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Research Article

Alpine ungulates adjust diel activity to the natural return of wolves amid anthropogenic pressures

Charlotte Vanderlocht[1,2,3,4,5], Valerio Donini[6,7], Andrea Corradini[1,8], Simone Dal Farra[1], Benjamin Robira[1,9], Andrea Gazzola[10], Giorgia Galeotti[1], Laura Limonciello[1], Noemi Squillaci[1,11], Maël Van Dam[1], Giada Zeni[1], Marta Gandolfi[4], Elisa Iacona[6,7], Lucrezia Lorenzetti[6,7], Matteo Nava[6,12], Federico Ossi[1,8], Heidi C. Hauffe[2,8], Francesco Ferretti[7,8], Luca Corlatti[6,13], Luca Pedrotti[4,6] and Francesca Cagnacci[1,8]

[1]Animal Ecology Research Unit, Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy
[2]Conservation Genomics Research Unit, Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy
[3]Centre Agriculture Food Environment (C3A), University of Trento, San Michele all'Adige, Italy
[4]Stelvio National Park Office – Sustainable Development and Protected Areas Service, Autonomous Province of Trento, Cogolo di Peio, Italy
[5]Department of Biological, Geological and Environmental Sciences, University of Bologna, Bologna, Italy
[6]Stelvio National Park – Direzione ERSAF Lombardia, Bormio, Italy
[7]Department of Life Sciences, University of Siena, Siena, Italy
[8]National Biodiversity Future Centre (NBFC), Palermo, Italy
[9]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
[10]Association for the Conservation of Biological Diversity (ACDB), Focșani, Romania
[11]Estação Biológica de Mértola (EBM), Mértola, Portugal
[12]University of Milan, Department of Veterinary Medicine and Animal Sciences, Lodi, Italy
[13]Chair of Wildlife Ecology and Management, University of Freiburg, Freiburg, Germany

Correspondence: Charlotte Vanderlocht (charlotte.vanderlocht@fmach.it, charlotte.vanderlocht@gmail.com)

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As wolves recolonise their historical range across Europe, ungulates face predation once more – but in landscapes profoundly altered by human activity. This shift raises crucial questions about their capacity to express adaptive antipredator behaviours. Using a quasi-experimental camera-trap design, we examined diel activity responses of ungulates along the ongoing wolf recolonisation in the south-eastern Alps. Red deer showed higher summer diurnality in sites with a longer history of wolf presence (7% increase over five years, on average) and progressively reduced nocturnality within sites as local wolf establishment advanced (5% decrease per year, on average), also heightening activity overlap with humans. This 'diel shield effect' disappeared when human hunting occurred. Roe deer and Alpine chamois did not exhibit significant diel activity shifts in relation to wolves, though both species responded to human disturbance, with roe deer adjusting activity to hunting (18% less diurnal, on average) and chamois reducing diurnality in areas of intense outdoor use (up to 38% difference in diurnality between undisturbed and highly disturbed areas). Red deer, too, were less diurnal (up to 27% difference) and more nocturnal (up to 37% difference) in such highly disturbed areas, as well as near human settlements (up to 42% difference in diurnality between remote areas and villages). Our findings show that wolf recovery can induce

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detectable diel activity shifts in large herbivores over relatively short timescales, yet responses depend on species biology and behavioural plasticity. Importantly, human risk and disturbance can offset or override these behavioural adjustments, potentially altering the ecosystemic effects of returning large carnivores.

Keywords: antipredator behaviour, diel activity, human disturbance, human shield effect, hunting, wolf recolonisation

Introduction

Large carnivores are returning to their historical ranges throughout Europe (Chapron et al. 2014) and North America (Gompper et al. 2015), decades, and even centuries after their extirpation by humans (Estes et al. 2011). Classical predator–prey theory (Sih 1980, Lima and Dill 1990) poses that predation risk can induce antipredator responses in their prey (Curio 1993, Caro and Girling 2005), which may be expressed in the context of predator recolonisation, too. However, in highly anthropogenic landscapes, the extent to which large carnivores can exert their ecological functions remains questioned (Dorresteijn et al. 2015), as anthropogenic pressures not only strongly affect the behaviour of large herbivores and large carnivores, but they also interfere with the predator–prey interactions (Kuijper et al. 2015, Wilson et al. 2020). Indeed, functioning as ‘super-predators’ (Darimont et al. 2015, Suraci et al. 2019), humans can trigger strong antipredator behaviours in mammals (Potratz et al. 2024), especially when human disturbance (Frid and Dill 2002) is combined with lethal activity (Ciuti et al. 2012, Courbin et al. 2022). Such human-induced behaviours include spatial avoidance (Corradini et al. 2024), disrupted movement (Tucker et al. 2018, Doherty et al. 2021), and increased nocturnality (Gaynor et al. 2018). Within ecological communities, these one-on-one influences can create complex three-way interactions between humans, predators, and prey. On one hand, a growing body of literature reports that humans have a greater impact on prey species, whether through changes in behaviour (Proffitt et al. 2009, Ciuti et al. 2012, Clinchy et al. 2016, Proudman et al. 2021, van Beeck Calkoen et al. 2022) or physiology (Zbyryt et al. 2018). In some cases, human hunters can even facilitate natural predation when hunter avoidance increases prey exposure to predators (Gehr et al. 2018), or increase predator kill rates by creating fear so that predators abandon carcasses sooner (Smith et al. 2015). On the other hand, prey may prefer human presence over that of natural predators when the mortality risk associated with humans is lower, thus creating a ‘human shield effect’ (Berger 2007), which can be spatial (Leighton et al. 2010, Muhly et al. 2011), temporal (Van Scoyoc et al. 2023, Bassing et al. 2024), or spatiotemporal (Lamichhane et al. 2023).

When large carnivores are absent for long periods over a large geographical area, prey may become less sensitive to these predators, hence less prone to adopting effective antipredator behaviours (Lahti et al. 2009). During natural recolonisation, prey may be especially vulnerable to initial predator encounters (Berger 1999). For example, the hunting success of recolonising brown bears *Ursus arctos* and grey wolves *Canis lupus* on moose *Alces alces* was higher at the edge of their recolonisation front than in the centre of their range (Berger et al. 2001) or areas of continuous presence (Sand et al. 2006), respectively. On the other hand, the ability of prey species to detect and recognise predators may persist throughout their absence (Coss 1999, Blumstein 2006, Carthey and Banks 2016); for example, under experimental conditions, black-tailed deer *Odocoileus hemionus sitkensis* (Chamaillé-Jammes et al. 2014), fallow deer *Dama dama* (Sahlén et al. 2016), and Père David’s deer *Elaphurus davidianus* (Li et al. 2011) responded to olfactory, auditory, or visual cues of their co-evolved predators despite decade- to century-long absences. However, the resumption of adaptive antipredator behaviours themselves may require selection over the course of several prey-generations (Flecker 1992) and/or individual relearning across lifetimes (Berger et al. 2001, Laundré et al. 2001, Mao et al. 2005). The latter may occur in species with high behavioural flexibility and plasticity, as seen in generalist species or species that have evolved in highly unpredictable environments (Gabriel et al. 2005, Sih et al. 2011).

Modifying diel activity could be a first plastic response to a novel threat. Even before modifying habitat selection, temporal avoidance of predators can effectively minimise encounter probabilities without limiting access to favourable (but risky; Lima and Dill 1990, Brown et al. 1999) habitats. Diel adjustments to avoid humans and natural predators are common across mammalian taxa (Fenn and Macdonald 1995, Cunningham et al. 2019), with diel activity shifts towards nocturnality being particularly widespread to avoid both human disturbance (Gaynor et al. 2018, Burton et al. 2024, Smith et al. 2024) and human lethality (Kilgo et al. 1998, Sönnichsen et al. 2013, Oriol-Cotterill et al. 2015, Patten et al. 2019, Frey et al. 2022). Previous research has shown that large herbivores experiencing simultaneous lethal risk from humans and nocturnal or crepuscular large carnivores face a diel exposure tradeoff, as both influence prey diel activity, with a marked dominance of human-related effects (Crosmary et al. 2012, Bonnot et al. 2020). However, the dynamics of these complex three-way interactions remain understudied, especially during the natural recolonisation of predators, where initial prey naïveté may elicit extreme responses to newly arrived predators. The timing and dynamics of these behavioural modifications in anthropogenic landscapes is indeed difficult to assess, as it ideally requires experimental or quasi-experimental study designs (Butsic et al. 2017, Montgomery et al. 2019, Peacor et al. 2022) which explicitly take human activity and presence into account (Kuijper et al. 2016, Fardell et al. 2021).

