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Proactive and reactive movement behaviours shape the antipredator sequence in a large herbivore

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Abstract

Background Prey species can display antipredator movement behaviours to reduce predation risk, including proactive responses to chronic or predictable risk, and reactive responses to acute or unpredictable risk. Thus, at any given time, prey movement choice may reflect a trade-off between proaction and reaction. In previous studies, proaction and reaction have generally been considered separately, which neglects their potentially simultaneous influence on animal movement decisions and overall space use.

Methods In this study, we analysed how proaction and reaction interact to shape the movements of GPS-collared red deer (*Cervus elaphus*) in response to hunting by humans. Using an exhaustive inventory of red deer hunting events and very high-resolution canopy cover density (LiDAR), we combined movement metric (displacement and path length) models and integrated step selection functions to investigate antipredator movement responses to lethal risk on various spatiotemporal scales, considering a dynamic landscape of risk.

Results Our results show that red deer either proactively avoided areas of chronic risk, or they selected canopy cover where and when risk was predictably high. However, when risk was encountered anyway, canopy cover was no longer selected, but only modulated a reactive response along a remain-to-leave continuum. This reaction was even more evident when the environment was unfamiliar, underlining the importance of memory in such reaction patterns.

Conclusions We describe how proaction and reaction fuse in an *antipredator sequence* of interconnected movement decisions in a large herbivore, and discuss how this result may help disentangle the ecological consequences of behavioural responses to predation. Finally, we lay the foundations for further investigations into the origins of similarities and differences between proactive and reactive movement responses.

Keywords Predator–prey dynamics, Landscape of fear, Schedule of fear, Bio-logging, Displacement, Path length, iSSA, Integrative approach, Hunting, *Cervus elaphus*

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Background

Avoiding predation while ensuring sufficient resource acquisition is a constant challenge for wild prey species. As prey seek feeding opportunities, they often expose themselves to higher predation risk [1] as predators, in turn, also seek to maximize fitness gains by hunting when and where encounter and capture probabilities are high [2, 3]. Antipredator behaviours may reduce predation risk, but these are offset by other fitness-related costs [4] such as reduced reproduction [5, 6], slower growth [7] and/or decreased survival [8]. Ultimately, prey individuals must continuously make cost–benefit assessments [9, 10], trading-off between predation avoidance and resource acquisition, which in turn also affects space use, among other behaviours.

As predation risk and resource distribution vary in space and time, prey movement decisions and space use also reflect knowledge about these variations, and of deviations to both spatial and temporal predictability. Paradoxically however, most of the current approaches to quantifying the food-risk trade-off [11] and its consequences on prey behaviour [12] generally assume fixity in one or both of these dimensions [13], either focusing on behavioural time allocation (e.g. vigilance [14], 'giving up densities' of resources [15]) or habitat selection in relation to long-term spatial patterns of risk, referred to as the 'landscape of fear' ([16]; see [17] for a review). Conversely, the risk allocation hypothesis [18, 19] proposes that prey adjust the intensity of their antipredator responses not only based on the immediate level of risk (or acute risk), but also in relation to how risk is distributed over time — considering its frequency and intensity relative to background levels (or chronic risk). Here, we contribute to this framework by considering how the proactive responses to chronic or predictable risk, and reactive responses to acute or unpredictable risk [20] simultaneously emerge along the entire 'predation sequence' [21, 22].

As predation can be segmented into various steps at different spatiotemporal scales (the 'predation sequence' [21]: encounter—detection—identification—attack—subjugation—consumption), antipredator movement behaviours can target various steps of this sequence [21, 23]: *proactive* antipredator behaviours generally aim at reducing encounter and/or detection probabilities based on cumulative former experience of risk, which may be perceived as chronic in the landscape [24], predictably variable in time [18, 25] and/or predictably associated with environmental contexts (e.g. habitat type [26]; habitat feature [27]). On the other hand, *reactive* antipredator behaviours generally aim at reducing attack and/or kill probabilities based on direct, sudden cues of risk which are acute or unpredictable to the prey [20, 27] (e.g. [28, 29]). The display of these antipredator behaviours in prey species requires sensory and cognitive abilities [30]. Indeed, reactive behaviour involves the perception of risk cues while proactive behaviour additionally requires associations between risk and context (e.g. risky time of day, risky habitat feature), and can be 'innate' [31, 32], and/or triggered by knowledge of past experience [33] and the memory thereof [34]. Accordingly, familiarity with the surrounding area [35, 36] can modulate habitat selection [37] and behaviour choice [29].

The success of proactive and reactive antipredator behaviours adopted by prey depends on the hunting strategy of the predator, which may have spatial and temporal consequences for the perception of risk [38]. For example, coursing predators tend to increase risk perception of their prey in open areas, while ambush predators have this effect in covered habitats [39]. Human hunters, while exhibiting a large diversity of hunting modes, tend to select areas with good visibility to improve hunting success [40]. Human disturbance alone is also a form of risk [41, 42], and ungulates in anthropogenic landscapes are known to switch between forested areas during the day, and open areas at night as a consequence [43]. Therefore, in grazing or mixed-feeding ungulates that have coevolved with coursing predators such as wolves (*Canis lupus*), and/or with human hunters and disturbance, the food-risk trade-off is often translated into a compromise between grazing in open areas, where grass biomass [44, 45] and palatability [46] may be higher, and selecting canopy cover to evade predators, including humans [47]. Canopy cover can be proactively selected, in response to predictable or chronic risk, but the role of canopy cover in antipredation goes beyond simple selection or avoidance; for example, perception of risk in open habitat can be exacerbated by the distance to refuge cover [48], by the relative positions between the predator, the prey and the refuge [49], or even by crop phenology [50]. When exposed to direct and acute lethal risk, the classical hide *vs* flee decisional dilemma that ungulates face [48, 51, 52] (or the 'remain *vs* leave' dilemma, on a broader temporal scale than just instantaneous reaction (53)) can also be modulated by cover [54]. Therefore, ungulates can use canopy cover in both proactive *and* reactive antipredator behaviours.

Proaction and reaction coexist within the spectrum of behaviours available to prey species, but little is known about how this coexistence shapes prey space use through time. In this study, we thus leveraged high-resolution hunting data combined with hourly movement data of GPS-collared red deer (*Cervus elaphus*) from the same area to investigate the role of proaction and reaction in antipredator movement and habitat selection strategies along the predation sequence, at multiple spatiotemporal scales (Fig. 1). We considered three main research questions.

How do red deer respond to acute lethal risk through movement, given exposure to the risk, surrounding habitat features and site familiarity?

