more easily, as, for instance, compared to species with large, variable movement ranges. Not least, the study system in itself is relevant: Alpine regions are increasingly under pressure from growing global nature tourism, including within protected areas (Sato et al., 2013). Although Alpine marmots are not considered threatened currently (Gazzard and Ferrari, 2024), they are potentially sensitive to human disturbance because they rely on a short vegetative period during the Alpine summer to accumulate enough fat reserved for winter hibernation. Given additional stressors such as climate change (e.g. Rézouki et al., 2016), monitoring potential (negative) impacts of outdoor recreational activities on marmots is important.

We focused on the effects of non-consumptive summer outdoor recreational activities (e.g. hiking) on marmot (1) anti-predator behaviour, (2) foraging, and (3) physiological stress. We characterised outdoor recreation in terms of three different factors that, combined, allow us to better characterise fine-scale intensity and exposure: current on-site visitor numbers, the extent of areas within marmot territories used by visitors (e.g. along trails, unofficial footpaths or around picnic areas) and the distance of marmot's activity centre within their territory (i.e. the main burrow) to the main hiking trail, which was the major recreational infrastructure in the area. The number of visitors reflects the real-time intensity of human presence during each observation. In contrast, the extent of area use quantifies the general exposure of a full territory to recreational infrastructure and is fixed for each family group. Lastly, distance to the main trail focuses on how exposed a marmot's activity centre is to where visitors are primarily concentrated, independent of recreational use in the full territory. For example, a territory might not be used by visitors extensively (e.g. no picnic areas), but marmots may still be highly exposed when on-site visitor numbers are high, when their main burrow lies directly beside the main trail. These metrics are uncorrelated but biologically complementary: together, they allow us to test whether marmots' reactive behaviour to people depends not only on current human presence (i.e. on-site visitor numbers), but also on how their territory is structured in relation to recreational use. We hypothesised that marmots would increase anti-predator behaviour and physiological stress, and reduce foraging, at times when more visitors are present in the study area. We further hypothesised that the strength of this response would depend on territory structure in relation to recreational use, but unequivocal evidence from previous studies renders the direction of this effect uncertain. On the one hand, marmots might respond more strongly to increasing visitor numbers either when the extent of areas within their territory that is used by visitors is higher, or when their activity centre is located next to the main trail, because they may perceive a higher risk from people that are spatially closer (Ydenberg and Dill, 1986; Stankowich and Blumstein, 2005). When both the extent of areas used by visitors is high and activity centres are close to the trail, we would expect marmots to show peak responsiveness, reflecting an additive effect on perceived risk (H1; Fig. 1 a,b). On the other hand, marmots from territories that are spatially structured in a way that maximises overall exposure to recreational activity (i.e. high extent of area use by visitors within territories and/or activity centre close to the trail) may be less responsive to increasing visitor numbers in the study area, for example due to habituation-like processes (Bejder et al., 2009; Samia et al., 2015) (H2; Fig. 1c,d). Gaining a more refined understanding of the fine-scale context in which outdoor activities disturb wildlife is critical to accurately assess impacts and inform management that aims to minimize adverse effects of outdoor recreation while maintaining public access to nature.

2. Materials and methods

2.1. Study area

We studied free-living Alpine marmots in the Stelvio National Park (Northern Italy, 46°42′ N, 10°57′ E, hereafter PNS) during the summer seasons of 2022 and 2023. The study area extends over about 30 ha of alpine grasslands in Val Cedec (46°42′ N, 10°57′ E) at altitudes of 2178 to 2450 m above sea level. It is characterised by a typical Alpine climate with harsh winters, prolonged snow cover that can last up to seven months (October – April), and a short growing season in summer. Temperatures range from −14 °C to 24.5 °C (https://it.weatherspark.com/). The Stelvio National Park is a popular area for summer outdoor recreational activities. A main hiking trail runs through the study area, which in summer is primarily used by hikers and, to a lesser extent, by cyclists. Dogs are permitted in the areas when on a leash; however, on a few occasions, we observed off-leash dogs chasing marmots. Access to motorised transport is limited to a few authorized vehicles. Alongside the main trail, there are a few smaller, less frequented paths, as well as a few picnic areas nearby. Thus, while the main trail is the central axis of outdoor activity in the area, outdoor recreational activities can extend from it into marmot territories (see Fig. 2 for a map of the study area and spatial structure of marmot territories in relation to recreational use). Marmot hunting is prohibited in PNS, and there are no records of poaching. Natural marmot predators in the area include red foxes *Vulpes vulpes* and golden eagles *Aquila chrysaetos*.

