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Research article

Navigating a landscape of contrasting hunting regimes and habitats: red deer responses to risk and resources

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Habitat selection of ungulates is influenced by various factors, with human interactions playing a significant role. Human disturbances through hunting strongly affect ungulate behaviour, often forcing them to modify their habitat choices by avoiding areas where the risk from humans outweighs other habitat benefits. Gaining insights into these dynamics of human-wildlife interactions is essential for reducing conflicts between hunting objectives and wildlife conservation efforts. Here, we used GPS tracking data of 32 female red deer *Cervus elaphus* to derive resource selection functions, analysing habitat selection of animals with both hunting and no-hunting zones within their home range in Berchtesgaden National Park, Germany.

Red deer habitat selection differed distinctly between hunting and no-hunting zones. In the hunting zone, red deer more strongly selected closed forests, indicating a priority for safety. This pattern was particularly strong during daylight hours (i.e. the primary time of hunting) during which they also greatly reduced their movement. During night-time, when hunting risk was absent, red deer strongly selected open habitats and increased their movement rate. Conversely, red deer consistently selected open habitats and had similar movement rates during both day and night in the no-hunting zone, reflecting a preference for foraging grounds when not influenced by hunting. Our results highlight red deer's ability to distinguish between and adapt to areas of varying risk within their home range.

These insights are critical for targeted wildlife management and conservation. On the one hand, they demonstrated that hunting can be strategically used as a management tool to control red deer habitat use, reducing their presence and thus potentially their impact on specific areas. On the other hand, the finding that hunting distinctly influences red deer habitat selection and movement highlights the value of no-hunting zones for the conservation of natural behaviour of ungulate populations.

Keywords: habitat selection, hunting, national park, protected area, red deer, ungulates

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Introduction

Habitat selection is a complex process that represents the dynamic interactions between wild animals and their environment (Manly et al. 2002). It is shaped by a variety of biotic and abiotic factors, including food availability and quality, climatic and topographic conditions, as well as inter- and intraspecific interactions (Boyce and McDonald 1999). Notably, humans significantly influence the habitat selection process. Human infrastructure alters habitat composition and its attractiveness for wildlife (Ciuti et al. 2012), and even the mere presence of humans can impact wildlife behaviour (Visscher et al. 2023). Human disturbances, such as recreational activities and hunting, modify animals' habitat use and activity patterns, as they seek to avoid risky encounters (Courbin et al. 2022). These behavioural responses result in spatiotemporal variations in habitat use, which are based on an animal's perception of risk across different habitat types, a concept termed the 'landscape of fear' (Laundré et al. 2001).

For ungulates, the risk of predation plays a pivotal role in shaping the landscape of fear. Today, human wildlife management is the primary cause of mortality for ungulates in large parts of Europe, regardless of whether large predators are present or not (van Beeck Calkoen et al. 2020). Beyond direct effects on population densities and structures, hunting also profoundly affects the spatiotemporal behaviour of ungulates (Dwinnell et al. 2019, Parsons et al. 2022). In response to hunting pressure, ungulates frequently adopt increased nocturnality (Visscher et al. 2017, Spitz et al. 2019, Bonnot et al. 2020, Wiskirchen et al. 2022), reduce their activity and movement radius, and increase vigilance (Ciuti et al. 2012, Benoist et al. 2013, Marchand et al. 2014, Little et al. 2016). Additionally, they select refuge habitats that minimize risk, such as remote alpine environments, dense forests, or areas with low human disturbance, depending on species-specific preferences (Grignolio et al. 2011). While these behavioural adaptations enhance survival, they may impose fitness costs by restricting access to high-quality foraging areas and by allocating more time to fleeing and hiding than to foraging and resting (Bonnot et al. 2013).

Despite extensive research on broad-scale habitat shifts under hunting pressure (Tolon et al. 2009, Fattebert et al. 2019), the fine-scale effects of spatially variable risk within individual home ranges remain poorly understood. Our study addresses this gap by investigating how female red deer *Cervus elaphus* navigate trade-offs between foraging opportunities and predation risk across spatially heterogeneous hunting regimes. Specifically, we examined selection patterns between high-risk (hunted) and low-risk (non-hunted) zones within individual home ranges, assessing not only the broad-scale 'reserve effect' (Tolon et al. 2009, Grignolio et al. 2011) but also fine-scale habitat selection within these zones. The focus of our approach lies in analysing how individuals modulate their use of open (high forage, low canopy cover) versus closed (low forage, high canopy cover) habitats in response to different hunting regimes. By integrating habitat selection with localised risk exposure, our study provides new insights into the behavioural trade-offs that shape anti-predator strategies in an ungulate species.