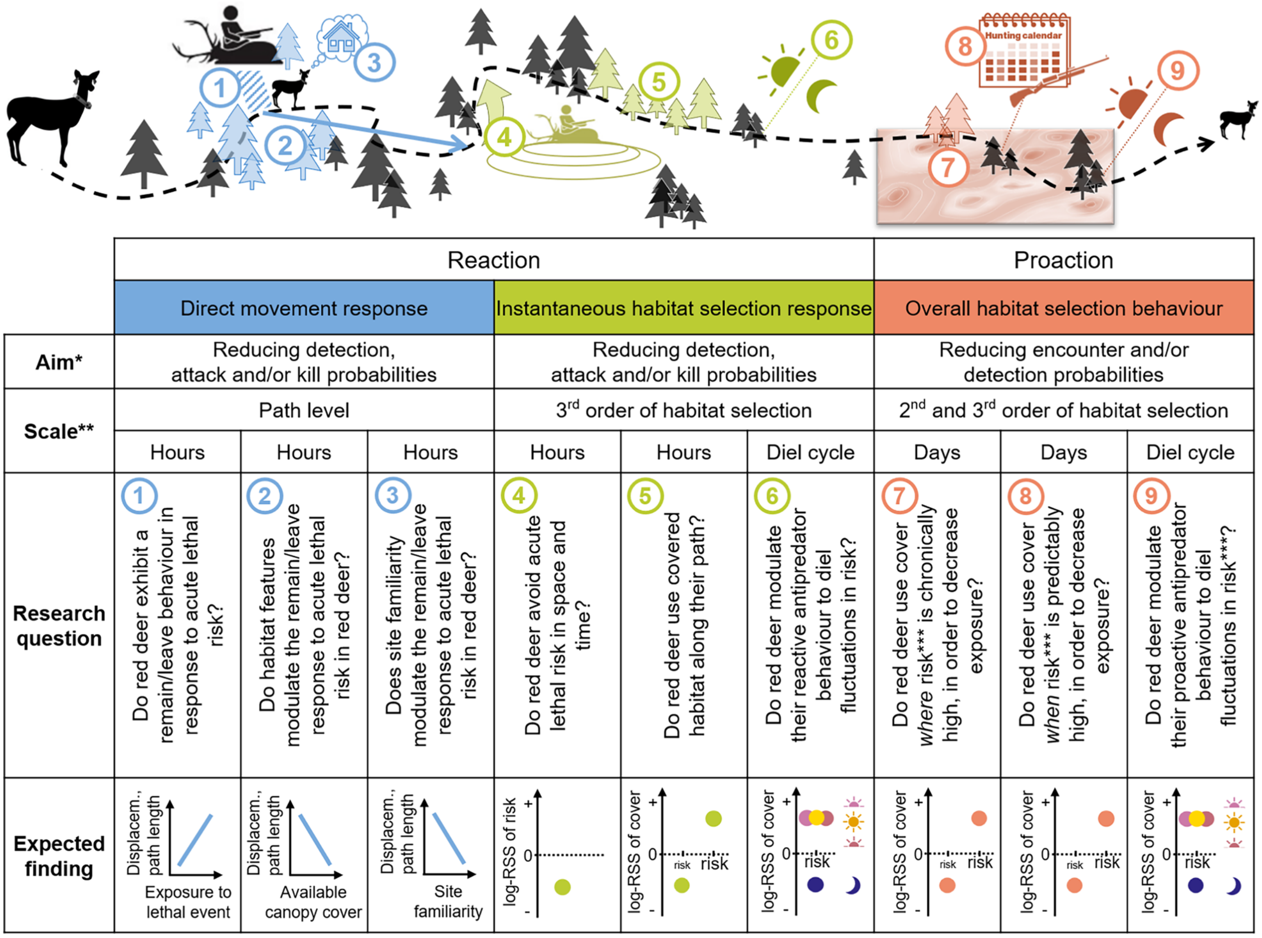
Chassagneux et al. [29] showed that 'remaining' behaviour in red deer was always followed by delayed flight, thus we expected that red deer would exhibit a reactive 'leaving' response in the 24 h following exposure to direct lethal risk, with a decreasing magnitude of response with distance to the hunting location (Q.1), available surrounding canopy cover (Q.2), and site familiarity (Q.3).

What is the instantaneous habitat selection response of red deer to acute lethal risk, given the diel period?

We expected red deer to avoid acute lethal risk (Q.4) and to select for forested habitat (Q.5) when exposed to high acute risk. In line with the risk allocation hypothesis, we expected these reactive antipredator behaviours to be strongest during the hours of the day in which hunting is allowed (i.e. dawn, day, dusk) (Q.6).

What is the overall habitat selection behaviour of red deer in a landscape of predictable spatial and temporal risk?

We expected that red deer would use cover where chronic spatial risk was high (Q.7), and that they would increase their selection for cover as hunting pressure increased throughout the year (Q.8). We also expected that proactive antipredator behaviour in red deer would be strongest during dawn, day and dusk, when hunting



	Reaction						Proaction		
	Direct movement response			Instantaneous habitat selection response			Overall habitat selection behaviour		
Aim*	Reducing detection, attack and/or kill probabilities			Reducing detection, attack and/or kill probabilities			Reducing encounter and/or detection probabilities		
Scale**	Path level			3rd order of habitat selection			2nd and 3rd order of habitat selection		
	Hours	Hours	Hours	Hours	Hours	Diel cycle	Days	Days	Diel cycle
Research question	① Do red deer exhibit a remain/leave behaviour in response to acute lethal risk?	② Do habitat features modulate the remain/leave response to acute lethal risk in red deer?	③ Does site familiarity modulate the remain/leave response to acute lethal risk in red deer?	④ Do red deer avoid acute lethal risk in space and time?	⑤ Do red deer use covered habitat along their path?	⑥ Do red deer modulate their reactive antipredator behaviour to diel fluctuations in risk?	⑦ Do red deer use cover *where* risk*** is chronically high, in order to decrease exposure?	⑧ Do red deer use cover *when* risk*** is predictably high, in order to decrease exposure?	⑨ Do red deer modulate their proactive antipredator behaviour to diel fluctuations in risk***?
Expected finding	Displacem., path length Exposure to lethal event	Displacem., path length Available canopy cover	Displacem., path length Site familiarity	log-RSS of risk + 0 -	log-RSS of cover + 0 - risk risk	log-RSS of cover + 0 - risk	log-RSS of cover + 0 - risk risk	log-RSS of cover + 0 - risk risk	log-RSS of cover + 0 - risk

* Aim refers to the steps of the predation sequence (21) hypothesised to be specifically targeted for each antipredator behaviour under investigation. / ** Scale refers to the spatiotemporal scale (*sensu* Nathan et al. (55)) under investigation, as well as the timespan considered for the analysis. Orders of habitat selection refer to those defined by Johnson (56). / *** *Hazard* is intended instead of *risk*, given the classical definition *Risk* = *Hazard* × *Exposure*. Here, *risk* was chosen for consistency with ecological literature. / Log-RSS refers to the logarithmic relative selection strength as defined by Avgar et al. (57).

Fig. 1 Schematic representation of predicted associations between predation risk and prey space use along the predation sequence, including our research questions and expectations is allowed and human disturbance is prevalent (Q.9), in accordance with the risk allocation hypothesis.

Methods

Study area and red deer hunting regime

The study took place in the hunting reserves of Lauregno and Proves, in the Non Valley (Central-eastern Alps, Autonomous Province of Bolzano, Italy), which cover a total surface of 32.7 km^2 (Fig.S1), characterised by rugged terrain (857–2613 m a.s.l.) and marked habitat heterogeneity, particularly in the distribution of open and forested patches (Data S1). Lower altitudes are dominated by conifer forests (*Abies spp.* and *Picea spp.*), as well as irrigated hay meadows, while higher elevations are covered successively by alpine shrublands and grasslands. The target species of this study, the red deer, is the largest ungulate in the Alps. This gregarious species tends to form sex-specific groups of typically 3–6 individuals in summer and 6–9 individuals in winter [58]. In May–June, pregnant females isolate to give birth, whereas they remain grouped in harems during the mating season in September–October.