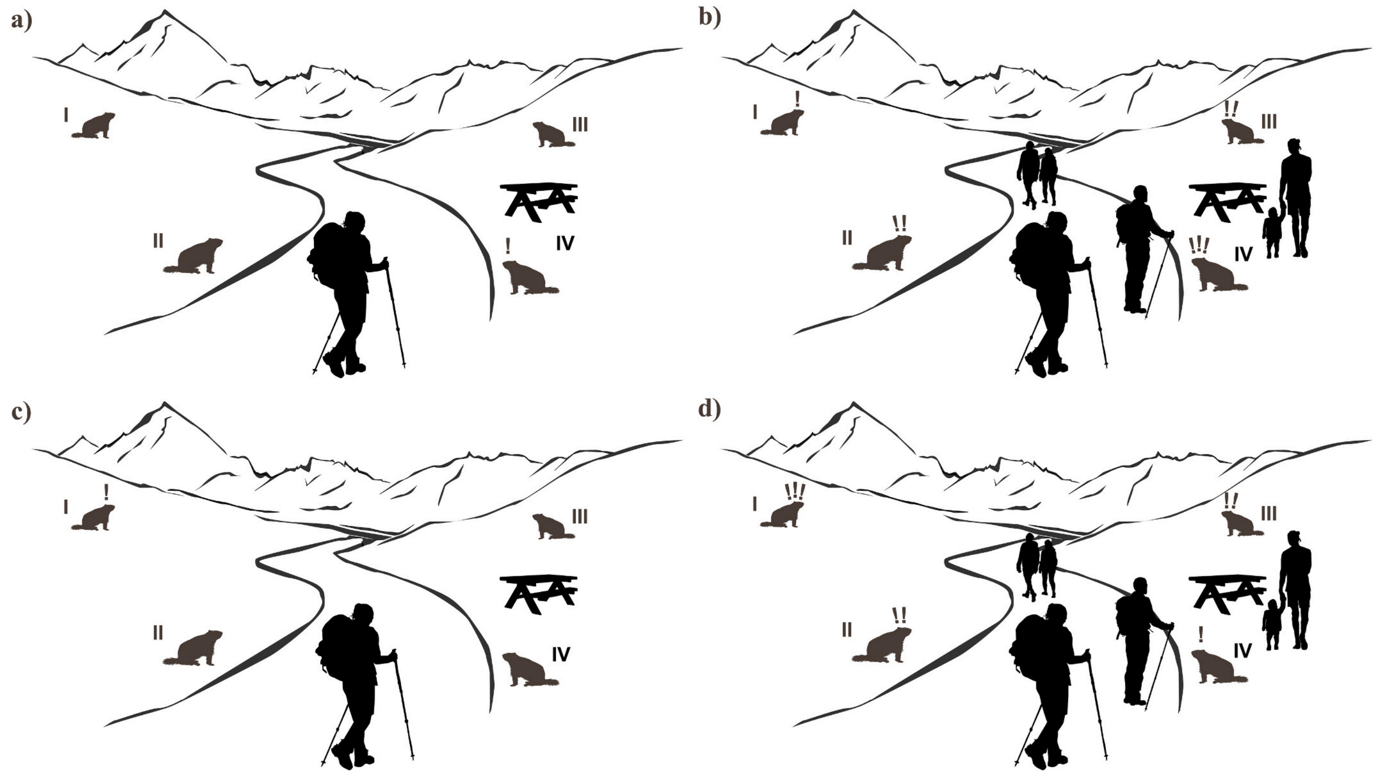

Fig. 1. Predicted effects of the real-time number of visitors present in the study area on marmot behavioural and physiological responses exemplified for low (a,c) and high (b,d) number of visitors and different territories that vary in how they are structured in relation to recreational use (I-IV), based on two contrasting hypotheses (H1: a,b; H2: c,d): I: low extent of areas that are used by visitors into the marmot's territory and activity centre located far from the main hiking trail; II: low extent of visitor use areas into the territory but activity centre close to the trail; III: high extent of visitor use areas (here a picnic area) into the territory, but activity centre far from the trail; IV: high extent of visitor use areas into the territory, and activity centre located close to the trail. Predicted strength of marmot behavioural and physiological responses is indicated by the number of exclamation marks (!) over the depicted marmots.

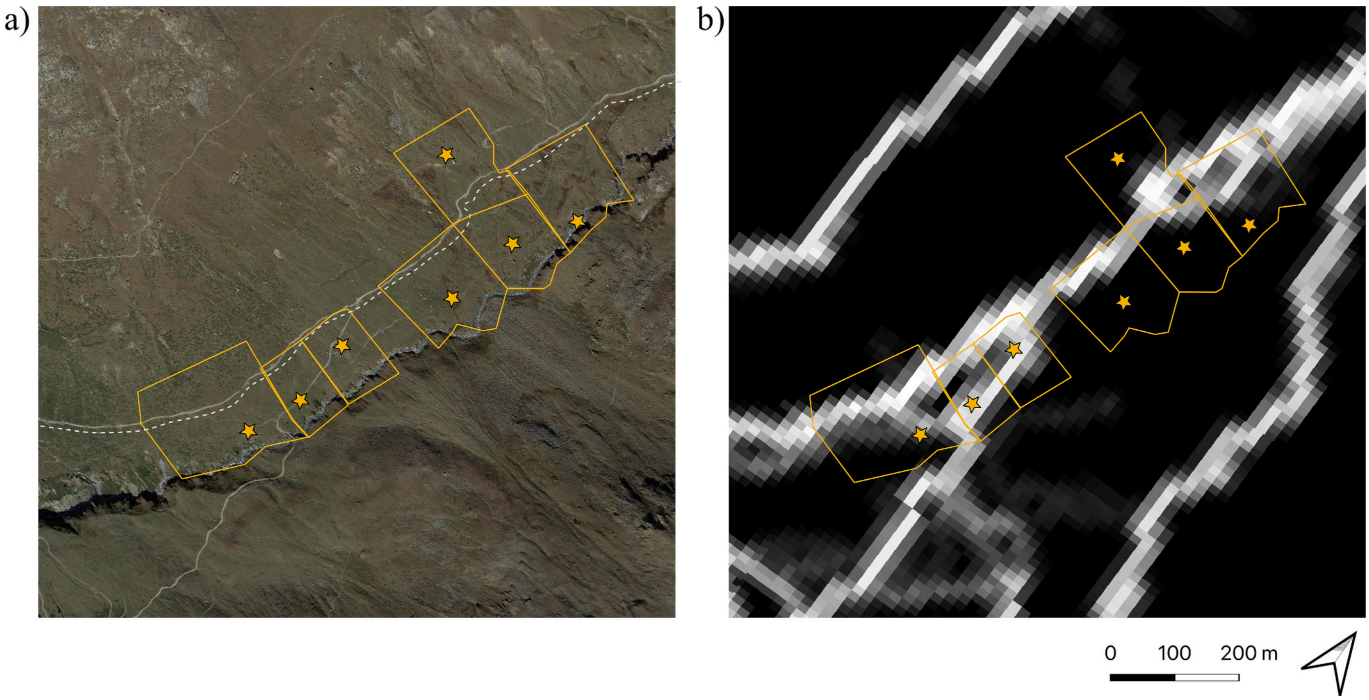

Fig. 2. Map of the study are in Stelvio National Park, as a) satellite and b) STRAVA heatmap view (areas with higher intensities of visitation use are depicted in brighter white tones; for details see section 2.5). Illustrated are marmot territory borders (yellow lines) and locations of main burrows (yellow stars), and the main trail is marked (dashed white line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Capture and marking of marmots

Marmots were captured to be individually marked, sexed and aged using 20 two-door tomahawk traps that were baited with dandelion *Taraxacum officinalis* and evenly distributed over the study area, close to the marmot's main burrow entrances. Captures took place in May (2022–2023), shortly after hibernation, when plant biomass in the area was still low, thus maximizing capture probability and avoiding disturbance during behavioural observations, which were initiated shortly after the capture period. Captures were stopped after about 10 days, when recaptures dominated, thus defining the final number of marked animals available for the study. Individuals were visually marked with different combinations of coloured plastic ear tags and a microchip, which was injected subcutaneously. We determined sex through the examination of anogenital morphology (Zelenka, 1965) and age class (yearling or subadult/adult) through biometric measurements (body mass and length). Additionally, other physiological measures such as heart rate and rectal temperature were taken within a long-term study on marmot behavioural ecology in the area. For details on the capture procedure, see Giari et al. (2024). Captures were authorized by the ISPRA (Italian Institute for Environmental Protection and Research) and conducted with the assistance of a veterinarian. The total handling time of animals never exceeded 25 min.

2.3. Behavioural observations

We observed tagged marmots throughout most of their active period (June to early September) and during their active hours (0700 h to 2000 h). Overall, 52 individual animals from seven family groups were observed. To avoid disturbance, observers were located on the opposite side of the valley from the marmots, across a river, at a minimum distance of 150 m. We used spotting scopes (Swarovski 60 × 20) to aid close observations. Behavioural observations were conducted using focal animal sampling (Altmann, 1974). Each focal animal was observed for 15 min within each session, for six to 18 sessions per season, depending on the animal. Observations were distributed roughly evenly across daytime hours and throughout the season for each individual. In 2022 and 2023, respectively, 9 and 5 individuals were observed fewer than six times because they disappeared during the seasons (presumably either because they died, dispersed or lost their marks). Additionally, some observations were shorter than 15 min because the focal animal went out of sight, for example, entering a burrow. In these cases, an additional observation of that focal animal was conducted to compensate for the missing minutes, either later on the same day or on a subsequent day. During a focal observation, all behaviours were scored as ‘events’, that is, instantaneous behaviours (Altmann, 1974). Anti-predator behaviours were recorded using all-occurrence sampling (i.e. all occurrences of anti-predator behaviour shown by the focal animal during an observation were recorded). These included ‘stand up’ (i.e. a vigilance behaviour where marmots rise to the hind feet to enhance their overview of the surroundings, often looking around), ‘alarm call bout’ and ‘escape’ (see Ethogram in Table 1). Additionally, to capture the amount of foraging (which by nature is a ‘state’ behaviour, i.e. has a considerable duration) within marmot time budgets, we used instantaneous sampling every minute, recording the focal's current activity state as ‘foraging’ or ‘other’ (see Ethogram in Table 2). During most focal observations, both anti-predator behaviours and foraging were recorded, with some additional focal observations of instantaneous sampling of foraging only.