Building resource selection functions from GPS tracking data of 32 female red deer collected over two consecutive years in Berchtesgaden National Park (BGNP), Germany, we assessed how habitat selection was influenced by contrasting risk regimes. We first investigated how the risk of being hunted influenced the spatial habitat selection of red deer by comparing habitats with different canopy cover between hunting and no-hunting zone. We hypothesised that red deer select closed habitat more strongly in the hunting zone, while the selection of open habitat is higher in the no-hunting zone. Second, we took a spatiotemporal perspective, examining if red deer show temporal flexibility in their behaviour with changing selection patterns across the day. Daytime poses a greater risk for red deer in the hunting zone due to hunting activity, while this risk is absent in the no-hunting zone. Therefore, we hypothesised that the circadian selection for closed and open habitats differed more strongly in the hunting zone compared to the no-hunting zone. Additionally, we assumed that this selection for safety is also seen in step length, as red deer move less in the hunting zone during the day than in the no-hunting zone and at night to reduce the risk of encounters with hunters.

Material and methods

Study area

Berchtesgaden National Park is situated in the northern Alps in Bavaria, Germany. The park encompasses an area of 20 808 ha and spans an elevational range between 603–2713 m a.s.l., with the tree line located at approximately 1650 m a.s.l. Forests cover about 12 000 ha (56%), with Norway spruce *Picea abies* being the dominant tree species. The area is a national park (IUCN category II) and has been protected since 1978. It still has a strong legacy of past forest management, with vegetation in transition towards the potential natural vegetation, which includes a higher proportion of silver fir *Abies alba*, sycamore maple *Acer pseudoplatanus*, and European beech *Fagus sylvatica* (Thom and Seidl 2022). Below the tree line, anthropogenic mountain pastures have existed for centuries. They are maintained by cattle grazing (1.4% of the park area), while natural grasslands (4%), interspersed with mountain pine *Pinus mugo* shrublands, scree and rock, mainly occur in the alpine zone.

The park is divided into two zones: a non-intervention zone covering 75% of the park (15 606 ha), where no management activities and consequently no hunting occur, and an intervention zone accounting for the remaining 25% (5202 ha), where forest restoration, wildlife management, and traditional land uses, such as alpine pastoralism take place (Nationalparkverwaltung Berchtesgaden 2023). Red deer are hunted in the intervention zone from 1 May to 31 January only during daylight hours by professional hunters employed by the park. Legal regulations define daylight from one hour before sunrise to one hour after sunset, during which hiding and stalking are permitted, and the use of night vision equipment for shooting is prohibited. The hunting density is approximately 4.2 animals per 100 ha per year, based on the area of the intervention zone, with males only being shot up to an age of four years, while females are hunted across all age classes.

The main study site was the Königssee valley, the largest of three valleys within BGNP, covering approximately 10 000 ha (Fig. 1). Of this area, 76% lies within the non-intervention zone, while the remaining 24% is designated as the intervention zone. The intervention zone is concentrated around Lake Königssee, covering 500 ha in the centre of the valley (i.e. the lowest part of the landscape), as well as in a series of interconnected mountain pastures on the valley's eastern slopes, located between 1200 and 1700 m a.s.l. The Königssee valley experiences high tourist activity due to easily accessible hiking trails and a boat service on the lake, enabling tourists to reach remote areas in the non-intervention zone. The valley is enclosed by mountains exceeding 2500 m a.s.l. on three sides, creating a natural barrier for red deer. At the northern end, the valley opens towards the village of Schönau, which acts as a barrier to deer dispersal. GPS tracking data showed no migration to areas outside the valley, so that we could treat the population in the Königssee valley as a distinct meta-population (home ranges in Fig. 1a).

Due to the loss of suitable overwintering habitats outside the national park and the blocking of migration routes by human infrastructure, red deer are fed during winter at four feeding sites within the park, two of which are located in the Königssee valley. The feeding sites are located on open grassland patches within closed forests, and hunting is prohibited within a 200 m radius around these sites. The duration of winter feeding depends on annual weather conditions, with a maximum feeding period from mid-November to mid-April. However, due to milder winters, feeding often started later and ended earlier in recent years. Approximately 4 kg of hay were provided per animal per day, or the dry matter equivalent of mixed feed (maize and grass silage). This quantity meets the animals' daily nutritional requirements, thus eliminating the need for natural foraging behaviour. As a result, the animals significantly restrict their range of movement around the feeding site, remaining on average within a 700 m radius during the feeding period, compared to a 3900 m radius outside the feeding period. Consequently, behavioural patterns are markedly altered by supplement feeding. No large carnivores were present in the park during the study period.