The population of red deer in this study area has been estimated as approximately 278 individuals (source: Autonomous Province of Bolzano), and is selectively hunted following the Italian law and regulations of the Province of Bolzano (https://provincia.bz.it/agricoltura-foreste/fauna-caccia-pesca/default.asp): that is, the hunting period is open from May 1st to December 15th, with demographic targets varying throughout the year. Hunting is banned at night (one hour after sunset to one hour before sunrise, Data S2). Ungulate hunters in this area use firearms, and adopt a sit-and-wait approach, either at ground level or in an elevated hunting blind, with most hunting events occurring in open habitats (Data S2). The grey wolf (*Canis lupus*) has been recolonising the area since 2017 [59]. Although wolf predation and telemetry data were not available during the 2021–2023 study period, earlier research conducted between 2018 and 2020 [60] on the local wolf pack — whose territory encompassed our study area — indicated that wolf predation had a considerably lower impact on red deer mortality than human hunting. Based on telemetry-informed kill site monitoring at the time, wolves were estimated to kill approximately 17 red deer annually within the study area, compared to about 59 taken by hunters over the same period [60].

Red deer captures

We captured 15 adult female red deer during the winters of 2021–2023, each of which were eartagged and collared with a GPS tracker (Vectronics Aerospace GmbH©, Vertex Plus), set to record one fix/hour, for *circa* 1.5 y after which the collars were programmed to drop off, reaching a total of 23 animal-years between 11/01/2021 and 20/11/2023. During captures, deer were immobilised through telenarcosis ('Vienna mix', i.e. Xylazine, Zoletil, and Antisedan).

Data pre-processing

We carried out data processing and analyses in R software [61] (v.4.2.2).

Trajectory data

We processed the GPS data by removing locations with low accuracy (dilution of precision > 10), and we added a small amount of time (10 s) to time duplicates and a small spatial shift (0.00001 degrees to the latitude and the longitude) to consecutive location duplicates (as advised in the *crawl* R package [62] guide). In order to exclude any capture effect from the analysis, we also removed all locations in the 10 days following capture [63]. In the resulting animal tracks, 83% of all fixes were separated from the previous and subsequent fix by 1 h (± 10 min). We did not interpolate missing locations, to only focus on 'true' locations. After data pre-processing, a total of 137,368 GPS locations were used for subsequent analyses (Fig. S1).

Hunting data

Hunting bag information was recorded in the database of the Südtiroler Jagdverband/Associazione Cacciatori Alto Adige (www.stat.jagdverband.it), with the bagged species, kill location (estimated precision of *circa* 15 m) and kill time (estimated precision of *circa* 20 min). In order to include all hunting events occurring in the study period, as well as estimate former experience of risk, we extracted hunting records for all red deer bagged on the territory since 2016 (i.e. the earliest available date; extraction on the 05/02/2024 with *qdapRegex* R package [64]), obtaining a total of 470 reported kills (annual mean of 58.8 ± 3.2 events). We excluded incomplete records (e.g. missing kill time or location), for a final total of 407 red deer hunting bags (Fig.S1).

Model variables

In order to assess antipredator behaviour at various spatio-temporal scales (Fig. 1), we extracted ecological variables from spatial layers accounting for a dynamic environment, as described below.

Environmental variables

We described the environment of red deer with four indices known to affect their movement in Alpine environments (altitude, terrain ruggedness, food resources, canopy cover density), using spatial raster layers at 10 m resolution, except for canopy cover, which was 20 m. We derived altitude and terrain ruggedness from the digital elevation model of the National Institute of Geophysics and Volcanology [65] for topographical description of the area (Data S3). We generated a canopy cover density map, calculated as the surface density of trees exceeding 2 m height in LiDAR's Canopy Height Model [66] to describe refuge distribution (Data S3). As a proxy for quality forage availability, we also estimated daily maps of new-growth forage biomass (hereafter referred to as 'food'), from spatiotemporal extrapolations based on the modelling of field-measured biomass of newly emergent graminoids, forbs and shrubs as a function of Normalized Difference Vegetation Index, habitat type, slope exposure, and Julian day (Data S3).

Lethal risk variables

Based on the kill location and time of all hunting events in the study area, we derived various components of lethal risk experienced by the collared red deer. First, we quantified *acute* spatiotemporal risk, to investigate reactive responses as a function of spatial and temporal distance to lethal events occurring throughout the monitoring period of red deer (11/01/2021–20/11/2023), considering the distance to the kills (direct movement response; Q.1–3), and hourly spatially-explicit risk maps (instantaneous habitat selection response; Q.4–6). Second, we quantified *chronic* spatial and *predictable* temporal risk by considering all lethal events since 2016, to investigate proactive movement behaviour as a function of canopy cover and risk (overall habitat selection; Q.7–9).

First, for every hunting event occurring throughout the monitoring period, we measured the Euclidean distance between the location of the hunting event and each GPS-collared red deer at the time of hunting (or at the closest fix before the hunting event within 1 h). Second, we created a series of hourly risk maps at a resolution of 10 m. We estimated the weighted kernel density considering hunting events that occurred within the previous 24 h (smoothing parameter of 2 km with *spatialEco* R package [67]; the threshold of 2 km was identified from the predictions of the reaction to lethal risk model, see 3.1; see also [28, 68]). The used weights were a function of time and decreased linearly from 1 to 0 throughout the 24 h following the hunting event, in order to simulate the decay of perceived acute risk. Each hourly risk map was then weighted overall by the highest weight occurring in that map, as a way of distinguishing high and low absolute risk values between hourly maps. Third, to create the chronic spatial risk map, we generated a map of cumulated spatial risk at a resolution of 10 m: we estimated the kernel utilisation distribution (ad hoc estimation of smoothing parameter with *adehabitatHR* R package [69]) of all locations of recorded hunting events between January 2016 and November 2023. To estimate the predictable temporal risk, we fitted a yearly circular kernel density (smoothing parameter of 0.1 with *circular* R package [70]) to the circular Julian dates of all recorded hunting events between January 2016 and November 2023.

All risk variables were constrained between 0 and 1. We extracted the risk for each location as the density value of the cell containing this location (acute or chronic risk), associated with its timestamp (temporal chronic risk).

Diel periods

We defined four diel periods in the 24 h of each day relative to the timing of sunrise and sunset (*suncalc* R package [71]): dawn and dusk were considered as the two-hour periods centred around sunrise and sunset, respectively, and day and night in the remaining hours from dawn to dusk, and from dusk to dawn, respectively. Hunting events occurred during dawn (10% of all hunting events), day (14%) and dusk (75%, Fig.S2); but not at night (< 1%, see Data S2).

Movement analyses

To investigate the role of proaction and reaction in antipredator movement responses along the predation sequence, we combined and integrated different analytical approaches at three different spatiotemporal scales of the predation sequence (Fig. 1), as described below.

Reaction to lethal risk: direct movement response over 24 h

To characterise reactive red deer movement following a lethal event, assuming a 'remain' or 'leave' dilemma [53], we measured red deer displacement (straight line distance between the first and last location) and cumulated path length over the 24 h following the lethal event (Data S4). We excluded travel sequences with missing hourly fixes in such time intervals. We then investigated how movement metrics (displacement and cumulated path length) varied as a function of risk, using a generalised linear mixed model with a negative binomial error distribution and a log family (*glmmTMB* R package [72]). Specifically, we modelled these metrics as a function of the distance to the lethal event at the time of hunting (Q.1), interacting with the canopy cover density surrounding the animal (mean within 500 m buffer, based on 95th percentile of step lengths; Data S5) at the time of hunting (Q.2), and site familiarity (local value, defined as the movement-based utilisation distribution value associated with the location at time of the lethal event; Data S6) (Q.3). We also controlled for the local terrain ruggedness (local value, Data S3) at the time and location of hunting, as well as individuals and years as random effects on the intercept. Continuous explanatory (distance to lethal event, terrain ruggedness) variables were scaled (to a standard deviation of 1) and centred (to a mean of 0), and proportional explanatory variables (canopy cover density, site familiarity) were first arcsine-square-root transformed. We analysed the effects of risk and environmental variables on displacement and cumulated path length in two separate models, and we verified the models' assumptions, as well as the fit quality by statistically assessing the prevalence of outliers and visually checking residual distributions (Tables S7.2 and S8.2, Fig.S7, Fig.S8; *DHARMa* R package [73]). We did not note any collinearity issue (maximum variance inflation factor < 2; Tables S7.4 and S8.4; *performance* R package [74]).