We studied three sympatric ungulates with contrasting ecologies: red deer *Cervus elaphus* (70–200 kg), roe deer *Capreolus capreolus* (18–28 kg), and Alpine chamois *Rupicapra rupicapra* (25–45 kg; Mustoni et al. 2002). Red deer are gregarious mixed feeders, roe deer tend to be more solitary concentrate selectors, and chamois are gregarious, mountain specialist mixed feeders, adapted to rugged high-elevation terrain (ca 1500–2500 m) (von Elsner-Shack 1985, Hofmann 1989). In the Alps, red and roe deer often exhibit partial altitudinal migration between summer alpine meadows and winter valleys (Cagnacci et al. 2011, 2024), while chamois can shift seasonally between high grasslands and lower, south-facing wintering slopes (Corlatti et al. 2021, 2022). All three are game species and confirmed wolf prey in the study area (Ferretti unpubl.).

Here, we took advantage of the ongoing natural recolonisation of the grey wolf in the Alps (Groff et al. 2019, since 2017 in our study area) (Fig. 1A–B) nearly 150 years after its extinction in this area (Ramponi 1923, 1928, Comincini 2002, Calabrese 2015). We developed a community-level study within a quasi-experimental design to examine the diel activity allocation of red deer, roe deer, and Alpine chamois in response to simultaneous risks from wolves and humans along a temporal gradient of recent wolf recolonisation (Fig. 2). Using camera-traps placed in four study sites along this gradient, we hypothesised that (H1) in the absence of human hunters, increasing prey exposure to wolves causes a shift in ungulate diel activity, decreasing nocturnal activity and increasing diurnal activity ('diel shield effect' hypothesis), but that (H2) in the presence of both (diurnal) human hunters and (nocturnal) wolves, ungulate diel activity is more strongly influenced by human hunting than by wolf presence, leading to an overall decrease in diurnality (Fig. 2). Given the perceptive and cognitive abilities of ungulates (Caicoya et al. 2021, Ranc et al. 2021, Schaffer et al. 2024), we expected the diel activity shift in response to wolf recolonisation to be detectable within less than a decade of gradual recolonisation and to persist in time, based on direct perception of risk (Fraker 2009) and working memory (Bracis et al. 2018). We also hypothesised that (H3) species-specific traits would shape the magnitude of diel responses to novel and multiple risk sources, with habitat generalists (red deer and roe deer) – characterised by high behavioural plasticity – responding more strongly than the mountain specialist Alpine chamois (Gabriel et al. 2005, Sih et al. 2011; Fig. 2).

Material and methods

Study sites and quasi-experimental study design

The study area was located in the Italian Alps, specifically in the Regions of Lombardy and Trentino-Alto Adige/Südtirol, including the Stelvio National Park (IUCN category II). Here, rugged mountainous terrain (900–3905 m a.s.l.)

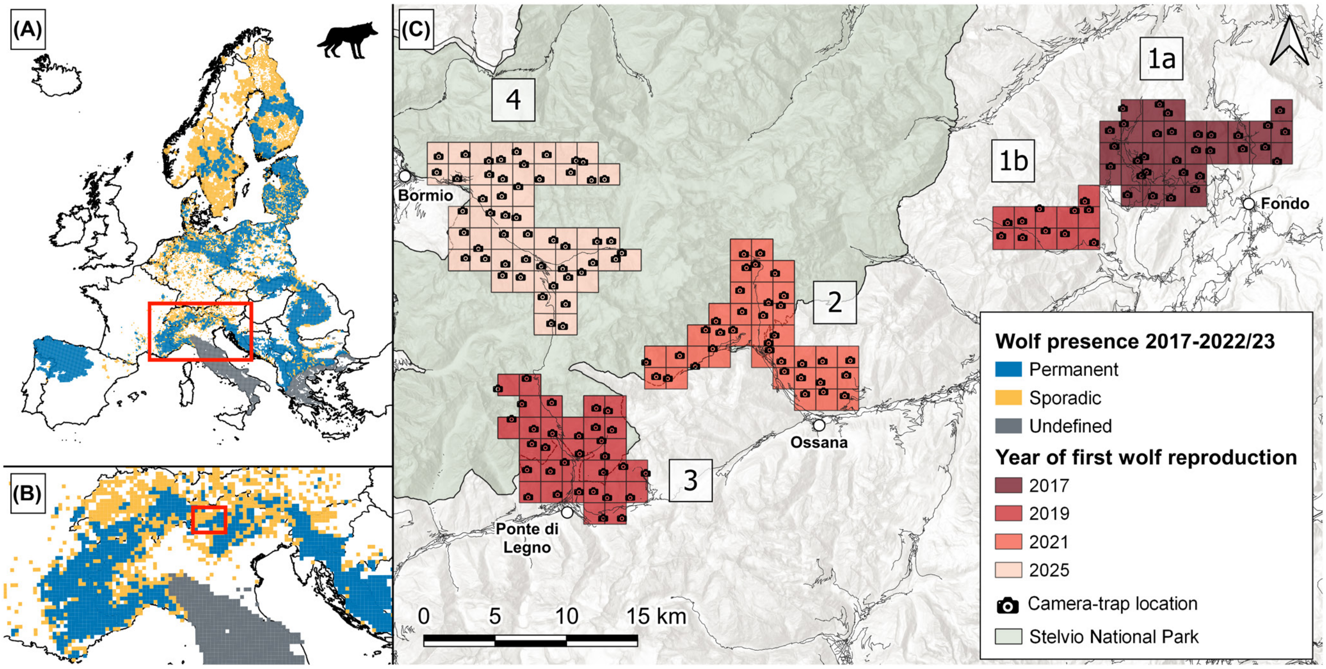

Figure 1. Quasi-experimental study design of camera-trap monitoring along the wolf recolonisation front in the south-eastern Alps, Italy. Wolf distribution at European (A) and Alpine (B) scales for the period 2017–2022/23 (Kaczensky et al. 2024); permanent, occasional, and undefined (i.e. presence is established but its status is unclear) presences are indicated in dark blue, dark yellow, and grey, respectively; the red frames indicate the Alpine region (A) and the location of the study areas therein (B). Four study areas (C) represent a temporal gradient since first wolf reproduction; shades of red indicate year of first wolf reproduction (from right to left: 1a) Upper Non Valley (2017); 1b) Bresimo Valley (2019); 2) Peio Valley (2021); 3) Tonale Pass (2019); and 4) Valfurva (2025)). Light green indicates the extent of Stelvio National Park.