GPS data

Annual counts at winter feeding sites, separated into males, females, and juveniles, estimated the red deer population in

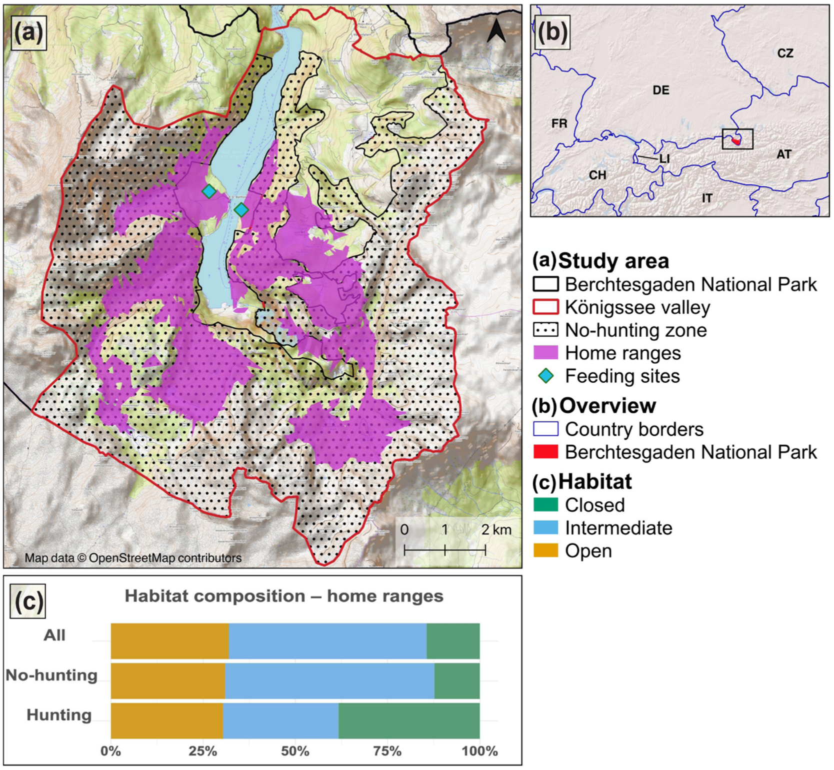

Figure 1. Map of the study area. (a) Königssee valley, the no-hunting zone is shown with a black-dot pattern. The home ranges of the two groups are highlighted in pink, the two feeding sites, where the GPS-collars were placed, are marked with blue rectangles. (b) Location of Berchtesgaden National Park (BGNP) in south-eastern Germany. (c) Distribution of habitat types (open, intermediate, closed) in the red deer home ranges in total and separated for hunting and no-hunting zone.

BGNP at approximately 500 individuals, with around 350 residing in the Königssee valley. 44% of them are male and 82% of the adult females (> 2 years) are with offspring. From 2022 to 2024, we collected data from 32 female red deer equipped with Vertex Plus GPS-collars (Vectronic Aerospace GmbH). The animals were captured and collared at the two feeding sites located east and west of Lake Königssee in January and February 2022 (Fig. 1a). We followed the capture protocol described in Heurich (2011). During all capture and handling operations, the German Animal Protection Act's guidelines were strictly followed, and all necessary permissions for trapping and animal handling were obtained prior to the study from the government of Upper Bavaria (ROB -55.2-2532.Vet_02-21-132). Of the initial 30 animals collared in February 2022, two individuals died in the following winter, so that two additional females were collared in February 2023. Therefore, we collected two years of data for 28 animals and one year for four individuals. Since animal home ranges of the two capture sites did not overlap, we considered them as two separate groups in the analysis (Fig. 1a).

We focused our analyses on the period from 1 May to 15 November in 2022 and 2023. During this time, hunting takes place continuously and no supplemental feeding is provided. We deliberately excluded the winter months from this study, as these months are characterised by feeding and the seasonal hunting ban. It would not be beneficial to study behaviour during the closed hunting season, as the supplemental feeding has a substantial impact on the animals' behaviour at this time, as it suppresses their natural activity patterns. The spatial distribution of GPS locations supported the exclusion of the feeding period for addressing our study objectives. During the closed hunting season (1 February–30 April), when feeding was provided continuously with the exception of the last two weeks, areas in the immediate vicinity of feeding sites (500 m radius) were strongly preferred, with 96% of all GPS locations in open-canopy habitats in the hunting zone occurring within a mere 1.3% of the total open-canopy area. In contrast, during the hunting season (1 May–31 January), in which feeding only took place during the last 2.5 months, this proportion dropped to 44%, and further to only 18% during our chosen study period when excluding the feeding period. These analyses highlight the substantial influence of feeding on habitat use when the hunting season is closed, suggesting that any analysis during this time would be unable to disentangle the effects of feeding from those of no-hunting. The pronounced selection for open-canopy habitats observed during the closed season (Supporting information) cannot be attributed solely to the absence of hunting but is most likely the effect of supplementary feeding. Hence, we have restricted our analysis to the feeding-free period.