Reactive and proactive habitat selection

We fitted integrated step selection functions [75] on individual movement tracks to estimate the relative probability of selecting covered habitat at various levels of lethal risk, as well as the relative probability of selecting spatial risk itself, both reactively (Q.4–6) and proactively (Q.7–9). To do so, we generated 50 potential steps ('available') for each observed step ('used'). These available steps were obtained by sampling their distances in a Gamma distribution and the turning angles in a Von Mises distribution, parameterised based on observed steps. We then fitted conditional logistic regressions (*amt* R package [76]) on all individual movement choices together, considering risk (see 2.4.2) and local environmental variables (see 2.4.1; with values constrained between 0 and 1) as predictors, controlling for movement variables (cosine of the turning angle and logarithm of the length of the step), and we used the individual-step ID as stratum. Due to unavailability of risk information outside of the hunting reserves, we removed 'used' steps with missing risk values, or individual-step IDs with more than 10 missing 'available' risk values.

Reaction to lethal risk: instantaneous habitat selection response To model the reactive behaviour of red deer to acute lethal risk, we considered the probability of a location to be selected as a function of the acute spatiotemporal risk (Q.4), the local canopy cover density (Q.5) and the diel period (Q.6.

Proaction to lethal risk: overall habitat selection behaviour To model the proactive behaviour of red deer to chronic lethal risk, we estimated the probability of a location to be selected as a function of the chronic spatial risk (Q.7), the predictable temporal risk (Q.8), the diel period (Q.9) and the local canopy cover density.

For both habitat selection models (reaction and proaction), we ran alternative models including some or all of the above-mentioned variables of interest: from simple additive terms to complex three-way interactions (Tables S9 and S10). Importantly, diel period and predictable temporal risk were included only as interaction terms, not as additive effects, since they do not vary within strata. We also included control variables to all tested models, namely food availability, altitude and terrain ruggedness (see 2.4.1. Environmental variables) as environmental additive control terms, and step length in interaction with turning angle as well as step length in interaction with diel period as movement-dependent control terms [75]. Among the alternative models, the most parsimonious was selected [77], minimising the Akaike Information Criterion (AIC). The quantitative effect of variables identified as influential in movement choices was estimated with logarithmic relative selection strengths (log-RSS, [57]), by computing the logarithm of the ratio between the model predictions when all variables were set to 0.5 (exception for Fig. 3B, see caption), while the variable of interest was set to 1 or 0, and the step length and turning angle to their mean values.

Results

Reaction to lethal risk: direct movement response

Our models for displacement (displ) and path length (pathl) explained 25% and 27% of variability observed in our data, respectively. Distance to the lethal event in interaction with surrounding canopy cover density strongly and significantly modulated red deer displacement ($\chi^2_1 = 11.093$, $p_{LRT} = 0.001$) and path length ($\chi^2_1 = 4.053$, $p_{LRT} = 0.044$) response in the 24 h following a kill. Specifically, when red deer were majoritarily surrounded by open areas, displacement decreased as distance to the lethal event increased (Fig. 2A – dotted red line). In contrast, when red deer were majoritarily surrounded by canopy cover, displacement increased as distance to the lethal event increased (Fig. 2A – solid green line). These opposing reactions intersected at about 2 km from the lethal event, and at this distance red deer showed similar displacements regardless of the canopy cover. Similar trends were observed for path lengths, but the converging response intensity regardless of surrounding cover only occurred when red deer were very close to the lethal event (< 100 m) (Fig. 2C). Interestingly, displacement and path length were significantly lower when red deer were familiar with their surroundings (Fig. 2B, D; $\beta_{displ} = -0.370$, $SE_{displ} = 0.052$, $z_{displ} = -7.09$, $p_{displ} < 0.001$; $\beta_{pathl} = -0.122$, $SE_{pathl} = 0.025$, $z_{pathl} = -4.95$, $p_{pathl} < 0.001$). Local terrain ruggedness did not affect the direct movement response of the deer ($\chi^2_{1,displ} = 0.249$, $p_{LRT,displ} = 0.618$; $\chi^2_{1,pathl} = 0.340$, $p_{LRT\text{-}pathl} = 0.560$).

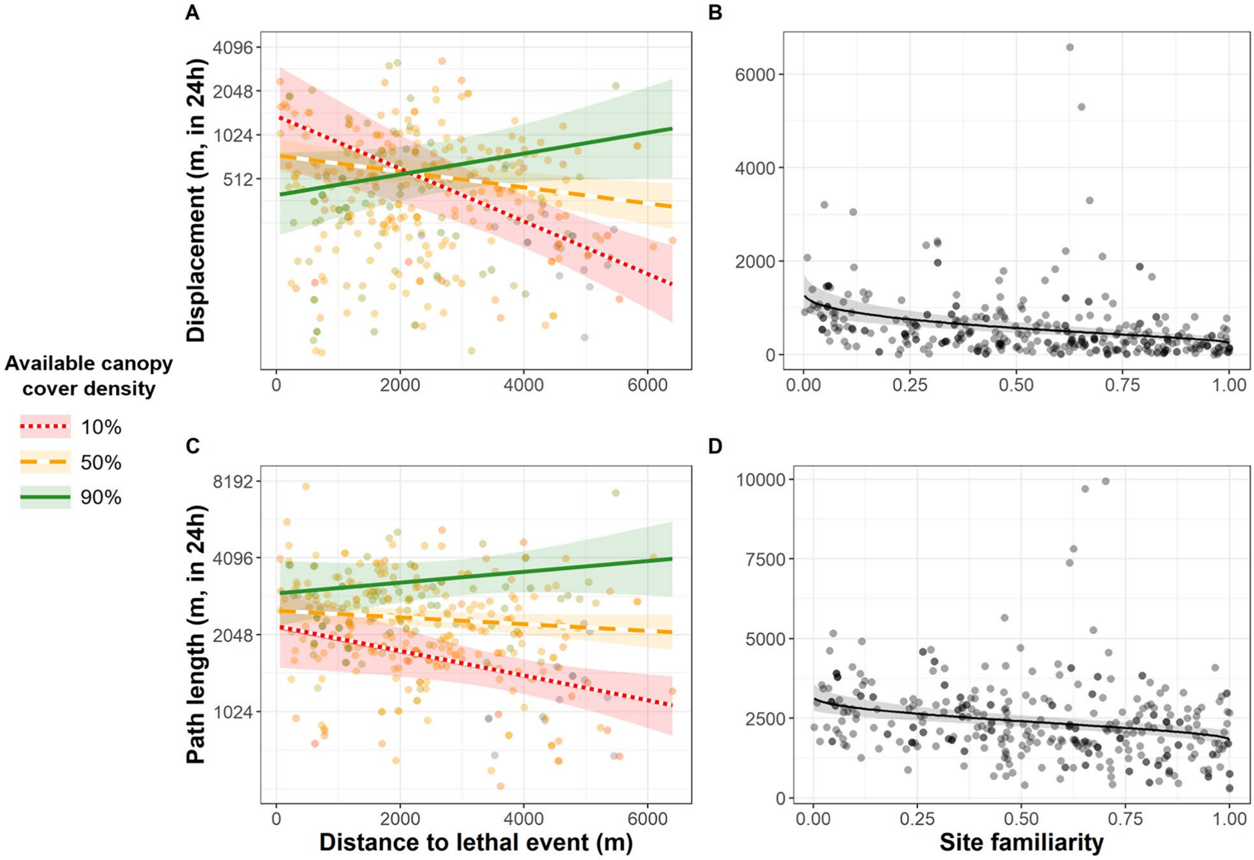


Fig. 2 Predictions of red deer movement metrics in the 24 h following a hunting event (**A–B**; displacement, **C–D**; path length). Panels show effects of interaction between distance to the lethal event and available canopy cover density to the red deer at the time of the lethal event (**A–C**), and of site familiarity at the red deer location at the time of the lethal event (**B–D**). Lines with shaded areas represent the model prediction (mean effect with 95% CI), and dots represent observed data. For **A–C**: data are log-transformed for visual purposes; colour/dash patterns refer to three reference canopy cover densities