Table 1
Ethogram of Alpine marmot anti-predator behaviours (‘stand up’, ‘alarm call bout’, ‘escape’) recorded during all-occurrence focal sampling.

Behaviour (TYPE)	Description
Stand up (EVENT)	Marmot stands up on its two hind feed only, appearing alert and without foraging at the same time, while often looking around and/or alarm calling.
Alarm call bout (EVENT)	Marmot emits a short, distinct series of alarm calls, with calls separated by <2 s considered as part of a single alarm call bout.
Escape (EVENT)	Marmot suddenly starts running, typically towards a burrow entrance, while appearing alerted and not in context of social interaction (e.g. play or agonistic encounters).

Table 2
Ethogram of Alpine marmot foraging behaviour (‘forage’) to record the foraging ratio within marmots' time budgets recorded during instantaneous focal sampling.

Behaviour (TYPE)	Description
Forage (EVENT)	Marmot is sitting, standing or slowly moving with nose close to food plants, or head up while chewing at the same time.
Other (EVENT)	Focal engaging in any other activity that foraging.

Behaviours were scored live in the field and recorded using a handheld audio recording device or an audio recorder app on a smartphone. Behaviours were later transcribed in the software BORIS 7.13.9 (Friard and Gamba, 2016).

2.4. Measurement of faecal cortisol metabolites

We quantified faecal cortisol metabolites (FCMs) to track variations in physiological stress. Marmot faecal samples were collected non-invasively from the study area in the same period that behavioural observations were conducted (June to early September 2022–2023). Because FCM concentrations can change with time after defecation (Palme, 2019), we collected only faeces that appeared fresh (i.e. presumed to be less than one day old), judged by the sample's colour, moisture, and texture. Moreover, to ensure accurate assessment, samples were collected only on and following rain-free days, as rainfall can obscure age estimation due to moisture, which can artificially increase FCM levels (Washburn and Millspaugh, 2002). Upon collection, faeces samples were immediately cooled on ice packs and, after a maximum of 8 h, transferred to −20 °C storage.

For laboratory analysis, FCMs were extracted by dissolving a 0.5 g sample aliquot in 80 % methanol on a shaker for 30 min. The samples were then centrifuged at 2500g for 10 min at 8 °C and diluted 1:10 with assay buffer (Palme et al., 2013). We used an 11-oxoetiocholanolone (‘72 T’; for details see Möstl et al., 2002) assay to measure FCM levels, which has been successfully validated for Alpine marmot (Zenth et al., 2025).

2.5. Assessment of outdoor recreational activity

Data on the current on-site number of visitors were retrieved from a people counting device installed by the National Park personnel along the main hiking trail running through the study area, located at around 60 min walking distance from the centre of the study area (46°45′ N, 10°57′ E). The system operated with laser measurement technology, counting every passing object (e.g., a person on foot) as a single count. To approximate current intensity of outdoor activity within the study area, for the analysis of (1) anti-predator behaviour and (2) foraging, we considered the sum of people counted within a three-hour window around each focal observation. For the analysis of (3) FCM levels, we considered the total number of people in the study area two days before the sample collection to account both for the delay between defecation and collection of a faeces sample, which was assumed ~1–24 h, and the fact that FCMs are an integrative measure of adrenocortical activity which is pooled over a few hours and reflected with a time delay that roughly corresponds to the species-specific gut passage time (Palme, 2019). In Alpine marmots, the delay between a stressful event and a peak in FCM levels was estimated at ~18 h based on a biological validation experiment (Zenth et al., 2025). Thus, FCM levels can reasonably be assumed to reflect marmot plasma cortisol levels about 18–42 h before collection.

Some marmot territories were only bordered by the main trail, while others were intersected by it or by smaller paths or contained a picnic area. To capture this difference in the extent of areas used by visitors, for each territory, we calculated a spatially explicit Cumulative Outdoor activity Index (COI) from the STRAVA heatmap (www.strava.com/maps/global-heatmap) following the procedure described in Corradini et al. (2021). STRAVA displays a heatmap of the cumulative intensity of outdoor activity in a location by overlapping recorded GPS tracks of users engaging in outdoor activities; a higher number of overlapping tracks in each pixel results in a higher ‘heat’ count, depicted in more bright tones (i.e. higher pixel intensity) in the STRAVA heatmap (Corradini et al., 2021). We focused on on-foot activities such as hiking, running and walking, which were the main summer outdoor activities in the study area, and displayed them at a zoom level of 13 (for a resolution of 20 m). The derived COI for each pixel ranged between 0 and 1, depicting users' relative intensity of use for each pixel over the last 12 months. Thus, in contrast to the current on-site visitor number, the COI is not a real-time measure, but a fixed characteristic of each territory. Importantly, the COI was shown to be spatially and temporally representative of overall levels of outdoor activity (Corradini et al., 2021). We calculated the average COI in each studied marmot group's territory using the “raster” R package (Hijmans et al., 2015). Territory borders were estimated by visually tracking the locations of marked individuals.

We considered the marmot's main burrow (i.e. the burrow used for hibernation) to be the activity centre of a marmot territory (Arnold, 1999). This burrow could easily be identified in spring (April) by snow tracks centring to this burrow from different directions and was typically also the largest complex within a territory. Observations confirmed that all group members spend a considerable amount of time near this burrow, for example, resting on earth and rock ledges in front of their burrows (FZ, personal observation) (Arnold, 1999). We measured the shortest distance between a respective main burrow and the main trail using the ruler function in QGIS (Version 3.32.3 – Lima).

2.6. Statistical analysis

All analyses were conducted in R 4.4.2 (R Core Team, 2024) through RStudio 2024.09.1 + 394 (Posit Team, 2024). To assess the relationship of the real-time number of visitors in the study area, average COI within a marmot's territory and distance of the activity centre to the main trail with (1) anti-predator behaviour, (2) foraging, and (3) FCM levels, we adopted a generalized linear (mixed) modelling approach.