To further elucidate the effect of the study period on our results, we tested a subdivision into two-month intervals corresponding to key biological phases of female red deer – calving, lactation, and rut. However, we found no substantial differences in selection patterns across these periods (Supporting information). Consequently, we conducted our analyses using the entire study period as a single unit. The GPS collars provided hourly locations and we only used locations that had a dilution of precision (DOP) < 10 (D'Eon and Delparte 2005) and applied the protocol described in Bjørneraas et al. (2010) to remove outliers from the dataset. The median DOP of all used GPS locations was 3.6, indicating high accuracy. Due to computational and statistical reasons we down-sampled the data to one location information every five hours per individual, which ensured an equal representation of all hours of the day, and reduced autocorrelation in the modelling process (Noonan et al. 2019). Visual data inspection revealed similar results for the full and thinned dataset (Supporting information). For the final analyses, we had on average 1583 (± 347) GPS locations per individual. The original timestamps of the data had limited biological relevance, as day length strongly varied during both 6.5-month study periods. Therefore, we converted them to values based on the position of the sun with the package 'overlap' (ver. 0.3.4; Meredith and Ridout 2022) in R ver. 4.3.2 (www.r-project.org), so that sunrise and sunset always had the same value, expressed in radian ($\pi/2$ and $3\pi/2$, respectively).

Predictor data

Open and closed habitats provide the most important resources for red deer, namely forage and safety (De Groeve et al. 2023). To distinguish between these resource types we used forest canopy closure, with closed canopy structures expected to be primarily selected for resting and hiding, while open areas offer abundant forage (Hebblewhite and Merrill 2009).

We used canopy cover above 5 m in height (in %) in 1-m horizontal resolution derived from high resolution LIDAR data collected in 2021 (Mandl et al. 2023). We classified the data into open, intermediate and closed habitat with a resolution of 30 m, as grass and herb layers that are characteristic for open habitat and attractive for ungulates only occur in patches of this size and larger (Walters et al. 2016). Open habitat was defined as areas with less than 30% canopy cover (including forests with canopy cover < 5 m in height and open areas such as mountain pastures and natural grasslands), which we hypothesised to be primarily selected for foraging. Intermediate habitat, defined as 30–80% canopy closure, combined a mixture of foraging areas and cover. Areas with canopy cover greater than 80% were classified as closed habitat, likely selected primarily for hiding and resting, as reduced light penetration in these areas limits understory plant growth (Braziunas et al. 2024). This classification was supported by relating canopy cover with understory cover, showing an inverse relationship between the two strata (Supporting information).

Additional predictor variables representing topographic features were elevation and slope in 1-m resolution. They were rescaled to a mean of 0 and a standard deviation of 1 for statistical analyses. To account for differences in hunting regime, we used the two zones of the park (i.e. hunting versus no-hunting) as predictors. To assess multicollinearity among predictor variables, we calculated the variance inflation factor

(VIF). All values were below 2, indicating low multicollinearity (Zuur et al. 2009).

Statistical analysis

To examine habitat selection of red deer, we used third order resource selection functions (RSF) (Johnson 1980, DeCesare et al. 2012). RSFs are binomial logistic regression models with a use-availability design (Northrup et al. 2022). For the third order, the used points are represented by GPS locations, the available points are randomly generated within the individual's home ranges. For the calculation of home ranges, we used the time integrated local convex hull nonparametric kernel method (t-LoCoH) in the R-package 'tlocoh' (ver. 1.4.07, Lyons and Getz 2019), as this method aligns home ranges much closer to GPS coordinates as more widely used methods such as kernel density or minimum convex polygon approaches (Noonan et al. 2019). Therefore, it is especially suitable for analyses in mountainous areas with steep slopes and physical barriers for animal movement such as lakes and mountain ridges (Getz et al. 2007). By setting the parameter k, the number of closest neighbours with which each polygon is calculated is determined. The parameter s defines the temporal proximity. We used $k = 21$, $s = 0.003$ and a 95% kernel to create realistic home ranges for red deer that reflect their use of the landscape well and do not include steep rock walls or water bodies.