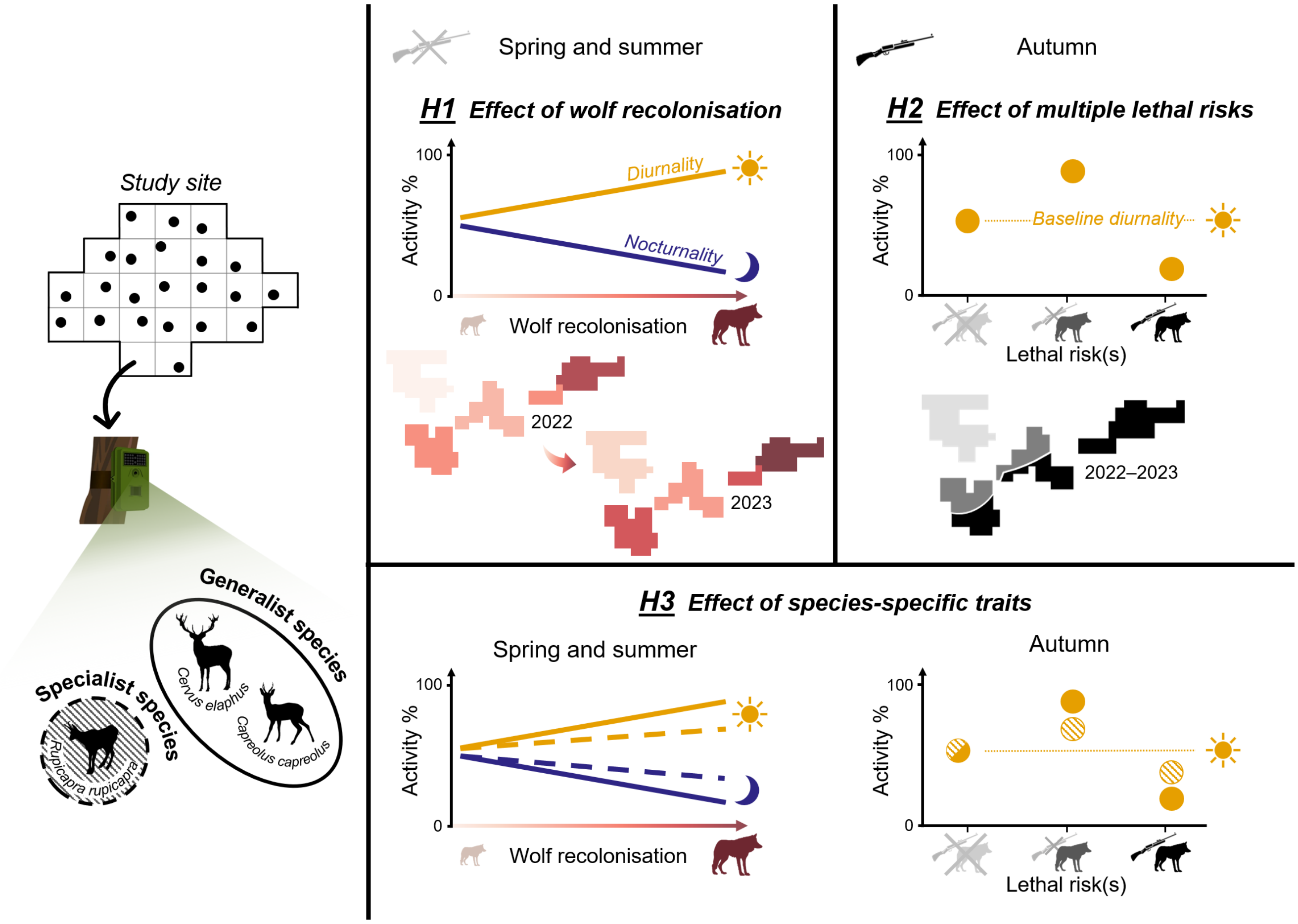

Figure 2. Schematic representation of the overall framework of our camera-trap study design and analysis, including the expected findings per hypothesis (H1–H3), for ungulate responses to wolf recolonisation gradients, and hunting. H1: wolf recolonisation measured as space-for-time across sites and time-for-time within sites (shades of red; 2022 versus 2023); H2: gradient of lethal risk across sites (shades of grey; both 2022 and 2023); H3: expected responses for generalist (continuous lines, full shapes) and specialist (dashed lines, striped shapes) ungulate species.

features alpine pastures at higher elevations and coniferous forests with managed meadows at lower altitudes. The large ungulate community includes herbivores such as red deer, roe deer, and chamois, which have rebounded following a population bottleneck after WWII, notably increasing since the 1950s (Passoni et al. 2024). Taking advantage of the ongoing natural wolf recovery in the Alps (Groff et al. 2019), we designed a quasi-experimental study (Fig. 1) – using a non-randomised but structured approach to analyse changes in time and space (Butsic et al. 2017, Siegel and Dee 2025) – with four study sites (total area 355.5 km^2; mean 88.9 km^2 [range 69.75–112.5]) within a single continuous ecosystem, chosen for similar landscape characteristics and ungulate occurrence (Corlatti et al. 2019, Cagnacci et al. 2024, Cagnacci and Nicoloso 2025, Vanderlocht et al. 2025a). The sites spanned a temporal gradient of wolf recolonisation, with reproductive wolf pairs established in 2017, 2019, 2021, and 2025 (Fig. 1, Supporting information). As the study was repeated for two consecutive years (2022 and 2023), our quasi-experimental design integrated a space-for-time substitution (between sites) and a time-for-time component within sites (Fig. 2). Hunting is restricted to areas outside Stelvio National Park (established in 1935; Fig. 1, 2) and to the legal season (in place since the second half of the 20th century, see the Supporting information).

Standardised camera-trapping

The study area was divided into 158 gridcells (1.5 × 1.5 km each), grouped into four sites, with one camera-trap randomly placed in each cell (Fig. 1). We followed a standardised protocol to maximise homogeneity of detection rates and ranges (50 cm height, north-facing, unbaited; see the Supporting information for details). From May to October 2022–2023, motion-triggered cameras operated with minimal inactivity delays (1–5 s, depending on the model). Regular field checks were conducted to replace battery and SD cards.

Each camera-trap media file was annotated using the software Timelapse (https://timelapse.ucalgary.ca; Greenberg et al. 2019), yielding a dataset of all sighted species per camera-trap location and timestamp.

Independent ungulate trapping events

To aggregate consecutive animal trapping events into independent events, we applied a data-driven maximum likelihood approach to determine species-specific time-to-independence thresholds (red deer, roe deer, chamois). Specifically, we used the bout-ending criterion (Luque and Guinet 2007), fitting a mixture of two Poisson processes to time intervals between camera sightings, assuming a 'fast' process for closely triggered, non-independent images, and a 'slow' process for truly independent events at the camera-trap site (Supporting information). We determined the 'time-to-independence criterion' as the most likely minimum time period needed to distinguish two independent camera-trap events, constraining the search space broadly between 1 min and 12 h to avoid bias and facilitate computation, using the 'diveMove' R package (Luque 2024).

This approach enabled us to ensure data independence in the statistical analysis, while remaining sensitive to the different biologies of the species (e.g. sociality, speed of movement and recursion frequency).

Diel activity modelling

We aimed to investigate the diel activity of ungulates in response to wolf recolonisation and hunting, without specifically considering total activity per se. As such, we used multinomial logistic regressions to estimate the probabilities of any given independent trapping event being diurnal or nocturnal with respect to being crepuscular (where crepuscularity was considered the reference; Georgii and Schröder 1983, Pachlatko and Nievergelt 1985, Pagon et al. 2013, Ensing et al. 2014), as a function of the risk from wolves and/or hunters, and other control variables.

Accounting for variation in sunrise and sunset times across the year, each camera-trap event was classified as crepuscular (2-h intervals centred around sunset and sunrise), diurnal (1 h after sunrise to 1 h before sunset) and nocturnal (1 h after sunset to 1 h before sunrise) using the 'suncalc' R package (Thieurmel and Elmarhraoui 2022).

Effect of gradual wolf recolonisation (H1 and H3)

Firstly, we investigated the effects of wolf recolonisation on ungulate diel activity through time during spring (May–June) and summer (July–August). To capture a biologically meaningful proxy for gradual and cumulative prey exposure to wolves, we used the year of first wolf reproduction as a reference point in the recolonisation process. This event was reliably detected across the study area, independently of monitoring effort, and marks stable territorial establishment together with an increase in predation rate (Sand et al. 2008). We also acknowledge that wolves may be present prior to reproduction, e.g. transient individuals or non-reproductive pairs (Åkesson et al. 2022). Because ungulates may respond throughout these stages, we expressed time as a continuous variable, with 0 denoting first reproduction and negative values indicating years prior to this milestone (−3 to +6 years; Fig. 1). First reproduction was determined using ongoing opportunistic camera-trapping and genetic monitoring (Marucco et al. 2022, Groff et al. 2024).

For each species (red deer, roe deer, and chamois), we modelled the relative probability of any trapping event being diurnal or nocturnal versus crepuscular ('mclogit' R package; Elff 2022) as a function of the time since first wolf reproduction (H1), while accounting for possible interactions with season, and controlling for tree cover density (European Environment Agency 2012), slope (Tarquini et al. 2023), minimum distance to human settlements (Marsoner et al. 2023), and the cumulated outdoor activity index (Corradini et al. 2021; Supporting information). Identical model structures were applied to each ungulate species in order to identify species-specific differences (H3).

To account for confounding among time since first wolf reproduction (TWR), study sites, and years, we decomposed TWR into a between-site mean (space-for-time gradient) and a within-site deviation (time-for-time signal). Shared annual shocks (e.g. climatic variability) were modelled through year fixed effects, while random intercepts for site and camera-trap location captured residual spatial heterogeneity. This modelling strategy (see Table 1 for the model equation, and the Supporting information for detailed model description) – combining a group mean centering and fixed effects approach (Mundlak 1978, Van De Pol and Wright 2009, Wooldridge 2010, Byrnes and Dee 2025) – mitigates endogeneity in the within-site signal, improves inference for between-site differences, and overall helps move closer towards causal interpretation (Dee et al. 2023, Wu et al. 2023, Byrnes and Dee 2025, Siegel and Dee 2025).

Effect of multiple lethal risks (H2 and H3)

Secondly, we focused on the autumn hunting period (September–October) to model the relative probability of any trapping event being diurnal or nocturnal versus crepuscular ('mclogit' R package; Elff 2022) as a function of potential lethal risk(s) – namely no lethal risk, only wolf, wolf and hunting (H2) – controlling for vegetational variability (tree cover density) as a fixed effect, as our sample size was too limited for a more complex model structure. To account for baseline spatial and temporal variations, we added study sites, camera-trap locations, and years as random intercepts in the models. Continuous explanatory variables were scaled and centred. Identical model structures were applied to each ungulate species in order to identify species-specific differences (H3).