For anti-predator behaviour, the number of anti-predator behaviours recorded during a focal observation was divided by the duration of a respective observation (in minutes) to obtain a rate, which we then divided by the maximum rate measured over all observations to normalize it on the (0,1) interval for subsequent modelling. Because anti-predator behaviour ratios are continuous data with upper and lower bounds, we assumed a conditional ordered Beta distribution with a logit link function, which accommodates data on the [0,1] interval (Kubinec, 2023). Specifically, the anti-predator behaviour ratio (response variable) was fitted as a function of a three-way interaction between the number of visitors (numeric count variable), COI (continuous variable with theoretical possible values from 0 to 1 [no outdoor recreational activity – comparably highest outdoor recreational activity within the study region]), and distance from the activity centre to the trail (numeric variable in meters) as target explanatory variables using the ‘glmmTMB’ R package (Brooks et al., 2017). Marmot sex (factor: male, female) and age class (factor: yearling, subadult/adult), as well as the year of the observation (factor: 2022, 2023) and Julian day (numeric variable), were also included as covariates. Based on data exploration, we allowed for a non-linear relationship between Julian Day and anti-predator behaviour ratio by including a smoothing term with three natural cubic splines in the model formula with the ‘ns’ function in the R package ‘splines’ (R Core Team, 2024). Because of repeated observations of the same individuals, marmot identity (ID) was fitted as a random intercept. Additionally, we tested a model that also included family group identity as a random intercept to account for the fact that several individuals from each family group were observed. However, that model did not converge, likely because family group was collinear with COI and distance to trail, which are both fixed characteristics of the territory that a family group occupies. Thus, they likely account for most of the between-family variation – making the inclusion of a family-level random intercept redundant, and we decided to drop this term from the model. Lastly, we included the duration of observation as weights in the model to correct for heteroskedasticity due to the higher variance of shorter observations. Multicollinearity between explanatory variables was deemed inconsequential based on the Variance Inflation Factor (VIF < 3) assessed with the 'vif' function in the 'car' R package (Fox and Weisberg, 2018). Residual diagnostics assessed through the R package 'DHARMa' (Hartig, 2022) indicated violations of model assumptions, which appeared to stem from six extreme data points. After dropping these six outliers (out of 750 total data points) from the dataset, the residuals complied with the model assumptions. Comparing two models with and without the six outliers showed that their removal did not substantially change estimates or statistical significance. In addition, we tested for spatial autocorrelation due to territories located near each other using Moran's I test for distance-based spatial autocorrelation of model quantile residuals through 'DHARMa', which indicated no evidence for autocorrelation.

To model foraging, we used the same approach as above. First, for each observation, we divided the number of scans scored as 'forage' by the total number of scans recorded to obtain a foraging ratio on the [0,1] interval. Then, we modelled the foraging ratio (response variable) as a function of the three-way interaction between visitor count, COI, and distance from the activity centre to the trail (target explanatory variable), while also controlling for sex, age class, year, and Julian day. Again, we assumed an ordered Beta distribution with a logit link function. ID was fitted as a random intercept, and the total number of scans (i.e. duration of the observation) was included as weights. Residual diagnostics in 'DHARMa' confirmed the adequacy of the model.

To assess the effect of the same target explanatory variable, as well as their statistical interaction on FCM levels (response variable), we fit a generalized linear model, assuming a conditional Tweedie distribution with log-link function, which extends various exponential dispersion models and is versatile enough to accommodate a wide range of data types, both continuous and discrete (Dunn and Smyth, 2018). Year and Julian day (fitted as non-linear effect as in [1,2]) were fitted as cofactors. Because faecal samples were collected non-invasively in the study area, no information was available on age class, sex or ID. Residual diagnostics indicated no major violations of model assumptions.

3. Results

The average number of visitors in the study area during the study period (May–September) was 85 (min – max: 0–396) people within a three-hour window during behavioural observations. COI within the territories of studied marmot groups averaged 0.34 (0.12–0.50), and marmot groups' activity centres were located an average of 76 m (62–125 m) away from the main hiking trail running through the area.

(1) Anti-predator behaviour

We conducted a total of 744 focal all-occurrence sampling of anti-predator behaviour on 42 individual marmots (12 females and 30 males, 15 yearlings and 25 adults/subadults [note that some individuals were observed across years, transitioning from yearlings to adults/subadults]). Observed rates of anti-predator behaviour averaged 0.1 (min – max: 0–1), which corresponds to 2 (0−20) behaviours during an observation, which typically lasted 15 min.

Anti-predator behaviour was statistically significantly associated with the number of visitors in the study area, in interaction with both COI and the distance of the marmots' activity centre to the trail. Specifically, the rate of anti-predator behaviour increased with higher number of visitors, but only in marmots from territories with a low COI and the activity centre located at far to medium distances from the main trail. Notably, while marmots from territories with low COI and activity centres far from the trail increased anti-predator behaviour about 5-fold at peak visitor times, this effect weakened either when COI increased or when the distance of activity centres to the main trail decreased. As soon as both COI increased and distance to trail decreased, anti-predator behaviour no longer increased with rising number of visitors. At maximum values of COI and activity centre distance, anti-predator behaviour was even slightly reversed (Table 3; Fig. 3).

Additionally, there was evidence for a non-linear effect of Julian day (rate of anti-predator behaviour peaking in July), marmot age class (lower odds of antipredator behaviour in adults/subadults as compared to yearlings) and year (higher rate of anti-predator behaviour in 2022 as compared to 2023) (Fig. 4). Conversely, sex did not seem to affect the anti-predator behaviour rate in marmots. Last, there was substantial individual variation in anti-predator behaviour.

(2) Foraging

We conducted a total of 972 focal instantaneous samplings of foraging on 52 individual marmots (16 females and 36 males, 19 yearlings and 33 adults/subadults). The foraging ratio during an observation averaged 0.42 (min – max: 0–1).

The foraging ratio was associated with the number of visitors in the study area, in interaction with COI and the distance of the marmots' activity centre to the trail, with similar (opposite) patterns to those observed in (1). Marmots in territories characterised by low COI and with main burrows located far from the trail decreased foraging with increasing number of visitors, whereas the foraging ratio did not change with rising number of visitors in marmots from territories with medium and comparably high values of COI and/or activity centre closer to the hiking trail (Table 4; Fig. 5). Additionally, Julian day had a non-linear effect on foraging, with marmots increasing foraging time towards the

Table 3
Rate of anti-predator behaviour as a function of the number of visitors in the study area in a time window around the observation, average Cumulative Outdoor activity Index (COI) within a marmot's territory, and distance of marmots' activity centre to the main trail running through the study area (distance to trail; in meter). Covariates include Julian day, marmot age class (yearling, subadult/adult), sex (female, male), and year of the observation (2022,2023). Effects are given as odds ratios (OR), with 95 % confidence intervals (CIs). Significant effects ($p < 0.05$) are shown in bold.