For each individual, we created random points with a ratio of 1:5 to the mean number of thinned GPS locations (1583:7915) (Northrup et al. 2013). The random points were evenly sampled in their home ranges so that they well represented the availability of different landscape features, such as hunting regime and topography. The random points were assigned with the same timestamps as their counterparts from the GPS data to calculate circadian selection. For all used and available point locations we extracted habitat type, hunting regime, elevation, and slope as covariates. We used infinite weighting of the available points to determine a stable selection function using logistic regression without decreasing the computational speed by increasing the number of points (Fithian and Hastie 2013, Northrup et al. 2022).

We used the R-package 'lme4' (Bates et al. 2023) to set up a generalized linear mixed model to calculate habitat selection. To test our first hypothesis, the selection of open and closed habitats in the hunting and no-hunting zones, we constructed a model with two-way interaction between habitat type and hunting regime, and included slope and elevation as quadratic terms. Initial model comparison revealed lower AIC values for the model with quadratic terms for elevation and slope than for its linear inclusion. We included random intercepts and slopes for each individual within its respective group to account for differences in habitat availability between individuals but also for the autocorrelation of an individual's data points (Muff et al. 2020). For the second hypothesis focusing on spatiotemporal differences, we included a three-way interaction with time, hunting regime, and habitat type – instead of the two-way interaction, while keeping the rest of the model structure the same. To account for the cyclical and nonlinear nature of selection across the day we used four trigonometric functions of time: sin(time), cos(time), sin(2time), cos(2time) (Richter et al. 2020). We calculated the logarithmic relative selection strength (log-RSS) of the different habitat types for the first hypothesis following the approach described by Fieberg et al. (2021), using the fitted model coefficients. For the second hypothesis, we employed the generic predict function to estimate log-RSS across different habitat types and hunting regimes over a 24-hour period, while holding all other covariates constant (Avgar et al. 2017). Specifically, we set elevation and slope to their mean values, time to 'noon', habitat to 'closed' and hunting regime to 'no-hunting'.

To further examine the influence of hunting regimes on circadian movement patterns, we calculated the distances between consecutive hourly GPS locations. We then compared these distances between day (sunrise to sunset) and night (sunset to sunrise) within hunting regimes and habitat types using a generalised linear mixed model with step length as gamma distribution and individuals as random effect.

Model validation

We performed a five-fold cross-validation (CV) for both models. For this we subdivided the data into training and test data by withholding data for six randomly selected individuals for validation (Roberts et al. 2017). In each of the five model runs of the CV, we used the training data to generate maps of predicted relative probability of selection in the study area. As we expected circadian differences in selection, we validated the model for our second hypothesis for three different timesteps: 0.2 radian representing night-time (around midnight), 1.5 radian representing dawn and 3 radian representing daytime (around noon). We transformed the pixels of the predicted maps into ten ordinal ranks of equal area bins, each bin with the same number of pixels (Boyce et al. 2002, Morris et al. 2016). We overlaid the used GPS locations of the test data on the binned maps and obtained the number of points per bin. As we generated time-sensitive maps for the second hypothesis, we only retained GPS points that matched the respective timestep with a buffer of ± 0.2 radian. The Spearman rank correlation coefficient between bin number and number of points per bin was used to assess model accuracy, with a high correlation coefficient representing a good model fit (Morris et al. 2016). The averaged correlation coefficient across the five CV results then indicated the overall predictive performance of the model.

Results

Open habitats dominate the Königssee valley (54.3%, compared to 35.4% intermediate and 10.3% closed habitat). Within the individual home ranges of red deer, intermediate habitat was most present (53.6 ± 4.6%), followed by open (32 ± 9.5%) and closed habitat (14.4 ± 7.3%; Fig. 1). In the parts of the home ranges that overlapped with the no-hunting zone, open habitat was more than two times more abundant than closed habitat (31 ± 9.3% versus 12.3 ± 7.3%), while in the parts that overlapped with the hunting zone, closed habitat was more abundant than open habitat (38.3 ± 27.6% versus 30.3 ± 21.9%). The average home range size was 243 ha (± 51 ha), with the large majority of the home range area (84% ± 12%) located in the no-hunting zone, where also 88% (± 12%) of the GPS locations per animal were sampled. Only five animals had no GPS points in the hunting zone during the study period.