For all models (H1–3), we verified the performance of each model and fit quality by computing Nagelkerke's pseudo-R^2 (Nagelkerke 1991) and other performance indices (Supporting information; 'performance' R package; Lüdecke et al. 2024). We checked for variable correlation a priori (rho < |0.4|; Supporting information).

We tested for each predictor whether it improved model fit using likelihood-ratio χ^2 tests of nested models (χ^2, p_{LRT}, Table 1, 2). For each predictor significantly improving model fit (and only those), we reported the level-specific parameter

Table 1. Odd ratios with 95% confidence intervals and β estimates with standard errors for diurnal activity (day versus crepuscule) and nocturnal activity (night versus crepuscule) of red deer, roe deer, and Alpine chamois in spring and summer, in relation to between-site and within-site variation in time since first wolf reproduction (TWR), season of the year (reference: spring), year, and a set of environmental covariates. Overall significance of each predictor was evaluated using likelihood-ratio χ^2 tests of nested models (χ^2, p_{LRT}). When a predictor significantly improved model fit ($p < 0.05$), the level-specific Wald p-values (p_{Wald}) for categories relative to the baseline are reported. Significant effects ($p < 0.05$) are highlighted in bold. Test values for single terms involved in significant interactions are not shown, as their interpretation is not meaningful in isolation. The rightmost columns report the number of grid cells in which each species was observed, the total number of observations, and Nagelkerke's pseudo-R² (Nagelkerke 1991). The models' formula is reported in the first row of the table.

$$\text{Dielactivity} \sim \text{TWR}^{\text{Between}} + \text{TWR}^{\text{Within}} + \left(\text{TWR}^{\text{Between}} + \text{TWR}^{\text{Within}}\right) \times \text{Season} + \text{Season} + \text{Year} + \text{TCD} + \text{Slope} + \text{distHumSett} + \text{dCOI} + 1|\text{site} + 1|\text{gridcell}$$

	Day			Night							
Predictors	OR [95% CI]	β ± SE	p_{Wald}	OR [95% CI]	β ± SE	p_{Wald}	χ^2	p_{LRT}	Gridcells	Obs.	Nagelkerke's pseudo-R²
Red deer *Cervus elaphus*											
(Intercept)	0.69 [0.42; 1.13]	−0.37 ± 0.25	0.143	0.54 [0.34; 0.88]	−0.61 ± 0.24	0.012	-	-	152	7341	0.30
Between-site TWR (scaled and centred) **× Season (summer)**	**1.16 [1.01; 1.33]**	**0.14 ± 0.07**	**0.039**	0.95 [0.84; 1.08]	−0.05 ± 0.06	0.445	**6.58**	**0.037**			
Within-site TWR (scaled and centred) × season (summer)	1.21 [1.06; 1.38]	0.19 ± 0.07	-	1.15 [1.01; 1.30]	0.14 ± 0.06	-	4.27	0.118			
Between-site variation in time since wolf recolonisation ($\text{TWR}^{\text{Between}}$) (scaled and centred)	1.19 [0.75; 1.86]	0.17 ± 0.23	-	1.20 [0.77; 1.87]	0.19 ± 0.23	-	6.48	0.166			
Within-site variation in time since wolf recolonisation ($\text{TWR}^{\text{Between}}$) (scaled and centred)	0.83 [0.64; 1.08]	−0.19 ± 0.13	0.161	**0.78 [0.62; 0.99]**	**−0.25 ± 0.12**	**0.041**	**12.77**	**0.012**			
Season (summer)	0.55 [0.48; 0.63]	−0.60 ± 0.07	-	1.53 [1.35; 1.73]	0.42 ± 0.06	-	-	-			
Year (2023)	1.47 [0.93; 2.30]	0.38 ± 0.23	-	1.17 [0.79; 1.75]	0.16 ± 0.20	-	−4.27	1.000			
Tree cover density (TCD) (scaled and centered)	**1.28 [1.05; 1.56]**	**0.25 ± 0.10**	**0.015**	0.87 [0.73; 1.03]	−0.14 ± 0.09	0.112	**7.40**	**0.025**			
Slope (scaled and centered)	1.04 [0.87; 1.26]	0.04 ± 0.09	-	0.92 [0.78; 1.08]	−0.09 ± 0.08	-	1.30	0.521			
Distance from human settlements (distHumSett) (scaled and centered)	**1.45 [1.19; 1.76]**	**0.37 ± 0.10**	**< 0.001**	0.91 [0.77; 1.08]	−0.09 ± 0.09	0.303	**12.21**	**0.002**			
Density cumulated outdoor activity Index (dCOI) (scaled and centered)	**0.76 [0.63; 0.91]**	**−0.28 ± 0.09**	**0.004**	**1.22 [1.05; 1.40]**	**0.20 ± 0.07**	**0.007**	**13.88**	**< 0.001**			
Roe deer *Capreolus capreolus*											
(Intercept)	1.83 [0.88; 3.77]	0.60 ± 0.37	0.103	0.44 [0.26; 0.73]	−0.82 ± 0.26	0.001	-	-	117	2,439	0.22
Between-site TWR (scaled and centered) × Season (summer)	1.06 [0.86; 1.31]	0.06 ± 0.11	-	0.74 [0.55; 1.01]	−0.29 ± 0.16	-	5.83	0.054			

(*continued*)

Table 1. Continued.

$\text{Dielactivity} \sim \text{TWR}^{\text{Between}} + \text{TWR}^{\text{Within}} + \left(\text{TWR}^{\text{Between}} + \text{TWR}^{\text{Within}}\right) \times \text{Season} + \text{Season} + \text{Year} + \text{TCD} + \text{Slope} + \text{distHumSett} + \text{dCOI} + 1|\text{site} + 1|\text{gridcell}$

	Day			Night							
Predictors	OR [95% CI]	β ± SE	p_{Wald}	OR [95% CI]	β ± SE	p_{Wald}	χ^2	p_{LRT}	Gridcells	Obs.	Nagelkerke's pseudo-R^2
Within-site TWR (scaled and centered) × season (summer)	0.84 [0.68; 1.05]	−0.17 ± 0.11	-	1.02 [0.76; 1.37]	0.02 ± 0.15	-	3.20	0.202			
Between-site variation in time since wolf recolonisation ($\text{TWR}^{\text{Between}}$) (scaled and centered)	0.94 [0.44; 2.03]	−0.06 ± 0.39	-	1.45 [0.89; 2.38]	0.38 ± 0.25	-	6.65	0.156			
Within-site variation in time since wolf recolonisation ($\text{TWR}^{\text{Between}}$) (scaled and centered)	0.98 [0.74; 1.29]	−0.02 ± 0.14	-	1.05 [0.73; 1.51]	0.05 ± 0.19	-	6.05	0.195			
Season (summer)	**0.66 [0.54; 0.81]**	**−0.41 ± 0.11**	**< 0.001**	**1.82 [1.37; 2.43]**	**0.60 ± 0.15**	**< 0.001**	**59.29**	**< 0.001**			
Year (2023)	1.22 [0.81; 1.82]	0.20 ± 0.21	-	0.76 [0.46; 1.27]	−0.27 ± 0.26	-	3.54	0.171			
Tree cover density (TCD) (scaled and centered)	1.15 [1.00; 1.32]	0.14 ± 0.07	0.054	0.91 [0.79; 1.06]	−0.09 ± 0.26	0.226	**7.87**	**0.020**			
Slope (scaled and centered)	1.07 [0.94; 1.23]	0.07 ± 1.00	0.313	**0.84 [0.72; 0.97]**	**−0.18 ± 0.08**	**0.019**	**8.25**	**0.016**			
Distance from human settlements (distHumSett) (scaled and centered)	0.99 [0.85; 1.14]	−0.01 ± 0.08	-	1.04 [0.89; 1.21]	0.04 ± 0.08	-	0.31	0.857			
Density cumulated outdoor activity index (dCOI) (scaled and centered)	0.89 [0.75; 1.06]	−0.11 ± 0.09	-	1.05 [0.88; 1.25]	0.05 ± 0.09	-	1.90	0.388			
Alpine chamois *Rupicapra rupicapra*											
(Intercept)	2.77 [1.54; 5.01]	1.02 ± 0.30	0.001	0.24 [0.11; 0.53]	−1.42 ± 0.40	< 0.001	-	-	102	1,085	0.50
Between-site TWR (scaled and centered) × Season (summer)	1.25 [0.92; 1.70]	0.22 ± 0.16	-	1.40 [0.80; 2.45]	0.34 ± 0.28	-	−0.78	1.000			
Within-site TWR (scaled and centered) × Season (summer)	1.11 [0.82; 1.49]	0.1 ± 0.15	-	0.93 [0.54; 1.60]	−0.07 ± 0.28	-	0.73	0.694			
Between-site variation in time since wolf recolonisation ($\text{TWR}^{\text{Between}}$) (scaled and centered)	1.09 [0.70; 1.69]	0.08 ± 0.023	-	0.74 [0.43; 1.26]	−0.31 ± 0.27	-	6.72	0.152			

(*continued*)

Table 1. Continued.