Reaction to lethal risk: instantaneous habitat selection response

The model considering two-way interactions between acute spatiotemporal risk, canopy cover density, and diel period (i.e. Alternative model 1; Table S9) was retained as the most parsimonious. Red deer avoided acute spatiotemporal risk during the day (Fig. 3A, log-RSS [95% CI] = -2.772 [−4.590; −0.955]) and at dusk (Fig. 3A, log-RSS [95% CI] = −2.256 [−3.679; −0.834]), while they selected for these areas at night (Fig. 3A, log-RSS [95% CI] = 0.926 [0.099; 1.752]). At dawn, movement choices were independent of the acute spatiotemporal risk (Fig. 3A, log-RSS [95% CI] = −0.664 [−2.789; 1.460]). In the absence of risk, red deer selected for cover during the day (Fig. 3B, log-RSS [95% CI] = 0.517 [0.339; 0.694]) and at dawn (Fig. 3B, log-RSS [95% CI] = 2.137 [1.782: 2.492]), and they avoided cover at night (Fig. 3B, log-RSS [95% CI] = -1.072 [−1.204; −0.940]) and at dusk (Fig. 3B, log-RSS [95% CI] = −2.331 [−2.630; −2.032]). However, selection for cover decreased as acute spatiotemporal risk increased (Fig. 3C, $\text{slope}_{\text{log-RSS}} = -1.363$). Given the absence of the three-way interaction in this model, this slope of selection for cover as a function of acute spatiotemporal risk was invariable across diel periods.

Proaction to lethal risk: overall habitat selection behaviour

The model considering the three-way interaction between chronic spatial risk, canopy cover density and diel period, and the two-way interaction between predictable temporal risk and canopy cover (i.e. Alternative model 8; Table S10) was retained as the most parsimonious. When simultaneously considering selection for chronic spatial risk and selection for canopy cover, we found that at dusk, red deer showed neutral to avoidant behaviour towards spatial risk (Fig. 4B, Table 2), but they avoided cover as risk increased (Fig. 4A, Table 1). During the day, they were neutral towards spatial risk (Fig. 4B, Table 2), and they selected less for cover as the level of chronic spatial risk increased — but only to a certain level of risk (*circa* 0.75 on a scale from 0 to 1),

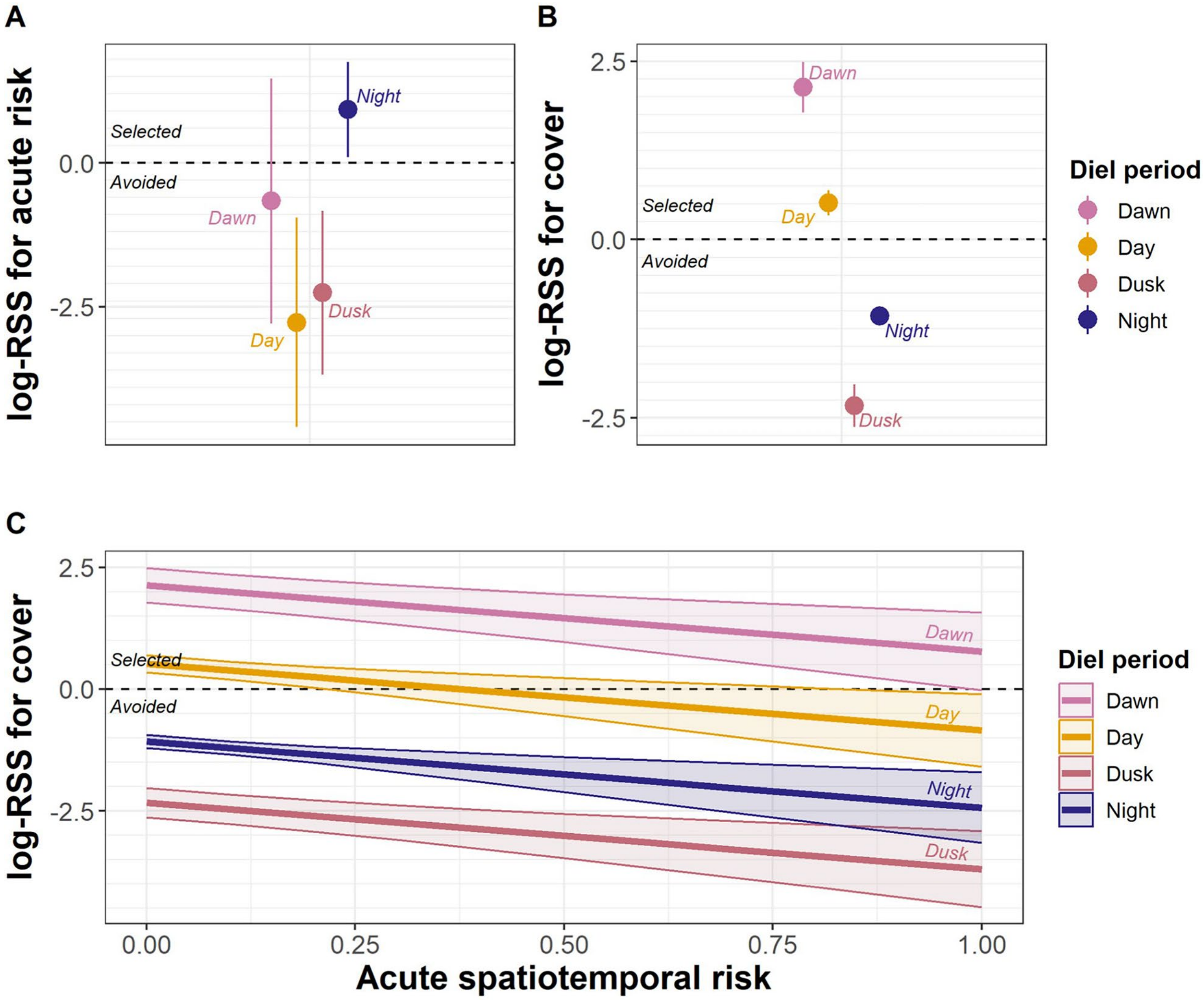


Fig. 3 Relative selection strength (log-RSS, [57]) with 95% confidence intervals for (**A**) acute spatiotemporal risk and for (**B–C**) canopy cover by red deer, at different diel periods (see legend). For **B**, note that the acute risk value was set to 0 in the calculation of log-RSS in order to reflect red deer behaviour in the absence of risk. For **C**, note that diel period affects the absolute level of canopy cover selection (see B), but not its relationship with acute spatiotemporal risk; however, these were plotted for clarity

beyond which cover was used according to availability (Fig. 4A, Table 1). Red deer selected areas of higher risk at dawn and at night (Fig. 4B, Table 2), but they increasingly selected or avoided cover as risk increased, respectively (Fig. 4A, Table 1). In parallel to the annual fluctuation of hunting pressure, red deer increased their selection for cover as predictable temporal risk increased (Fig. 4C, Δlog-RSS$_{\text{max-min}} = 0.555$). Given the absence of the three-way interaction in the most parsimonious model, this fluctuation throughout the year was invariable across diel periods. Interestingly, selection for cover reached its maximum in mid-September, when the hunting pressure was highest (Fig. 4C).