Testing our first hypothesis, we found significant differences in selection strategies between the hunting and no-hunting zones of BGNP. Model performance was good with a Spearman rank correlation coefficient of 0.77 ± 0.03 in the five-fold cross validation, demonstrating the model's ability to represent habitat selection. The model indicated a stronger selection of habitats in the no-hunting zone compared to the hunting zone. In addition, the order of relative selection strength within the zones was reversed. In the no-hunting zone, open habitat was selected most frequently (0.53 ± 0.2 log-RSS; Fig. 2), followed by intermediate habitat (0.33 ± 0.14 log-RSS) and closed habitat (0 (as it was the reference and comparison class)), whereas in the hunting zone closed habitat was most frequently selected (−0.80 ± 0.28 log-RSS), followed by intermediate (−0.84 ± 0.06 log-RSS) and open habitat (−1.12 ± 0.06 log-RSS). The differences in selection between habitat types within a hunting regime were significant for the no-hunting zone and the comparisons open – closed ($p = 0.02$) and open – intermediate ($p = 0.03$), for all other pairs of comparison the differences were not significant ($p > 0.05$). When comparing the same habitat type between zones, significant differences were found for all habitat types ($p < 0.05$). Slope was a significant covariate in the model, with lower slopes being preferentially selected, while intermediate elevations had the highest selection strength (Table 1).

Testing our second hypothesis, we observed distinct differences in circadian selection patterns between the hunting and no-hunting zones with a stronger circadian variation in selection in the hunting zone. The model's predictive performance was best during daylight, the Spearman rank coefficient was 0.77 (± 0.05) for the prediction at noon, followed by the prediction at dawn (0.69 ± 0.06) and at night (0.65 ± 0.08). In the no-hunting zone, closed habitat was the least selected habitat type throughout the entire day, with significantly lower selection compared to the other two habitat types (Fig. 3). Peak selection of closed habitat was at midday, the lowest selection was at sunrise and sunset. Open habitat was most strongly selected almost throughout the entire day, the selection was highest during the night and decreased during the day, whereas selection for intermediate habitat followed the opposite pattern, with higher selection during the day and lower selection at night. The log-RSS for closed habitat had the strongest circadian variation, it ranged from −0.45 to 0.02, followed by intermediate habitat with −0.08 to 0.34 and open habitat with 0.21 to 0.53. In the hunting zone, circadian variation in selection between habitat types was much more pronounced. Closed and open habitat exhibited a strong inverse selection pattern between day and night. The log-RSS for closed habitat differed from −2.16 during night to −0.60 during day, and from −1.69 during day to −0.03 during night for open habitat, whereas intermediate habitat only showed little variation in selection throughout the day (−0.83 to −0.50). Closed habitat was significantly more selected than open habitat from sunrise until late afternoon, after sunset open habitat became the most selected habitat

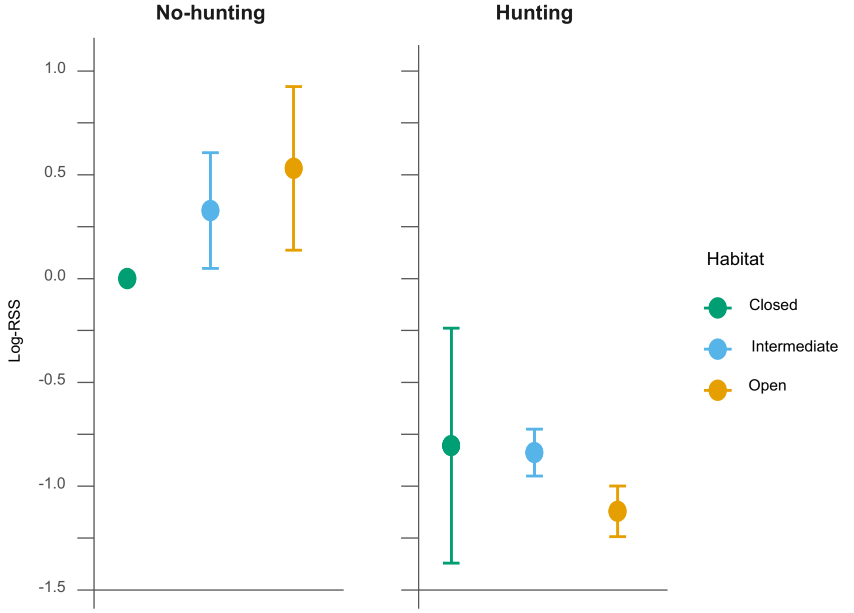

Figure 2. Selection of closed (> 80% canopy cover), intermediate (30–80%) and open (< 30%) habitat in the hunting and no-hunting zones of BGNP. The values of log(relative selection strength) compare to the reference category closed habitat in the no-hunting zone. Values above 0 indicate stronger selection, values below 0 indicate avoidance.

Table 1. Output of the model to investigate habitat selection in the no-hunting and hunting zones in Berchtesgaden National Park. The table shows the model output for the variables used in the analysis. The intermediate and open habitats are set in relation to the reference category closed, the hunting zone to the no-hunting zone. Slope and elevation were added to the model as quadratic terms.