$\text{Dielactivity} \sim \text{TWR}^{\text{Between}} + \text{TWR}^{\text{Within}} + \left(\text{TWR}^{\text{Between}} + \text{TWR}^{\text{Within}}\right) \times \text{Season} + \text{Season} + \text{Year} + \text{TCD} + \text{Slope} + \text{distHumSett} + \text{dCOI} + 1|\text{site} + 1|\text{gridcell}$

Predictors	Day			Night							
	OR [95% CI]	$\beta \pm$ SE	p_{Wald}	OR [95% CI]	$\beta \pm$ SE	p_{Wald}	χ^2	p_{LRT}	Gridcells	Obs.	Nagelkerke's pseudo-R^2
Within-site variation in time since wolf recolonisation ($\text{TWR}^{\text{Between}}$) (scaled and centered)	1.04 [0.71; 1.52]	0.04 ± 0.19	-	1.22 [0.59; 2.54]	0.20 ± 0.37	-	1.00	0.909			
Season (summer)	0.94 [0.70; 1.27]	−0.06 ± 0.15	-	1.76 [1.03; 3.01]	0.57 ± 0.27	-	5.93	0.431			
Year (2023)	0.89 [0.45; 1.78]	−0.11 ± 0.35	-	0.67 [0.20; 2.20]	−0.41 ± 0.61	-	0.35	0.837			
Tree cover density (TCD) (scaled and centered)	1.16 [0.93; 1.46]	0.15 ± 0.11	-	1.19 [0.88; 1.61]	0.17 ± 0.16	-	−1.24	1.000			
Slope (scaled and centered)	0.92 [0.75; 1.12]	−0.09 ± 0.10	-	1.23 [0.91; 1.66]	0.21 ± 0.15	-	3.71	0.157			
Distance from human settlements (distHumSett) (scaled and centered)	0.95 [0.77; 1.17]	−0.06 ± 0.11	-	0.94 [0.69; 1.28]	−0.06 ± 0.16	-	0.34	0.843			
Density cumulated outdoor activity index (dCOI) (scaled and centered)	**0.77 [0.63; 0.93]**	**−0.27 ± 0.10**	**0.006**	1.23 [0.96; 1.58]	0.21 ± 0.13	0.099	**11.68**	**0.003**			

Table 2. Odd ratios with 95% confidence intervals and β estimates with standard errors for diurnal activity (day versus crepuscule) and nocturnal activity (night versus crepuscule) of red deer, roe deer, and Alpine chamois in autumn, in relation to different scenarios of lethal risk(s) (reference: only wolf) and tree cover density. Overall significance of each predictor was evaluated using likelihood-ratio χ^2 tests of nested models (χ^2, p_{LRT}). When a predictor significantly improved model fit ($p < 0.05$), the level-specific Wald p-values (p_{Wald}) for categories relative to the baseline are reported. Significant effects ($p < 0.05$) are highlighted in bold. The rightmost columns report the number of grid cells in which each species was observed, the total number of observations, and Nagelkerke's pseudo-R^2 (Nagelkerke 1991). The models' formula is reported in the first row of the table.

Dielactivity ~ Lethalrisk + TCD + 1|area + 1|gridcell + 1| year

	Day			Night							
Predictors	OR [95% CI]	β ± SE	p_{Wald}	OR [95% CI]	β ± SE	p_{Wald}	χ^2	p_{LRT}	Gridcells	Obs.	Nagelkerke's pseudo-R^2
Red deer *Cervus elaphus*											
(Intercept)	0.73 [0.40; 1.31]	−0.32 ± 0.30	0.287	0.92 [0.42; 1.99]	−0.09 ± 0.39	0.828	-	-	146	4275	0.30
Lethal risk (none)	**0.45 [0.21; 0.97]**	**−0.80 ± 0.39**	**0.041**	0.94 [0.38; 2.28]	−0.07 ± 0.46	0.884	**16.55**	**0.002**			
Lethal risk (wolf and hunting)	**0.58 [0.34; 0.97]**	**−0.55 ± 0.26**	**0.039**	**1.84 [1.14; 2.95]**	**0.61 ± 0.24**	**0.012**					
Tree cover density (TCD) (scaled and centred)	1.08 [0.88; 1.31]	0.07 ± 0.10	-	1.02 [0.86; 1.22]	0.02 ± 0.09	-	−1.04	1.000			
Roe deer *Capreolus capreolus*											
(Intercept)	1.75 [0.86; 3.53]	0.56 ± 0.36	0.121	1.01 [0.50; 2.01]	0.01 ± 0.35	0.987	-	-	99	1219	0.10
Lethal risk (none)	0.67 [0.30; 1.51]	−0.40 ± 0.41	0.335	0.90 [0.40; 2.03]	−0.11 ± 0.41	0.798	**11.36**	**0.023**			
Lethal risk (wolf and hunting)	**0.38 [0.19; 0.73]**	**−0.98 ± 0.34**	**0.004**	1.09 [0.56; 2.11]	0.09 ± 0.34	0.798					
Tree cover density (TCD) (scaled and centred)	1.08 [0.86; 1.36]	0.08 ± 0.12	-	1.02 [0.82; 1.28]	0.02 ± 0.11	-	−4.36	1.000			
Alpine chamois *Rupicapra rupicapra*											
(Intercept)	1.71 [0.66; 4.42]	0.53 ± 0.48	0.270	0.58 [0.21; 1.60]	−0.54 ± 0.51	0.293	-	-	58	402	0.17
Lethal risk (none)	0.63 [0.20; 1.96]	−0.46 ± 0.58	-	1.14 [0.35; 3.74]	0.13 ± 0.60	-	−0.77	1.000			
Lethal risk (wolf and hunting)	1.10 [0.35; 3.40]	0.09 ± 0.58	-	1.34 [0.37; 4.88]	0.29 ± 0.66	-					
Tree cover density (TCD) (scaled and centered)	0.94 [0.61; 1.43]	−0.07 ± 0.22	-	0.91 0.56; 1.46]	−0.10 ± 0.24	-	−1.57	1.000			

estimates for each category (diurnal, nocturnal) relative to the baseline (crepuscular) as estimated slopes β with standard errors, Wald p-values (p_{Wald}), and odds ratios with 95% confidence intervals (Table 1, 2). Marginal conditional probabilities were extracted from the model outputs using the 'emmeans' R package (Lenth et al. 2024). All data processing and analyses were performed in R software (ver. 4.2.2; www.r-project.org).

Results

Time criterion for independent camera-trapping events

Camera-trap deployments resulted in 43 906 effective camera-days, yielding a total of 184 649 ungulate sightings, 507 wolf sightings, and 19 638 human sightings (excluding field operators). We estimated that consecutive images of red deer, roe deer, and chamois were most likely independent if separated by at least about 21, 16, and 20 minutes, respectively (Supporting information). After aggregating consecutive imagery into independent events based on this species-specific time criterion, we obtained 11 616 independent red deer trapping events, 3658 independent roe deer trapping events, and 1487 independent chamois trapping events across the entire study period. In autumn specifically, we obtained 4275 independent red deer, 1219 independent roe deer, and 402 independent chamois trapping events.

Diel activity allocation in response to time since wolf establishment and anthropogenic pressures (spring and summer, H1 and H3)

Red deer showed higher summer diurnality in sites with a longer history of wolf recolonisation ($\beta \pm SE = 0.14 \pm 0.07$, $p_{\mathrm{Wald}} = 0.039$), corresponding to an average 6.6% increase in diurnality between sites differing by five years in wolf establishment history (Fig. 3A). Within sites, red deer reduced nocturnality as local wolf establishment progressed ($\beta \pm SE = -0.25 \pm 0.12$, $p_{\mathrm{Wald}} = 0.041$), with nocturnal activity decreasing by an average of 4.9% per year (Fig. 3D). In contrast, roe deer and chamois did not show significant shifts in diel activity in relation to wolf establishment, either between sites or within sites (Fig. 3B–C, E–F). The fixed effect term for years did not show significant impact of broad yearly fluctuations on ungulate diel activity. Overall, roe deer were more nocturnal ($\beta \pm SE = 0.60 \pm 0.15$, $p_{\mathrm{Wald}} < 0.001$) and less diurnal ($\beta \pm SE = -0.41 \pm 0.11$, $p_{\mathrm{Wald}} < 0.001$) in summer compared to spring, and they were less nocturnal on steeper slopes ($\beta \pm SE = -0.18 \pm 0.08$, $p_{\mathrm{Wald}} = 0.019$). Red deer were more diurnal in areas of high tree cover density ($\beta \pm SE = 0.25 \pm 0.10$, $p_{\mathrm{Wald}} = 0.015$) and in areas further away from human settlements ($\beta \pm SE = 0.37 \pm 0.10$, $p_{\mathrm{Wald}} < 0.001$). Red deer were less diurnal and more nocturnal in areas of high outdoor activity use ($\beta \pm SE = -0.28 \pm 0.09$, $p_{\mathrm{Wald}} = 0.004$ and $\beta \pm SE = 0.20 \pm 0.07$, $p_{\mathrm{Wald}} = 0.007$). Chamois, too, were less diurnal in those highly disturbed areas ($\beta_{\mathrm{Cham}} \pm SE = -0.27 \pm 0.10$, $p_{\mathrm{Wald}} = 0.006$). Full model outputs are reported in Table 1, and environmental and anthropogenic effects can be visualised in the Supporting information.