Discussion

Given the pivotal role of ungulates in ecosystems [78, 79], landscape-scale effects of predation on this taxon are fundamental to understanding ecosystem dynamics, especially in anthropogenic ones [80–82]. Taking advantage of the spatiotemporal scalability of movement paths [55], and a unique, complete dataset of hunting bags, we investigated how proaction and reaction interact to shape movement behaviours of a prey species at various spatiotemporal scales in their natural environment. We showed how canopy cover and familiarity with the landscape modulate antipredator responses to chronic and acute lethal risk to answer the questions outlined in

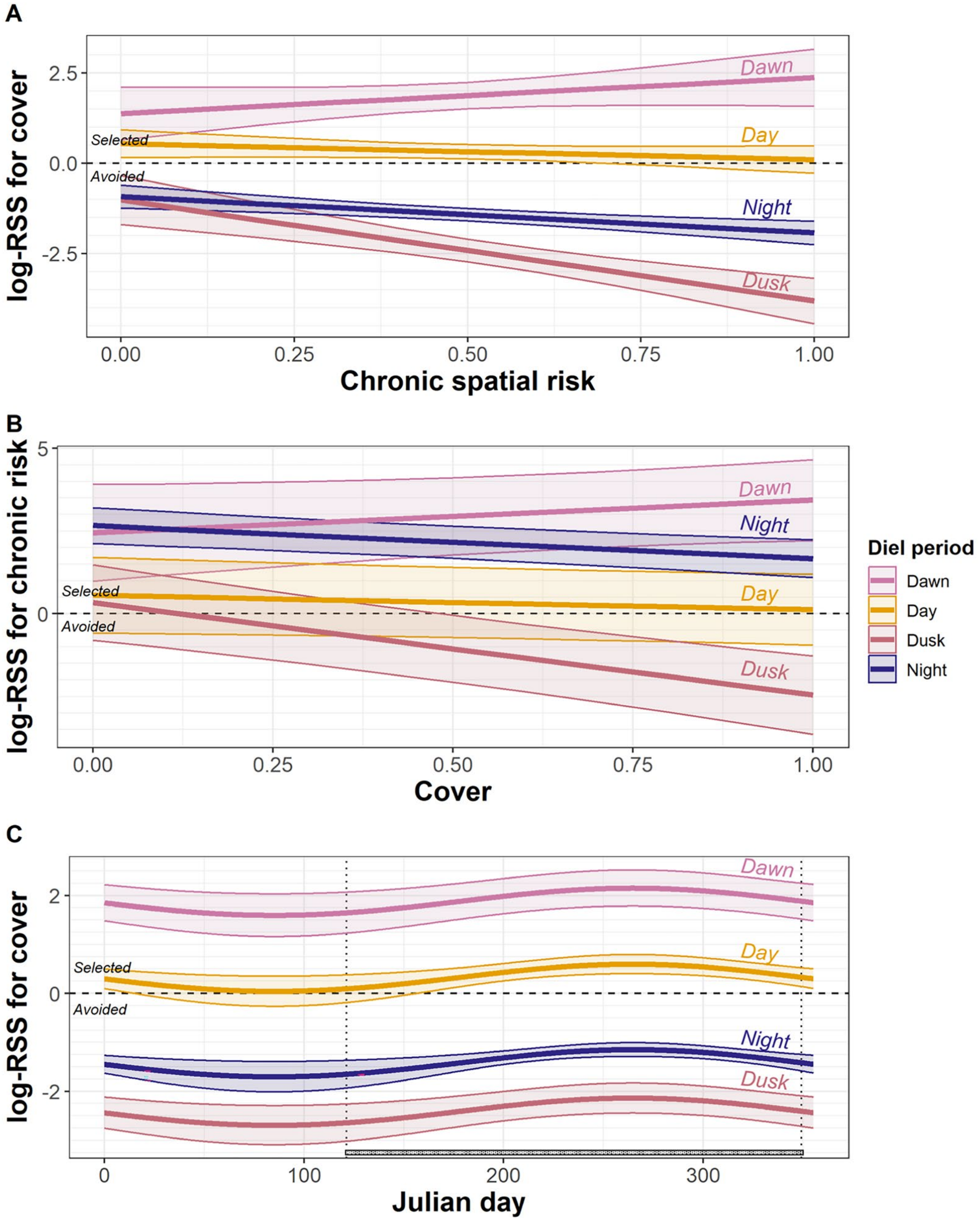


Fig. 4 Relative selection strength (log-RSS, [57]) with 95% confidence intervals (**A**) for canopy cover in response to chronic spatial risk and (**B**) for chronic spatial risk in response to canopy cover, and (**C**) for canopy cover in response to predictable yearly risk, by red deer at different diel periods. For **C**, note that the diel period affects the absolute level of canopy cover selection (see Fig. 3B), but not its relationship with predictable yearly risk. The hunting period is indicated with the textured line above the *x*-axis

Fig. 1. Specifically, the differential role of canopy cover in proactive and reactive antipredator behaviour revealed a decisional sequence: during the most hazardous diel period (i.e. dusk), deer tended to proactively avoid areas of chronically high risk altogether (Fig. 4B), whereas during a less — but still — hazardous period (i.e. dawn), they proactively selected for cover in chronically high-risk areas (Fig. 4A; Q.7). Cover was also proactively selected when risk was predictably high at a broader temporal scale – namely, annually (Fig. 4C; Q.8). When red deer occasionally exposed themselves to acute lethal risk despite proactive efforts, they responded within the following 24 h by adjusting their movement along a remain-to-leave continuum, modulated by the level of risk

Table 1 Relative selection strengths (log-RSS, [57]) with 95% confidence intervals for canopy cover by red deer in response to low and high chronic spatial risk, for each diel period (dawn, day, dusk, night)

	Low chronic spatial risk (set to 0)		**High chronic spatial risk (set to 1)**	
Diel period	**log-RSS**	**95% CI**	**log-RSS**	**95% CI**
Dawn	1.378	[0.641; 2.115]	2.370	[1.579; 3.162]
Day	0.540	[0.154; 0.927]	0.101	[−0.280; 0.481]
Dusk	−1.017	[−1.695; −0.339]	−3.812	[−4.442; −3.182]
Night	−0.922	[−1.239; −0.606]	−1.927	[−2.248: −1.605]

Table 2 Relative selection strengths (log-RSS, [57]) with 95% confidence intervals for chronic spatial risk by red deer in areas of low and high canopy cover, for each diel period (dawn, day, dusk, night)

	Low canopy cover (set to 0)		**High canopy cover (set to 1)**	
Diel period	**log-RSS**	**95% CI**	**log-RSS**	**95% CI**
Dawn	2.447	[0.985; 3.909]	3.440	[2.217; 4.662]
Day	0.562	[−0.584; 1.707]	0.122	[−0.953; 1.196]
Dusk	0.337	[−0.802; 1.477]	−2.457	[−3.642; −1.272]
Night	2.665	[2.121; 3.209]	1.660	[1.091; 2.230]

(distance to the lethal event), surrounding canopy cover, and site familiarity (Fig. 2; Q.1–3). In particular, deer tended to reduce movement if they were in covered areas offering them inconspicuousness (i.e., tending towards a hiding tactic), and to escape/leave if they were in open habitats, but less so when the environment was familiar, confirming the importance of memory and cognition in decision-making. As expected, avoidance of acute risk itself was strongest during the day and at dusk (Fig. 3A; Q.4, 6), when hunting was most probable (89% of hunting events; Fig.S2). However, we found no evidence of selection for cover along the chosen response path in these contexts of acute spatiotemporal risk (Fig. 3C, Q.5), indicating that cover at the time of acute lethal event encounter only conditioned the remain-to-leave choice (Fig. 2A, C).