Parameters	Estimate	SE	z value	Pr(>|z|)
Intercept	−10.23	0.82	−12.53	< 0.001***
habitat.intermediate	0.33	0.14	2.30	0.02*
habitat.open	0.53	0.20	2.64	0.008**
zone.hunting	−0.80	0.29	−2.79	< 0.005**
Elevation	1.10	1.78	0.60	0.55
Elevation^2	−0.83	0.74	−1.13	0.26
Slope	1.71	0.35	4.94	< 0.001***
Slope^2	−0.39	0.03	−11.15	< 0.001***
habitat.intermediate:zone.hunting	−0.09	0.06	−1.50	0.13
habitat.open:zone.hunting	−0.36	0.06	−5.87	< 0.001***

until early morning. During the middle of the night, open habitat within the hunting zone exhibited high attractiveness comparable to the reference level – closed habitat in the no-hunting zone at midday. In contrast, closed habitat in the hunting zone was the most selected habitat at midday but remained less attractive than the reference level. Slope and elevation had comparable effects to the model for hypothesis 1 (Table 2).

The comparison of movement patterns, specifically hourly step length, revealed more pronounced differences between day and night across all habitat types within the hunting zone (Fig. 4). Step length differences were significant for all habitats ($p < 0.05$), with nocturnal movements being consistently longer. The most pronounced difference was observed in closed habitat (44 m), followed by open habitat (25 m) and intermediate habitat (20 m). In contrast, within the no-hunting zone, circadian differences in movement across habitats averaged less than five meters and were only statistically significant for open habitat. Overall, red deer exhibited the shortest step lengths in closed habitat during the day and the longest step lengths in open habitat during the night within the hunting zone.

Discussion

We examined how hunting shaped female red deer habitat selection in Berchtesgaden National Park, Germany. Comparing selection patterns between hunting and no-hunting zones, we accepted our first hypothesis, finding distinct differences in habitat selection dependent on the hunting regime: red deer preferred closed habitats in the hunting zone but selected open habitats more frequently in the no-hunting zone. The spatiotemporal analysis supported our

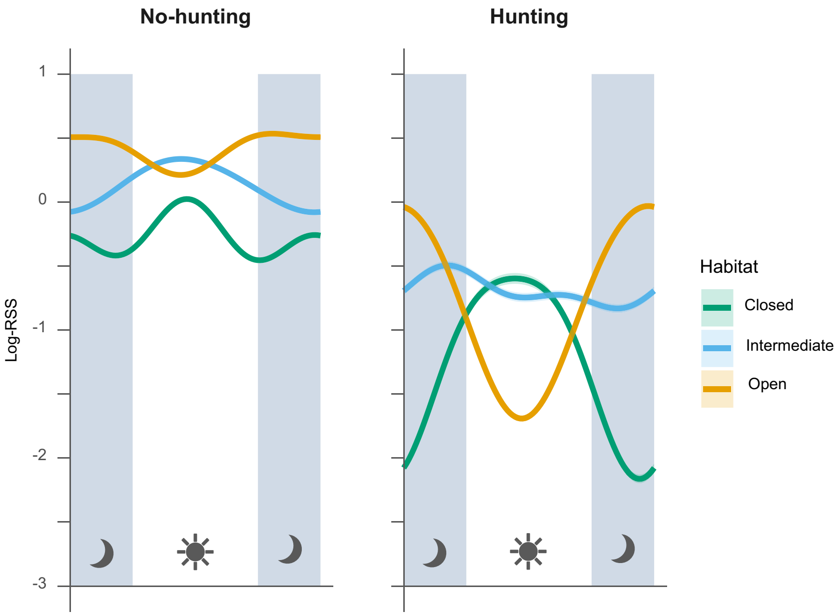

Figure 3. Circadian selection of closed (> 80% canopy cover), intermediate (30–80%) and open (< 30%) habitat in the hunting and no-hunting zones of BGNP. The x-axis displays time, with the grey shaded areas representing night, the light areas day. The transition between day and night corresponds to sunrise and sunset. The values of log(relative selection strength) compare to the reference category closed habitat in the no-hunting zone at midday. Values above 0 indicate stronger selection, values below 0 indicate avoidance.