	Rate of anti-predator behaviour		
Predictors	*OR*	*CI*	*p-value*
(Intercept)	0.01	0.000–4.793 × 10^4	0.573
Number of visitors (n)	0.90	0.864–0.929	<0.001
COI	8.83 × 10^6	0.000–6.025 × 10^{23}	0.419
Distance to trail (in m) [log]	1.94	0.054–69.709	0.716
Julian day [1st degree]	1.11	0.974–1.274	0.115
Julian day [2nd degree]	1.69	1.278–2.247	<0.001
Julian day [3rd degree]	0.43	0.364–0.514	<0.001
Age class [subadult/adult]	0.82	0.749–0.905	<0.001
Sex [male]	0.90	0.683–1.179	0.437
Year [2023]	0.84	0.792–0.886	<0.001
Number of visitors × COI	1.25	1.136–1.374	<0.001
Number of visitors × distance to trail [log]	1.03	1.018–1.035	<0.001
COI × distance to trail [log]	0.02	0.000–205.997	0.411
(Number of visitors × COI) × distance to trail [log]	0.95	0.927–0.970	<0.001
Random Effects			
σ^2	0.38		
$\tau_{00\ \mathrm{uid}}$	0.16		
ICC	0.29		
N_{uid}	42		
Observations	744		
Marginal R^2 / Conditional R^2	0.116 / 0.373		

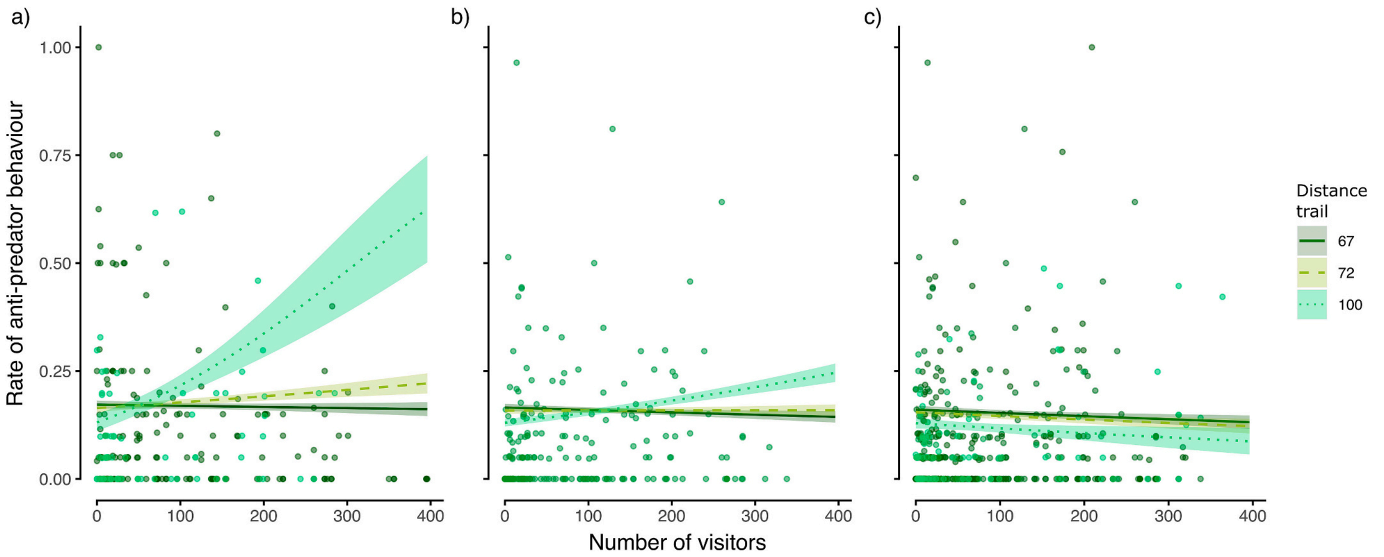

Fig. 3. Conditional relationship between rate of anti-predator behaviour and the number of visitors in the study area for a) 1st quantile (0.2), b) median (0.36), and c) 3rd quantile (0.48) values of Cumulative Outdoor activity Index (COI) and 1st and 3rd quantile, and median distance of marmots' activity centre to the hiking trail (in meters) (coloured lines). Continuous covariates are set at their mean values and categorical covariates at the most common level (age class = subadult/adult, sex = male, year = 2023). Colour-shaded areas show 95 % confidence intervals. Subsets of raw data are shown in each panel as coloured points with colours indicating distance to trail, including data with a) COI ≤ 0.2, b) 0.2 < COI ≤ 0.36, and c) COI > 0.36.

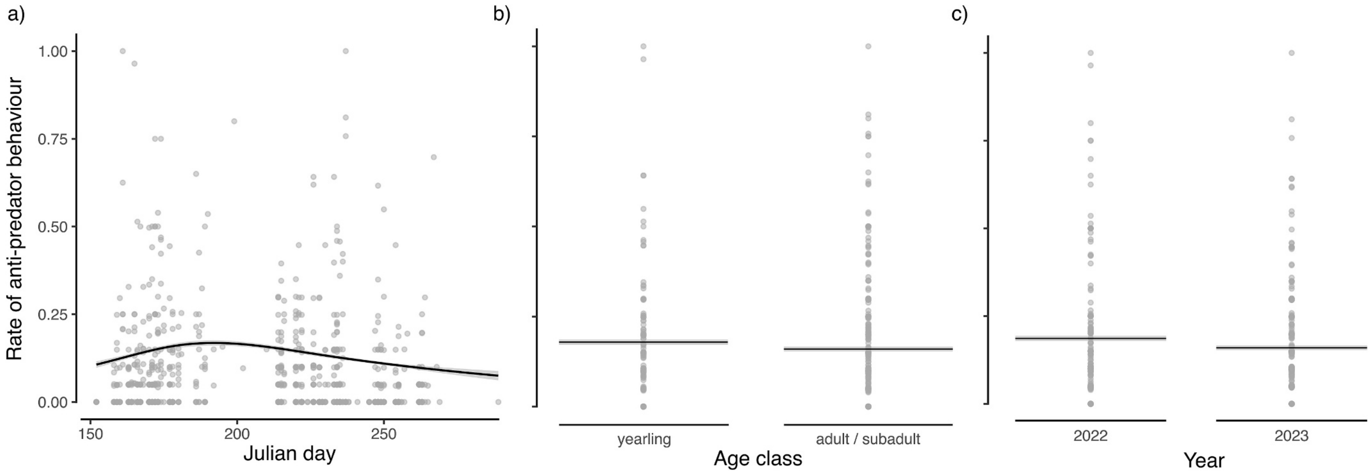

Fig. 4. Conditional effects of a) Julian day, b) year and c) age class on rate of anti-predator behaviours in marmots. Continuous covariates are set at their mean values and categorical covariates at the most common level (age class = subadult/adult, sex = male, year = 2023). Grey-shaded areas show 95 % confidence intervals. Raw data are shown as grey points.

end of the summer (Fig. 6).

(3) Faecal cortisol metabolites (FCMs)

We collected a total of 101 faecal samples from the field during the two summer study periods for FCMs analysis.

FCM data were highly variable, and there was no clear evidence for an effect of the number of visitors, COI or distance of the activity centre to the trail, nor an effect of covariates (year and Julian day) (Table 5). Yet, despite statistically non-significant, visualization of the three-way interaction between the target explanatory variables on FCM hinted at a possibly matching pattern to (1) and (2), with FCM levels tending to rise with increasing visitor frequentation, but only in territories characterised by low values of COI and when the main burrow was comparably distant to the trail (Fig. 7). In territories with medium or high COI, or when the main burrow was located closer to the trail, FCM levels were not affected by visitor frequentation or even decreased with increasing frequentation.