Canopy cover and site familiarity modulate the response to acute risk on a remain-to-leave continuum

In reaction to direct acute risk, prey species typically choose between remaining or leaving [51, 53]. However, in the 24 h period after encounters with acute risk, we found that red deer displayed a continuum of behaviours, from reducing movement to increasing it, so that displacements and path lengths varied with the distance to risk, the availability of canopy cover, and site familiarity (Fig. 2).

At short distances from risk, cumulated path length remained constant regardless of cover (Fig. 2C), confirming a heightened level of alertness after a hunting event as noted by Chassagneux et al. [52]. Under similar conditions — but often using behavioural assessments at finer temporal scales, such as direct observations — other authors have investigated high reactivity to additional cues [83, 84]; active seeking of information to reassess risk [85, 86]; or an active exploration in search for safer areas [87]. Therefore, red deer response in densely covered habitat seemed to resemble a *restricted movement* response, rather than a strict *sit-and-hide* response.

Instead, exposure to lethal events in more open habitats induced more directional movements in deer (Fig. 2A *vs* 2C, red dotted lines: similar intercepts but slope associated with displacement far exceeds the one associated with path length), probably due to an increased perception of risk exposure in this type of environment [54], or possibly because they can simply be traversed more quickly. Instead, exposure to hunting events in habitats with high cover density induced movements that were consistently less directional, whether the deer was close to the hunting event or not (Fig. 2A *vs* 2C, green solid lines: higher intercept for path length than for displacement, but similar slopes). This pattern could reflect a reduced perception of risk exposure, a need to reassess the risk, or zig-zagging behaviour in order to hinder close pursuits [88] or confuse the predator [89] in habitats with lower visibility and more obstacles. However, given the hourly resolution of our movement data, such fine-scale behavioural mechanisms remain speculative in this context.

Furthermore, we found a behavioural switch in red deer displacements at *circa* 2 km from lethal events (Fig. 2A), suggesting a distance above which red deer decreasingly perceive hazard cues, or respond less as exposure decreased [90]. Further research and experimental set-ups are needed to disentangle perception from response [91]; nevertheless, the spatial scale of this switching distance was consistent with previously published studies. For example, elk (*Cervus canadensis*) were shown to move from grasslands to forested areas when wolves were detected within 1 km [28] and their movement rates decreased as distance to wolves increased up to 5 km, beyond which their movement rates were constant [68]. Finally, both displacement and path length became longer in more densely covered habitats as distance from lethal events increased (Fig. 2A, C), indicating in the absence of perceived risk a typical directional use of forested areas and a typical exploitative use of open areas (Fig.S4).

In addition, prey species have often been noted to escape risk more often and move at greater distances when cover is scarce, when understorey vegetation is scarce, or when far from a refuge (fleeing [92]). Our measurement of available canopy cover at the time of exposure to lethal events provided a single variable integrating all these various potential elements concurrently used in red deer decision making: the current position in refuge habitat; the nearest distance from refuge habitat; and the availability of refuge habitat. Unlike escaping, restricted movement behaviour may provide a more adequate response to avoid detection by predators [21, 93], especially in response to visual predators such as humans [40] in areas with dense canopy cover offering concealment [94]. Staying put, in contrast with restricted movements, may be more likely observed in prey that are physically unable to outrun their predator (e.g. ungulate fawns [95]) or in prey that can effectively be hidden in their environment (e.g. small, solitary, camouflaged and/or woodland species [94, 96]). However, unlike the findings of Chassagneux et al. [29] and Bojarska et al. [97] on red deer responses to drive hunts, the restricted movement responses that we observed were not followed by delayed flight within 24 h, and were significantly more likely if the deer were familiar with their surroundings (Fig. 2B, D). Restricted movement responses may indeed provide for more safety to sit-and-wait hunting, compared to spatially spread drive hunts [98]. The often hypothesised role of familiarity in antipredatory behaviour [35, 36, 99] may become more apparent with direct exposure to sit-and-wait hunting events, where risk is acute and precisely localised. Interestingly, high site familiarity reduced displacement (Fig. 2B) and path length (Fig. 2D) possibly as a consequence of a reduced need for active information seeking [100] and a more effective escape [35], facilitated by improved navigation abilities in familiar environments [101].

Here, we considered the reactive behaviours to risk over 24 h, providing evidence for a continuum of behaviours in red deer, from 'remaining' to 'leaving'. It should be noted, however, that the hourly resolution of our data limits our ability to capture immediate, short-term responses (e.g., freezing or hiding *vs* fleeing) in the seconds or minutes following exposure to acute risk [48]. Finer temporal scales and/or more targeted data collection strategies (see [54] for an example) would be needed to draw such inferences. The consideration of such additional fine-scale responses would not alter the overall framework of movement responses along the predation sequence (Fig. 1); rather, it would be integrated into an additional level of reactive movement responses at a finer spatiotemporal scale.

Red deer alternate between risk avoidance and exposure mitigation in response to temporal variation in attack rates

In our study, dusk emerged as the most hazardous diel period, with 74.7% of all red deer hunting events occurring during that time (Fig.S2). More strikingly, when considering hourly attack rates (sensu [18]), dusk hours were 7.4 times more hazardous than dawn hours, and 17.4–36.2 times more hazardous than daytime hours (the range reflecting day length variability). Following the Risk Allocation Hypothesis, we predicted the highest selection for canopy cover at dusk. However, red deer showed the strongest avoidance of cover at dusk (Fig. 3B), and avoidance intensified with increasing chronic spatial risk (Fig. 4A). Instead, rather than selecting cover to mitigate risk, the step selection analyses revealed that, at dusk, red deer avoided the risky areas *altogether* — both acute spatiotemporal risk (Fig. 3A) and chronic spatial risk (Fig. 4B). This contrasts with behaviour at dawn, when risk was still elevated but lower than at dusk: red deer did not avoid risk per se (Fig. 4B) but they selected for cover (Fig. 3B) to mitigate risk exposure, increasingly so with increasing chronic spatial risk (Fig. 4A). During the day, deer exhibited weak selection responses overall — likely due to reduced movement and activity (Fig.S11) — but still selected for cover (Fig. 3B) and strongly avoided acute spatiotemporal risk (Fig. 3A), while responding neutrally to chronic risk (Fig. 4B) and its interaction with cover (Fig. 4A). This suggests limited proactive avoidance during the day (when risk existed but was relatively low), but clear reactive responses when risk was encountered. At night, when hunting was not permitted and actual risk was minimal, deer appeared to take risk across metrics: they avoided cover (Fig. 3B), selected for both acute (Fig. 3A) and chronic risk (Fig. 4B), and avoided cover increasingly as chronic spatial risk rose (Fig. 4A) — likely because these areas offered greater forage with no real cost. Lastly, annual variation in attack rates also triggered varying antipredator responses in red deer, consistent with the risk allocation hypothesis, as deer selected more for cover during the peak hunting season (Fig. 4C), regardless of diel period.