Diel activity allocation in response to potentially co-occurring lethal risks during the hunting season (H2 and H3)

During the autumn hunting period, red deer were significantly less diurnal both where wolves and hunters were absent ($\beta \pm SE = -0.80 \pm 0.39$, $p_{\mathrm{Wald}} = 0.041$; probability of diurnality $P_{\mathrm{diurnality}} = 15.1\%$ on average) and where they co-occurred ($\beta \pm SE = -0.55 \pm 0.26$, $p_{\mathrm{Wald}} = 0.039$; $P_{\mathrm{diurnality}} = 13.7\%$), compared to where wolves were present but hunters were absent ($P_{\mathrm{diurnality}} = 27.8\%$; Fig. 4A). Red deer were also significantly more nocturnal in the additional presence of hunters ($\beta \pm SE = 0.61 \pm 0.24$, $p_{\mathrm{Wald}} = 0.012$), with average probabilities of nocturnality $P_{\mathrm{nocturnality}} = 39.3\%$ in the absence of wolves and hunters, 34.6% where only wolves were present, and 54.2% where both were present (Fig. 4A). Roe deer responded only to the presence of hunters ($\beta \pm SE = -0.98 \pm 0.34$, $p_{\mathrm{Wald}} = 0.004$), with average $P_{\mathrm{diurnality}}$ decreasing to 23.8% in the presence of both wolves and hunters, compared to 38.0% where neither were present and 46.3% where only wolves occurred (Fig. 4B). In contrast, chamois diel activity was not affected by lethal risk context (Fig. 4C). Full model outputs are reported in Table 2.

Discussion

Ungulates play a pivotal role in ecosystems, as prey, primary consumers, and nutrient cyclers (Pringle et al. 2023, Trepel et al. 2024). Understanding their behavioural responses to hunters and returning large carnivores is therefore fundamental to understanding how ecosystem dynamics may change in rewilding anthropogenic landscapes (Dorresteijn et al. 2015, Kuijper et al. 2016, Ausilio et al. 2021, Rahman and Candolin 2022). Our findings show that natural wolf recovery in the presence of human pressures can drive shifts in diel activity in a community of large herbivores, and that additional lethal risk from human hunters can substantially alter the outcome of this diel tradeoff. In partial support of our first hypothesis (H1), red deer exhibited higher summer diurnality across sites with a longer history of wolf recolonisation (+6.6% per 5-year difference; Fig. 3A), and within sites, they reduced nocturnality as local wolf presence increased over time (−4.9% per year; Fig. 3D). Increased diurnality occurred mainly in areas of lower disturbance and farther from infrastructure (Table 1), suggesting a 'diel shield effect' concurrent with fine-scale spatial avoidance. Interestingly, during the autumn hunting period, this 'diel shield effect' disappeared where human hunting occurred (Fig. 4A; support for H2). Roe deer did not respond to wolf recolonisation but reduced diurnality under human hunting (H2; Fig. 4B). Chamois showed no diel response to wolves or hunting but spatially avoided human activity during daytime. Differences in diel responses among these three sympatric ungulate species likely reflect a combination of species-specific traits, such as ecological generalism (H3), and the relative effectiveness of diel activity shifts as an antipredator strategy, which may depend on body size, sociality, or perceived risk of wolves and humans.

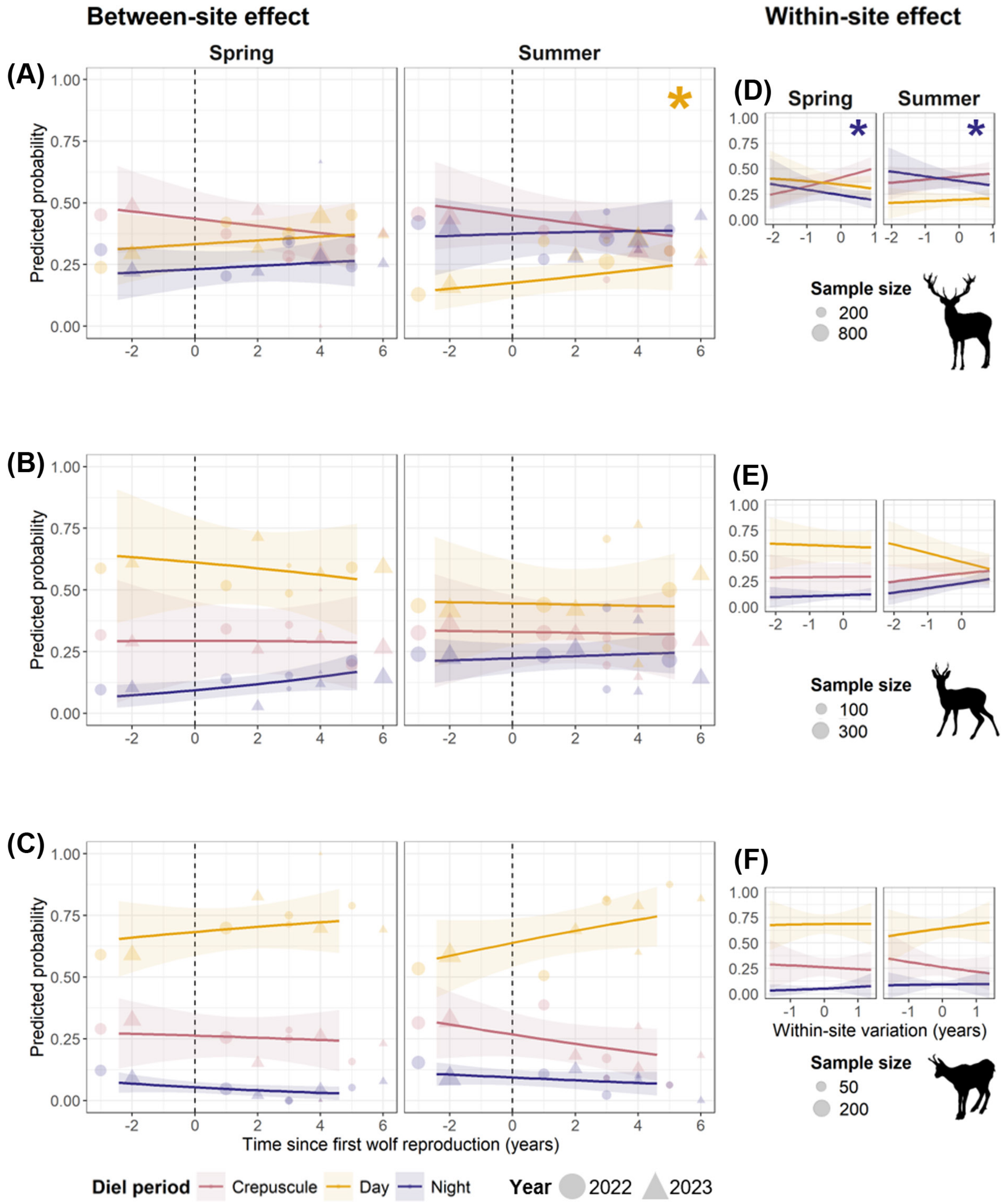

Figure 3. Predicted probabilities (using the 'emmeans' R package; Lenth et al. 2024) of crepuscularity (pink), diurnality (yellow), and nocturnality (blue), in response to between-site (A–C) and within-site (D–F) variation in time since wolf establishment, by season, for (A, D) red deer, (B, E) roe deer, and (C, F) Alpine chamois. Lines with shaded areas: model predictions (mean effect with 95% confidence intervals); dots and triangles: observed proportions from 2022 and 2023, respectively (symbol size indicating the relative number of observations). (A)–(C): 0 for the year of first wolf reproduction (vertical dashed line), negative values for years prior to wolf reproduction. (D)–(F): The x-axis shows deviations from each site's mean time since first wolf reproduction, with 0 representing the site-specific mean across the study period. All panels: an asterisk (*) denotes a significant effect of time since wolf establishment on predicted diel activity probabilities at α = 0.05.