4. Discussion

Anti-predator vigilance and foraging were associated with the number of visitors present in the study area at a given time. However, this effect depended on the combined effects of average COI in the marmot's territory and the distance of the activity centre within a territory to the main trail. In territories with low COI and the activity centre far from the trail, marmots increased anti-predator behaviours, and decreased foraging as a function of the number of visitors. However, this effect weakened when either the COI increased or the distance to the trail decreased. When both COI was medium to high and the activity centre closer to the trail, the rate of anti-predator behaviour and foraging ratio did not change any longer with the number of visitors. In territories with maximum values of COI and the activity centre close to the trail, marmots even slightly reduced anti-predator behaviour and

Table 4

Effects of the number of visitors, average Cumulative Outdoor activity Index (COI), distance of marmot activity centre to the main trail (distance to trail; in meter), and covariates (Julian day, age class [yearling, subadult/adult], sex [female, male], year [2022,2023] on foraging ratio of Alpine marmots. Effects are given as odds ratios (OR), with 95 % confidence intervals (CIs). Significant effects ($p < 0.05$) in bold.

	Foraging ratio		
Predictors	*OR*	*CI*	*p-value*
(Intercept)	0.00	0.000–0.316	0.032
Number of visitors (n)	1.09	1.055–1.118	<0.001
COI	3.43×10^{15}	1.163×10^{3}–1.013×10^{28}	0.015
Distance to trail (in m) [log]	24.03	1.461–395.359	0.026
Julian day [1st degree]	1.03	0.911–1.176	0.599
Julian day [2nd degree]	1.03	0.785–1.364	0.808
Julian day [3rd degree]	1.84	1.698–1.991	<0.001
Year [2023]	1.00	0.942–1.066	0.938
Age class [yearling]	1.11	1.000–1.243	0.051
Sex [male]	0.95	0.702–1.294	0.760
Number of visitors × COI	0.80	0.741–0.864	<0.001
Number of visitors × distance to trail [log]	0.98	0.974–0.987	<0.001
COI × distance to trail [log]	0.00	0.000–0.150	0.012
(Number of visitors × COI) × distance to trail [log]	1.05	1.035–1.073	<0.001
Random Effects			
σ^2	0.20		
$\tau_{00\ \text{uid}}$	0.24		
ICC	0.54		
N_{uid}	52		
Observations	872		
Marginal R^2 / Conditional R^2	0.122 / 0.598		

increased foraging, possibly related to human-shield effects (i.e. reduced predation risk in areas and at times with high human activity [Berger, 2007]). Notably, at maximum values of COI, the distance to trail was no longer associated with marmot behavioural responses to current presence of visitors. By contrast, when activity centres were located closer to the trail, COI appeared to be no longer relevant. FCM levels hinted at similar patterns as anti-predator behaviour, with increasing FCM levels as a function of the number of visitors in the study area, but only when the COI was low and activity centres were located further away from the trail. However, given the low sample size relative to the complexity of the fitted model and the high uncertainty around the estimated values of FCMs, we cannot rule out the possibility that the observed effect was due to chance. Thus, we have shown that disturbance effects through outdoor activity can vary on a fine spatial scale – even within a single population – and are modified by the combined effects of multiple

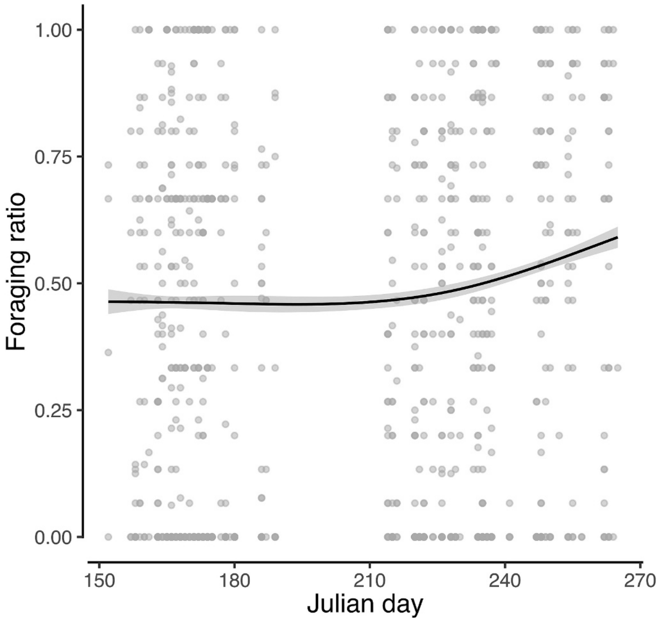

Fig. 6. Conditional relationship between foraging ratio and Julian day. Continuous covariates are set at their mean values and categorical covariates at the most common level (age class = subadult/adult, sex = male, year = 2023). Grey-shaded areas show 95 % confidence intervals. Raw data are shown as grey points.

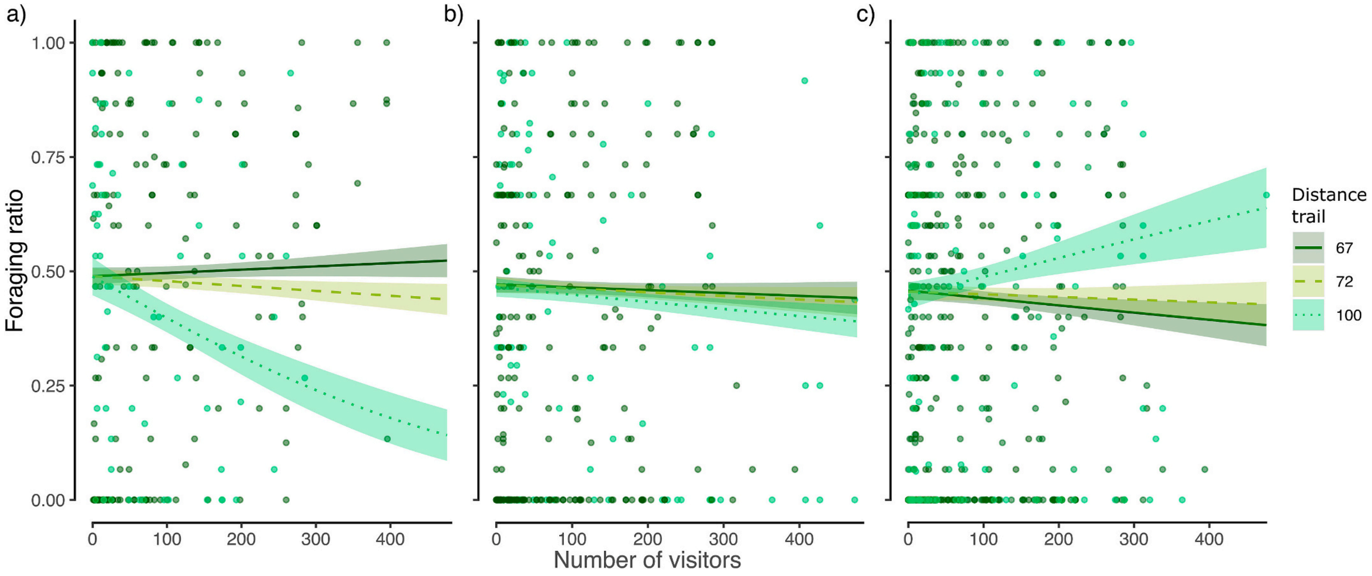

Fig. 5. Conditional relationship between foraging ratio and the number of visitors in the study area for a) 1st quantile, b) median, and c) 3rd quantile values of Cumulative Outdoor activity Index (COI) and distance of marmots' activity centre to the hiking trail (in meters) (coloured lines). Continuous covariates are set at their mean values and categorical covariates at the most common level (age class = subadult/adult, sex = male, year = 2023). Colour-shaded areas show 95 % confidence intervals. Subsets of raw data are shown in each panel as coloured points with colours indicating distance to trail, including data with a) COI ≤ 0.2, b) $0.2 < \text{COI} \leq 0.36$, and c) COI > 0.36.