Dusk, a critical time in the predator–prey space race

Despite proactive avoidance of high-risk areas at dusk, red deer were still exposed to lethal encounters, illustrating a classic case of the prey-predator space race [102, 103]. As discussed above, red deer selected open areas at dusk while avoiding areas of high chronic and acute risk, suggesting that individuals may exploit open areas not yet (commonly) used by hunters. Selecting these open areas at dusk may be a compensatory behaviour for lost grazing opportunities after dawn and day largely spent under canopy cover. The effect of accumulated lost feeding opportunities in the previous hours may also explain the difference in risk taking at dawn and dusk: at dawn, red deer have been able to forage abundantly throughout the night, making risk taking less necessary with respect to dusk. Whether this behaviour relates to other physiological or behavioural constraints (e.g. rumen functioning, alternate habitat use in a mixed feeder, intrinsic crepuscularity, hunger levels) requires further investigation. Moreover, observed responses may be modulated by additional factors beyond the scope of this study, including variation in vigilance [39] or grouping behaviour [26], reproductive status [104], individual body condition [105], and environmental conditions such as weather [106, 107] — all of which merit further investigation.

Diel cyclicity of lethal risk may be the key for red deer to face the food-cover trade-off

Sensitivity to diel cyclicity of risk is rarely considered in studies on reactive antipredator behaviour (but see [26, 108]), but is often described in association with proactive antipredator behaviour [25, 109–113]. In our study, predictability of risk across the diel cycle played a key role in shaping how individuals navigated the trade-off between cover and food, proactively and reactively. By highlighting how red deer perceive and respond to risk at fine diel scales, our results underscore the importance of integrating 'schedules of fear' [20] with the more commonly considered 'landscapes of fear' [17]. Indeed, as predation risk varies both in time and in space, integrating these axes of variation rather than investigating them separately may account for much of the observed variability in risk responses and non-consumptive effects [82, 114, 115].

Proactive choice for cover conditions following reactive behaviour

When acute risk was perceived, red deer integrated this information with local canopy cover availability and responded along a remain-to-leave continuum (Fig. 2A, C). These decisions reduced exposure to acute risk during the 24 h following the kill (Fig. 3A), without evidence of canopy cover selection along their paths (Fig. 3C). This suggests that habitat selection was no longer a viable response at this scale, and individuals instead reacted through movement under the constraints of their immediate surroundings. Deer tended to leave when in open habitats and remain when in closed ones (Fig. 2A), suggesting that selection coefficients — intrinsically reliant on movement — primarily captured "flight" in open areas, thereby explaining the counterintuitive pattern of increased canopy cover avoidance under higher acute risk (Fig. 3C).

Ensemble, the proactive and reactive uses of cover appeared to be different and underpinned sequential context-dependent choices, at different spatiotemporal scales. Indeed, although usually described separately, proaction and reaction coexist within the spectrum of behaviours available to prey species and they potentially contribute together to a multistage antipredator sequence [86], to context-dependent decision-making (e.g. if risk is unpredictable, prey invest only in reaction (20)) and even to proactive–reactive trade-offs within a decisional process (see speed-accuracy trade-off [116], see evidence- *vs* time-based mechanisms [117]) or within behavioural syndromes (see proactive–reactive personality axis [118]). Furthermore, even within reactive antipredator behaviours, there are still elements of predictable risk (i.e. diel cyclicity), allowing red deer to modulate their reactions to acute risk through proactive knowledge. In order to keep a clear and ecologically meaningful distinction between proaction and reaction, we recommend accounting for the predictability, and chronicity *vs* acuteness of risk (see Glossary in [20]), to articulate further the concept of temporal nature of risk (long *vs* short term sensu [26, 119]).

Conclusions

During this study, it is likely that human hunting was the most important risk for red deer (humans as a "super predator" [120, 121]; see Sect. "Study area and red deer hunting regime"), though the increasing presence of wolves and their different hunting mode with respect to humans (coursing vs human sit-and-wait) may also contribute to shaping red deer space use patterns. While fine-scale wolf behaviour or wolf predation data were not available for our study area during the period of our analysis, the integration of all lethal impacts into future analyses [111], as well as non-lethal human disturbance [122], may further contribute to understanding ungulate behavioural responses to multiple disturbance cues and trade-offs in anthropogenic ecosystems. Our fine-scale dataset provides a rare opportunity to disentangle how red deer coordinate proactive and reactive responses across temporal risk gradients, offering a coherent framework that aligns responses to acute and chronic risk. Building on this foundation, future research could explicitly test how background risk modulates acute reactivity, ideally through integrative modelling approaches and expanded temporal or individual sampling.

Our study revealed the ability of red deer to react to spatiotemporally varying risk in their environment by modulating their movement behaviour at large and fine scales, spatially and temporally, reactively and proactively. For the first time in a large herbivore, we described how proaction and reaction fuse in an *antipredation sequence* [86] of interconnected movement decisions. From these findings, several interesting questions emerge: what are the evolutionary origins of these similarities and differences between proactive and reactive antipredator behaviours? Do proactive behaviours emerge from accumulated reactive behaviours? Or do both behaviours undergo independent natural selection? Further research integrating individual and species life-histories may provide novel insights to these intriguing questions.

Abbreviations

iSSA	Integrated Step Selection Analysis
GPS	Global Positioning System
LiDAR	Light Detection And rRanging
Q	Question
AIC	Akaike Information Criterion
log-RSS	logarithmic Relative Selection Strength
displ	displacement
pathl	path length
SE	Standard Error
LRT	Likelihood Ratio Test

Supplementary Information

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Supplementary material 1 (R 9 KB)

Supplementary material 2 (R 113 KB)

Supplementary material 3 (CSV 67 KB)

Supplementary material 4 (CSV 259601 KB)

Supplementary material 5 (TXT 4 KB)

Supplementary material 6 (PDF 1241 KB)

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Author contributions

CV: Conceptualisation and study design; Data curation; Formal analysis; Investigation; Methodology; Software; Validation; Visualisation; Writing – original draft; Writing – review & editing. BR: Conceptualisation; Formal analysis; Methodology; Software; Validation; Visualisation; Writing – early drafts; Writing – review & editing. AC: Formal analysis; Investigation; Software; Visualisation; Writing – review & editing. SDF: Data curation; Investigation. FO: Data curation; Investigation; Project administration; Resources; Writing – review & editing. DR: Investigation; Resources; Project administration. HCH: Funding acquisition; Supervision; Writing – review & editing. LP: Funding acquisition; Supervision; Writing – review & editing. FC: Conceptualisation and study design; Investigation; Resources; Funding acquisition; Project administration; Supervision; Writing – early drafts; Writing – review & editing.

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Availability of data and materials

We provided the data as supplementary material, ensuring full reproducibility of analyses. We removed sensitive spatial information on red deer from data tables (while providing visuals – see Fig.S1 – and maintaining reproducibility: re-projection of single fixes) as these animals are selectively hunted under the regulations of the Autonomous Province of Bolzano, and spatial data were acquired or shared with us through agreements with this public body.

Declarations

Ethics approval and consent to participate

All animal handling and procedures were performed with ethical permission (permit approval by ISPRA-Wildbeobachtungsstelle) and led by a licensed veterinarian following Italian regulations. The administrative authorisation was granted by Decree No. 24664/2020 of the competent Provincial Council.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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