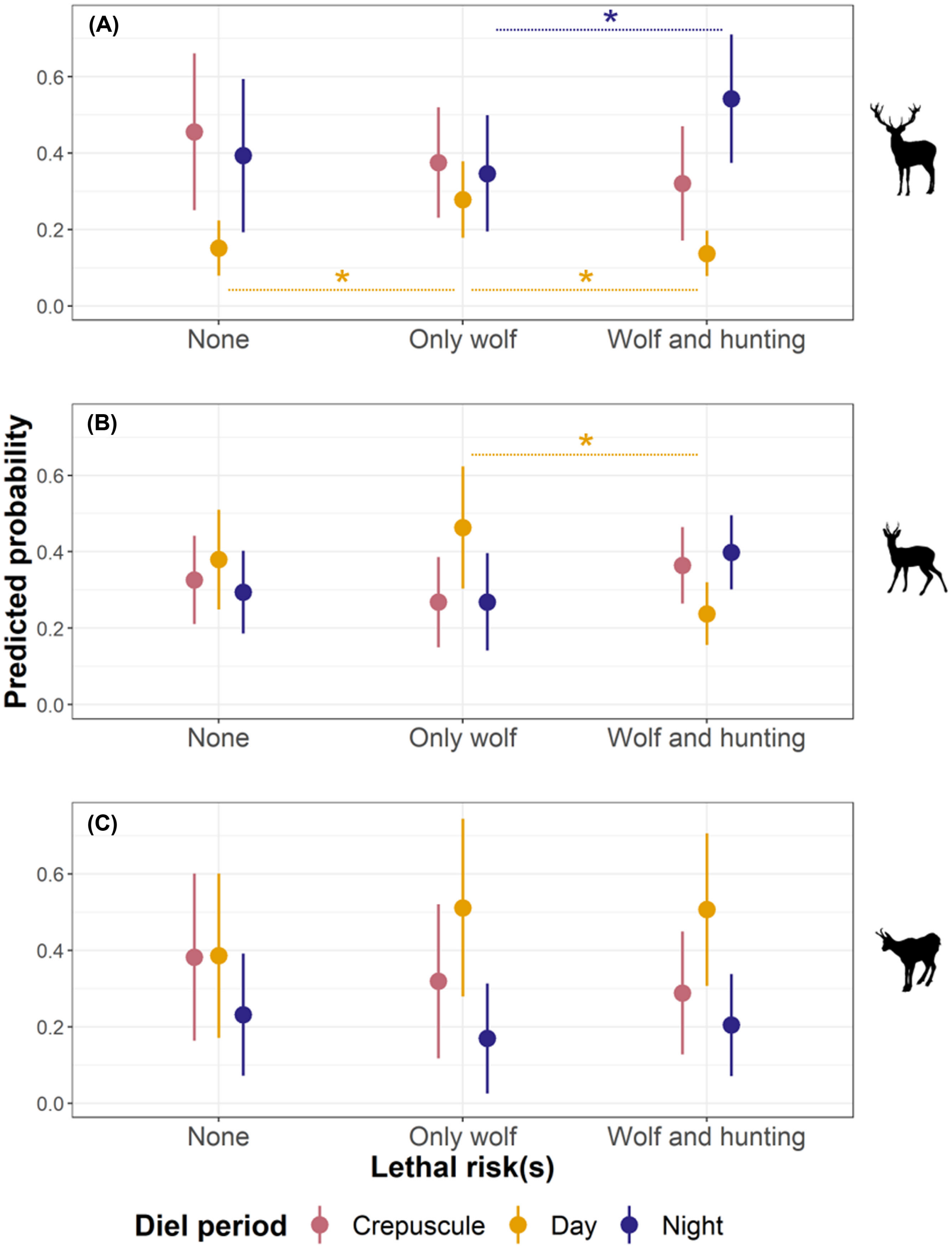

Figure 4. Predicted probabilities (with 95% confidence intervals; using the *'emmeans'* R package; Lenth et al. 2024) of crepuscularity (pink), diurnality (yellow), and nocturnality (blue) in (A) red deer, (B) roe deer, and (C) Alpine chamois, in response to no lethal risk, wolves only, or wolves and hunters. An asterisk (*) indicates a significant effect of the lethal risk scenario on predicted diel activity probabilities at $\alpha = 0.05$, with respect to the reference scenario ('Only wolf').

Diel activity shifts of red deer within less than a decade of wolf recolonisation

Given the typical nocturnal activity pattern of wolves (Merrill and Mech 2003) (Supporting information), decreasing nocturnal activity or increasing diurnal activity may represent adaptive strategies for prey species to minimise encounter probabilities. Our results, detected within less than a decade of gradual wolf recolonisation (between-site range < 8 years, within-site range < 3 years), suggest that diel responses may serve as an early behavioural strategy for ungulates facing novel threats (Lazzeri et al. 2024, Mirante et al. 2024). These responses may reflect behavioural plasticity, as well as the cognitive ability to process predator cues (and/or social signals and cues; Dall et al. 2005), anticipate diel patterns of risk (Bosiger et al. 2012), and exhibit adaptive antipredator behaviours consistently over time (Bracis et al. 2018, Heathcote et al. 2023). Given biological constraints on diel activity patterns (Kronfeld-Schor and Dayan 2003), we however expect diurnality levels of red deer to plateau in the near future once an optimal level compromising predator avoidance, resource acquisition, and other biological needs is reached.

Diverse (diel) antipredator responsiveness in an ungulate community

Species-specific traits likely explain some, but not all, of the observed differences among ungulates in responsiveness to wolf recolonisation. In particular, we tested ecological generalism as one species-specific trait, which is commonly associated with higher behavioural plasticity (Gabriel et al. 2005, Sih et al. 2011). Red deer had a lower baseline diurnality compared to roe deer and chamois (Fig. 3), which may have allowed for greater flexibility in diurnality shifts. Herd-level knowledge transfer may additionally confer adaptive advantages for facing recolonising large carnivores (Aureli et al. 2008, Caicoya et al. 2021). Roe deer, in contrast, are solitary and more elusive than red deer: their lack of diel response may be linked to the display of other antipredator strategies at different spatiotemporal scales, such as increased vigilance or modified space use (Benhaiem et al. 2008, Eccard et al. 2017). Alternatively, as a concentrate selector needing frequent feeding bouts (Hofmann 1989), roe deer diel flexibility may be more limited compared to mixed-feeders. Yet, roe deer populations coexisting with lynx (which predominantly prey on them) showed higher diurnal activity (Bonnot et al. 2020) – suggesting that prey–predator co-evolution plays a role in shaping current prey responses (Abom and Schwarzkopf 2016). Finally, if physiological constraints limit Alpine chamois' diel activity (e.g. heat exposure; Mason et al. 2014, Thel et al. 2024), they may instead rely on other anti-predatory strategies, such as habitat selection (e.g. steep slopes; von Elsner-Shack 1985, Anderwald et al. 2024). However, our conclusions about this species may also be limited by the limited sampling in steep, high-elevation grasslands due to logistical constraints (Supporting information).

Wolves are opportunistic carnivores (Newsome et al. 2016) that target high-profitability prey (Mech and Boitani 2007; see optimal foraging theory; Emlen 1966, MacArthur and Pianka 1966). Prey profitability (caloric gain, vulnerability, density, catchability, etc.) can be altered by predation, creating feedbacks between predator foraging decisions and prey antipredator responses (Prokopenko et al. 2023). In the Alps, wolves mainly feed on deer (Gazzola et al. 2005, Marucco et al. 2008), though primary reliance on chamois has also been reported (Palmegiani et al. 2013). At our study sites, preliminary results suggest red deer comprised 53–60% of wolf diet (Ferretti unpubl.), which may explain their stronger behavioural responsiveness (Stapley 2003, Lazzeri et al. 2024). However, focusing solely on predator diet limits understanding of prey behaviour (Creel and Christianson 2008); prey density, vulnerability changes, and indirect interactions (Abrams and Matsuda 1993, Matsuda et al. 1993) such as apparent competition (Holt 1977, Holt and Kotler 1987) or prey switching (Murdoch 1969, Garrott et al. 2007) also shape perceived risk and predator selectivity. These complex dynamics are often empirically studied from the predator's perspective (Becker et al. 2008, Mattioli et al. 2011, Tallian et al. 2017), but rarely from the prey's perspective and the drivers of antipredator decisions (but see Brown et al. 1999 for theory). By analysing concurrent responses within a prey guild exposed to predator recolonisation, our study provides a basis to discuss behavioural pathways linking antipredator responses to species traits. Further work should incorporate more species-specific information, such as prey density and predator impact, but also intra-guild interactions to rigorously test these dynamics.