Table 5
Effects of the number of visitors, average Cumulative Outdoor activity Index (COI), distance of marmot's activity centre to the main trail (distance to trail; in meter), and covariates (Julian day, year [2022, 2023]) on marmot faecal cortisol metabolites (FCMs), with 95 % confidence intervals (CIs).

	FCMs (in ng per g)		
Predictors	*Estimates*	*CI*	*p-value*
(Intercept)	4.05×10^3	$0.568–2.891 \times 10^7$	0.067
Number of visitors (n)	0.98	0.935–1.023	0.341
Distance to trail (in m) [log]	0.40	0.049–3.204	0.386
COI	0.00	$0.00–3.546 \times 10^5$	0.281
Year [2023]	1.15	0.890–1.479	0.289
Julian day [1st degree]	0.77	0.400–1.474	0.427
Julian day [2nd degree]	1.43	0.625–3.290	0.395
Julian day [3rd degree]	1.15	0.684–1.934	0.597
Number of visitors × distance to trail [log]	1.01	0.995–1.016	0.347
Number of visitors × COI	1.08	0.953–1.221	0.230
Distance to trail [log] × COI	34.03	$0.049–2.359 \times 10^4$	0.291
(Number of visitors × distance to trail [log]) × COI	0.98	0.954–1.011	0.228
Observations	101		

factors characterising how marmot territories are structured in relation to recreational use. As expected, we find evidence that outdoor recreation can disturb Alpine marmots when overall exposure is low, with a hint that disturbance also manifests at the physiological level (i.e. inducing stress). However, when territories are structured in a way that increases overall exposure to outdoor recreation, marmots seem to have higher behavioural tolerance to the presence of visitors, possibly due to habituation-like processes.

In marmots from territories with low overall exposure to outdoor activity (i.e., low COI and activity centre far from the trail), anti-predator behaviour increased with rising number of visitors in the study area, indicating that marmots were disturbed by people. If perceived as a threat, wildlife can respond to outdoor recreational activity with different behavioural strategies, including spatial or temporal avoidance or by increasing anti-predator behaviour, such as vigilance or alarm vocalisations (Salvatori et al., 2023). Because marmots occupy small, fixed territories (~2 ha) (Perrin et al., 1993), their ability to spatially avoid outdoor activity may be somewhat limited as compared to other species or involve retreating into a burrow. Similarly, temporal avoidance, such as shifting towards nocturnality as observed across a large number of mammalian species (Gaynor et al., 2018), is a limited option for diurnal marmots. Thus, increasing anti-predator behaviours, such as vigilance, should be a major anti-predator strategy in marmots, as confirmed by our data. Results indicated that, in Alpine marmots, anti-predator behaviour leads to a behavioural trade-off with foraging, with marmots reducing their foraging ratio by more than 50 % during periods of high tourist presence compared to times when tourists were absent. This makes sense because the considered anti-predator behaviours (i.e. standing up on the hind feet and looking, alarm calling and escaping) are incompatible with foraging. Similarly, a negative correlation between vigilance and foraging was shown in other marmot species, including yellow-bellied marmots (Chmura et al., 2016) and hoary marmots *Marmota caligata* (Holmes, 1984).

By triggering anti-predator behaviour at the cost of foraging, outdoor recreation could have biologically significant negative consequences for marmot fitness, in particular, because marmots rely on a relatively short summer growing season to accumulate fat reserves before hibernation (Arnold, 1999). This assumption is supported by a long-term study in yellow-bellied marmots, finding that marmots from populations that experienced higher levels of outdoor recreational activity allocated, on average, more time to anti-predator vigilance and had lower body mass gain as compared to less disturbed populations (Uchida and Blumstein, 2021). Long-term data on individual life-history traits are needed to confirm fitness and population consequences in Alpine marmots.

Besides behavioural responses, stress levels are generally considered to reflect the intensity of human disturbance (Tarlow and Blumstein, 2007). While our FCMs data hint in this direction, we cannot make definite conclusions as data were highly variable, while our sample size was low. Likely, 101 data points were not sufficient to support a complex generalized linear model with five predictors and three interactions. Thus, it is not surprising not to find significance if effect sizes are not very strong. Moreover, the high variability of measured FCMs is not surprising. This is because cortisol metabolites are pooled in faeces over

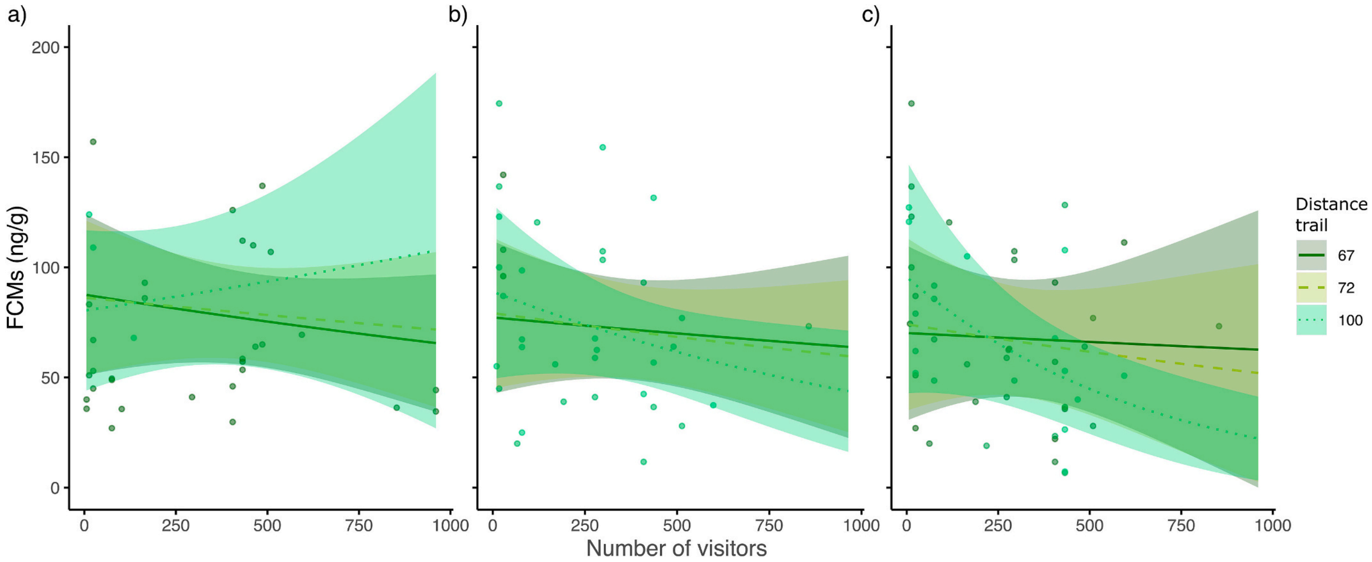

Fig. 7. Conditional relationship between marmot faecal cortisol metabolite (FCM) levels and visitor frequentation in the study area for a) 1st quantile, b) median, and c) 3rd quantile values of Cumulative Outdoor activity Index (COI) and distance of marmots' activity centre to the hiking trail (in meters) (coloured lines). Continuous covariates are set at their mean values and categorical covariates at the most common level (age class = subadult/adult, sex = male, year = 2023). Colour-shaded areas show 95 % confidence intervals. Subsets of raw data are shown in each panel as coloured points with colours indicating distance to trail, including data with a) COI ≤ 0.2, b) 0.2 < COI ≤ 0.36, and c) COI > 0.36.

a few hours (Palme et al., 2005) and thus could be influenced by different sources of stress, for example, agonistic encounters between marmots, both within or between family groups, or predator attacks. Additionally, because samples were collected non-invasively, the exact time of defecation was unknown. Thus, FCM levels could be matched only roughly to one of the target explanatory variables – current one-site visitor numbers. Additionally, due to lacking information on animal identity, we were unable to account for repeated sampling of the same individuals and individual differences in baseline and stress-induced FCM levels, which are known to be relevant in Alpine marmot (Zenth et al., 2025) and other species (Palme, 2019). However, in principle, not accounting for individual identity should have increased the precision of our estimates.

In contrast to marmots from territories with low COI and the activity centre far from the trail, marmots that occupied territories with higher comparative COI and/or with an activity centre closer to the trail seemed less disturbed by outdoor recreation. This suggests that Alpine marmots, similar to other taxa (Samia et al., 2015), can develop behavioural tolerance to humans in contexts where they are exposed to non-consumptive outdoor activities but not consumptive activities, such as hunting. In this context, behavioural tolerance to outdoor activity may have been achieved through habituation-like processes. Habituation to a (human-related) stimulus requires repeated exposure to it; if time intervals between stimuli are too long, habituation may not occur (Blumstein, 2016). In territories with higher COI, the probability of any marmot individual encountering a human at a distance close enough to be relevant may be higher compared to territories with lower COI. Similarly, on average, marmots that have their activity centre close to the trail should have a higher probability of relevant encounters with humans, thus facilitating habituation. This interpretation may also explain why, in territories with maximum values of COI, the distance to the trail is no longer relevant, and vice versa. In both cases, exposure to visitors may be sufficiently intense or frequent for learning processes to occur, whether driven by one factor alone or the combined effect of both. However, because we did not explicitly study behaviour change over time as required to demonstrate habituation, alternative mechanistic explanations for increased tolerance need to be considered. For example, there may have been spatial segregation between more and less tolerant individuals (Bejder et al., 2009): Individuals that are generally more tolerant to people (e.g., related to bolder personality types) and thus better at coping with outdoor activity may be more likely to occupy a burrow system near hiking trails. In contrast, less tolerant individuals, who respond strongly to immediate outdoor activity, may preferably select overall less disturbed areas.

Behavioural tolerance to humans can be adaptive to cope in anthropogenic landscapes primarily characterised by non-consumptive human activities (Samia et al., 2015), such as protected areas. In marmots, increased tolerance could mitigate negative effects of outdoor recreational activities by reducing energy and opportunity costs of antipredator behaviour towards harmless humans. If so, our findings add an interesting aspect to the discussion on how protected areas with a dual mandate of protecting biodiversity and providing public access to nature should be managed: medium-level exposure to outdoor activity – enough to create disturbance but not frequent enough to allow habituation – may create higher levels of disturbance as higher-level exposure. Thus, outdoor recreation's negative impacts on marmots could be reduced by concentrating human activities in a few areas and facilitating habituation there while closing off other areas. Nevertheless, caution is needed with this interpretation as it is based on the premise that habituation is positive for wildlife individuals. However, this need not necessarily be true (Bejder et al., 2009; Blumstein, 2016; Higham and Shelton, 2011; Uchida et al., 2023). In some contexts, increased tolerance to humans can have negative effects, for example, if it leads to generally decreased responsiveness, including to non-human predators, thus increasing vulnerability to predation (Geffroy et al., 2015). More research on behavioural tolerance in Alpine marmots and other species is required to better understand its consequences for individuals and cascading effects on populations. Regardless of whether promoting behavioural tolerance in wildlife individuals is desirable or not, our results underscore that conservation measures should not only manage visitor numbers, but also carefully consider spatial planning, such a positioning of picnic benches or recreational infrastructure.

In addition to the effect of the target explanatory variables, marmot vigilance was modulated by animal age class, which is in line with results in other species (Arenz and Leger, 2000), but not sex, and varied considerably between individuals. Individual variability could be related to unmeasured individual attributes, such as animal personality (Dammhahn and Almeling, 2012; Mella et al., 2015). Similarly, the foraging ratio varied individually but was not related to age class or sex, which again corresponds to findings in yellow-bellied marmots *Marmota flaviventer* (Chmura et al., 2016). Average higher levels of vigilance in mid-summer may be explained by the temporal overlap with pup emergence from burrows and, thus, increased vigilance in mothers (Burger and Gochfeld, 1994) and potentially other group members. Lastly, the effect of year on both vigilance and foraging suggests the presence of other correlated but unmeasured (environmental) variables.

Overall, our findings underscore the importance of fine-grained analyses that incorporate multiple factors to assess the impacts of outdoor recreational activities on wildlife. Specifically, our case study in marmots highlights the role of combined effects of intensity and spatial extent of exposure to outdoor activities on behavioural and physiological responses to human presence. Conservation measures aimed at mitigating negative effects of human disturbance should thus include both management of visitor numbers and carefully consider spatial planning of tourist infrastructure. Our case study suggests that non-consumptive outdoor recreational activities can disturb Alpine marmots, triggering behavioural and physiological responses, which potentially could have negative effects on individual fitness. On the other hand, marmots can also develop behavioural tolerance to human disturbance, but this requires a certain level of exposure to human activities. Similar patterns may also be found in other species, as learning generally follows similar principles. Further research assessing individual fitness and population parameters alongside behavioural responses to human presence is needed to confirm if behavioural tolerance to humans is adaptive in marmots or has negative consequences. Nonetheless, the fact that marmots are often found in areas with high human activity and have maintained stable populations over their distribution area (Gazzard and Ferrari, 2024) – despite being affected by the increase in alpine tourism – suggests that they cope well in tourist areas. Marmots' ability to develop behavioural tolerance to humans may be a key factor explaining this success.

CRediT authorship contribution statement

Friederike Zenth: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ilse Storch:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Chiara Giari:** Writing – review & editing, Investigation, Data curation. **Elena Morocutti:** Writing – review & editing, Investigation, Data curation. **Rupert Palme:** Writing – review & editing, Resources, Methodology, Investigation, Data curation. **Sabine Macho-Maschler:** Writing – review & editing, Resources, Methodology, Investigation, Data curation. **Andrea Corradini:** Writing – review & editing, Formal analysis, Data curation. **Daniel T. Blumstein:** Writing – review & editing, Supervision, Methodology. **Davide Tettamanzi:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Mira Huckfeld:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Luca Corlatti:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

We have no competing interests to declare.

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Data availability

Data will be made available on request.

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