'Diel human shield effect'... but also human avoidance

Red deer tended to be overall less diurnal and more crepuscular/nocturnal during summer, compared to spring (Fig. 3A). This lower summer diurnality may reflect warmer conditions (Berger et al. 2002) and increased human disturbance (Georgii and Schröder 1983), with tourist activity in the Alps peaking during this season (Robira et al. 2022). As wolves returned to an area and their presence became more stable, summer diurnality in red deer gradually increased (Fig. 3A), supporting the emergence of a 'diel shield effect'. Due to wolf biology and history of extirpation, wolves remain temporally avoidant of humans (Sunde et al. 2024) (Supporting information), providing prey a daytime temporal refuge. Red deer maintained spatial avoidance of settlements and recreational areas while exploiting this diel refuge. These findings further support the hypothesis that behaviour modulations by prey at a diel scale can offer solutions in multi-risk environments (Lone et al. 2017, Kohl et al. 2018, Palmer et al. 2022). Because of the multi-dimensional nature of human disturbance (Sih et al. 2011), complex avoidance/attraction mechanisms can be expected among predators, prey species, anthropogenic landscape features, and/or human activity (Murphy et al. 2021, Van Scoyoc et al. 2023). In Scandinavia, moose responses to wolf recolonisation have been suggested to be overshadowed by human activities (Sand et al. 2006, Gicquel et al. 2020, Ausilio et al. 2021). Consistent with this, we found a strong response to humans in Alpine ungulates, but we also detected early, progressive behavioural adjustments to wolves. Top–down effects, such as changes in prey abundance and browsing damage, may take longer to manifest than simpler behavioural shifts like diel activity changes.

In autumn, we found that human hunting could drastically modify the outcome of the diel trade-off. Red deer demonstrated a clear 'diel preference' for non-lethal humans over wolves, but also a 'diel preference' for wolves over human hunters (Fig. 4A), illustrating a hierarchy of fear (Rigoudy et al. 2022). Roe deer, although not responsive to wolf recolonisation (Fig. 3B), responded to human hunting by decreasing diurnality (Fig. 4B). These findings support comparative studies on diel plasticity under varying hunting contexts and predator densities (Cunningham et al. 2019), showing a marked dominance of hunter effects (Crosmary et al. 2012, Bonnot et al. 2020). Beyond diel shifts, stronger vigilance to humans than to large carnivores has been observed in red deer (Proudman et al. 2021) and elk *Cervus canadensis* (Ciuti et al. 2012), likely reflecting the need to respond proactively to the highly efficient 'super-predator' (Darimont et al. 2015, Montgomery et al. 2020, 2022) or the higher spatiotemporal predictability of human hunters during hunting seasons (Proffitt et al. 2009). Consistent with these findings, a supplementary analysis of sites spanning the park boundary (Sites 2–3; Fig. 1), shows that diel activity in hunted areas fluctuates sharply around the onset of hunting, whereas it remains more stable or changes more gradually in protected areas (Supporting information), illustrating how human hunting structures ungulate behaviour (Rempfler et al. 2025).

Marked diel plasticity in an ungulate community

Until recently, diel plasticity in wildlife was thought to be constrained by endogenous rhythms (Kronfeld-Schor and Dayan 2003), but has since been increasingly recognised (Kronfeld-Schor et al. 2017) and documented under rapid human-induced change (Gaynor et al. 2018, Patten et al. 2019, Burton et al. 2024). We show that such adaptations also occur in response to natural processes like wolf recolonisation in human-dominated landscapes, with diel shifts (i.e. ca 7% difference in diurnality across five years of recolonisation) comparable to those reported at the regional scale for large carnivores (e.g. ca 6% roe deer diurnality with increasing lynx density in the absence of human hunting; Bonnot et al. 2020) and at the global scale for human disturbance (e.g. ca 18% nocturnality in Gaynor et al. 2018, ca 19% in Burton et al. 2024).

By applying a community-view approach, here we provided a first glimpse at the diversity in diel antipredator strategies of prey species of the same ecosystem, emphasising the complex pathways linking risk perception and antipredator responses (Gaynor et al. 2019). Considering the spatial avoidance of human disturbance and diel avoidance of human hunters simultaneously, our results suggest that all ungulates perceived at least some level of risk from humans (Sih et al. 2011), and that this was taken into consideration when weighing the costs and benefits of displaying behavioural modifications to re-occurring natural predator risk (Lima and Dill 1990, Brown et al. 1999). Thus, we provided evidence for a rapidly occurring, plastic reassessment of the risk timescape in prey, but with clear interspecific differences. While our focus was on diel activity allocation, shifts in overall activity represent another key dimension of antipredator adjustment that warrants further investigation. Moreover, further research is needed to establish the cognitive and learning mechanisms underpinning these responses, and their limitations in multi-risk landscapes.

Leveraging natural gradients to reveal wildlife responses to change

Our quasi-experimental design, combining space-for-time and time-for-time contrasts along gradients of wolf recolonisation, provides a unique opportunity to examine prey responses to natural predator return. Large-scale ecological studies of natural phenomena rarely allow fully controlled experiments, making certain limitations – such as few, autocorrelated events, restricted randomisation, and residual pseudoreplication – almost inevitable (Hargrove and Pickering 1992). In our study, we leveraged the timing and spatial context to capture diel activity shifts of large herbivores along a wolf recolonisation gradient amid human disturbance. Despite extensive camera-trap deployment, combining multiple constraints within the space-for-time framework inevitably limited replication across sites. The time-for-time design covered only two years per site, reflecting the recent onset of monitoring and our goal of capturing behavioural responses as they emerge in real time. To address these limitations, we drew on recent advances in ecological modelling (Dee et al. 2023, Byrnes and Dee 2025, Siegel and Dee 2025), informed by earlier methodological work (Mundlak 1978, Van De Pol and Wright 2009, Wooldridge 2010) to strengthen inference. Specifically, we disentangled between-site from within-site behavioural responses, reducing endogeneity related to the study design, and providing complementary perspectives on prey behavioural change. This approach raises interesting questions – for instance, why between-site and within-site responses may diverge (as in red deer; Fig. 3A, D) or converge (as in chamois, albeit non-significantly; Fig. 3C, F). Such comparisons may help illuminate some of the variation observed across study systems – commonly described as 'context-dependence' – thereby contributing to a broader understanding of wildlife recovery at the continental scale (Kuijper et al. 2016, 2024, Gerber et al. 2024).

Moving forward, continued long-term monitoring in areas of ongoing or impending wolf recolonisation, combined with comparative and synthetic studies across sites and regions, will be essential to clarify these mechanisms and assess whether behavioural shifts scale up to landscape-level effects, including potentially nonlinear dynamics over longer timescales, and effects on lower trophic levels (Dorresteijn et al. 2015, Kuijper et al. 2016, Ausilio et al. 2021).

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Author contributions

Charlotte Vanderlocht: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Valerio Donini**: Data curation (equal); Investigation (equal). **Andrea Corradini**: Data curation (equal); Investigation (supporting); Software (supporting); Visualization (supporting); Writing – review and editing (equal). **Simone Dal Farra**: Data curation (supporting); Investigation (equal). **Benjamin Robira**: Investigation (supporting); Software (equal); Writing – review and editing (equal). **Andrea Gazzola**: Writing – review and editing (supporting). **Giorgia Galeotti**: Investigation (supporting). **Laura Limonciello**: Investigation (supporting); Writing – review and editing (supporting). **Noemi Squillaci**: Investigation (supporting); Writing – review and editing (supporting). **Maël Van Dam**: Investigation (supporting). **Giada Zeni**: Investigation (supporting). **Marta Gandolfi**: Investigation (supporting). **Elisa Iacona**: Investigation (supporting). **Lucrezia Lorenzetti**: Investigation (supporting); Writing – review and editing (supporting). **Matteo Nava**: Investigation (supporting). **Federico Ossi**: Investigation (equal); Writing – review and editing (supporting). **Heidi C. Hauffe**: Funding acquisition (equal); Supervision (equal); Writing – review and editing (supporting). **Francesco Ferretti**: Conceptualization (equal); Writing – review and editing (supporting). **Luca Corlatti**: Conceptualization (equal); Writing – review and editing (supporting). **Luca Pedrotti**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (supporting). **Francesca Cagnacci**: Conceptualization (lead); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

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Data are available from the Zenodo Digital Repository:https://doi.org/10.5281/zenodo.14841059 (Vanderlocht et al. 2025b). Analysis scripts are available at: https://doi.org/10.5281/zenodo.14840994 (Vanderlocht et al. 2025c).

Supporting information

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

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