Table 2. Output of the model to investigate circadian habitat selection in the no-hunting and hunting zones in Berchtesgaden National Park. The table shows the model output for the variables used in the analysis. The intermediate and open habitats are set in relation to the reference category closed, the hunting zone to the no-hunting zone. Slope and elevation were added to the model as quadratic terms. To incorporate the cyclical nature of time, trigonometric functions of time were included in the model sin(time)+ sin(2*time) + cos(time) + cos(2*time)

Parameters	Estimate	SE	z value	Pr(>|z|)
(Intercept)	−11.67	0.89	−13.13	< 0.001***
habitat.intermediate	0.56	0.10	5.69	< 0.001***
habitat.open	0.43	0.13	3.43	< 0.001***
sin(time)	0.28	0.05	5.21	< 0.001***
sin(2*time)	0.09	0.05	1.66	0.10
cos(time)	−0.73	0.06	−11.89	< 0.001***
cos(2*time)	−0.10	0.05	−1.87	0.06
zone.no-hunting	0.98	0.30	3.29	0.001**
elevation	2.47	2.33	1.06	0.29
elevation^2	−0.26	0.72	−0.35	0.72
slope	−1.85	0.26	−7.15	< 0.001***
slope^2	−1.76	0.28	−6.21	< 0.001***
habitat.intermediate:sin(time)	−0.16	0.06	−2.57	0.01*
habitat.open:sin(time)	−0.42	0.06	−6.80	< 0.001***
habitat.intermediate:sin(2*time)	−0.02	0.06	−0.32	0.75
habitat.open:sin(2*time)	−0.07	0.06	−1.09	0.28
habitat.intermediate:cos(time)	0.76	0.07	11.10	< 0.001***
habitat.open:cos(time)	1.55	0.07	22.12	< 0.001***
habitat.intermediate:cos(2*time)	0.07	0.06	1.15	0.25
habitat.open:cos(2*time)	0.06	0.06	0.91	0.36
habitat.intermediate: zone.no-hunting	−0.15	0.06	−2.48	0.01*
habitat.open: zone.no-hunting	0.25	0.07	3.69	< 0.001***
sin(time): zone.no-hunting	−0.23	0.06	−3.94	< 0.001***
sin(2*time): zone.no-hunting	−0.14	0.06	−2.43	0.02*
cos(time): zone.no-hunting	0.60	0.07	9.00	< 0.001***
cos(2*time): zone.no-hunting	0.24	0.06	4.13	< 0.001***
habitat.intermediate:sin(time): zone.no-hunting	0.16	0.07	2.43	0.02*
habitat.open:sin(time): zone.no-hunting	0.31	0.07	4.58	< 0.001***
habitat.intermediate:sin(2*time): zone.no-hunting	0.07	0.07	1.03	0.31
habitat.open:sin(2*time): zone.no-hunting	0.15	0.07	2.28	0.02*
habitat.intermediate:cos(time): zone.no-hunting	−0.82	0.07	−11.24	< 0.001***
habitat.open:cos(time): zone.no-hunting	−1.28	0.08	−17.03	< 0.001***
habitat.intermediate:cos(2*time): zone.no-hunting	−0.22	0.07	−3.36	< 0.001***
habitat.open:cos(2*time): zone.no-hunting	−0.24	0.07	−3.61	< 0.001***

second hypothesis, showing stronger circadian variation in selection under hunting conditions. In the hunting zone, red deer favoured open habitat at night and closed habitat during the day, reflecting risk avoidance, whereas open habitats were consistently preferred in the no-hunting zone. Overall, red deer selected stronger for habitats in the no-hunting zone compared to the hunting zone, suggesting habitat selection is primarily driven by risk levels rather than terrain characteristics, highlighting adaptive responses to hunting. Our findings demonstrate that female red deer exhibit highly flexible spatial and temporal strategies to navigate varying risk environments. By reversing their selection patterns for open and closed habitats between hunting and no-hunting zones, they effectively balance foraging opportunities with risk avoidance. The pronounced circadian shifts in habitat selection and movement rates further underscore the strong influence of hunting on their behavioural adaptations.

Adaptive behaviours, such as the increased selection for cover in response to hunting, as observed in our results, can negatively affect an animal's fitness, by restricting both spatial and temporal access to high-quality forage grounds (Dwinnell et al. 2019). For red deer, high-quality forage is primarily available in open areas with low canopy cover (Anderwald et al. 2016), while forests offer predominantly lower-quality forage (Spitz et al. 2019). As open areas only provide minimal protection against hunting, red deer select these habitats mainly at night in hunting zones, when darkness provides additional cover (Mysterud and Ostbye 1999) and hunting risk is low (Griesberger et al. 2022). Our findings further indicate that hunting influences movement patterns: by minimizing daytime movement, red deer reduce the likelihood of encountering hunters. However, as they predominantly remain in closed habitats during this period, access to optimal food resources is limited, potentially resulting in energy deficits. The increased step length observed at night within the hunting zone further suggests that they travel greater distances, likely to move from secure resting sites to high-quality foraging grounds, leading to increased energy expenditure. While movement reduction during the hunting season is a well-documented behavioural response

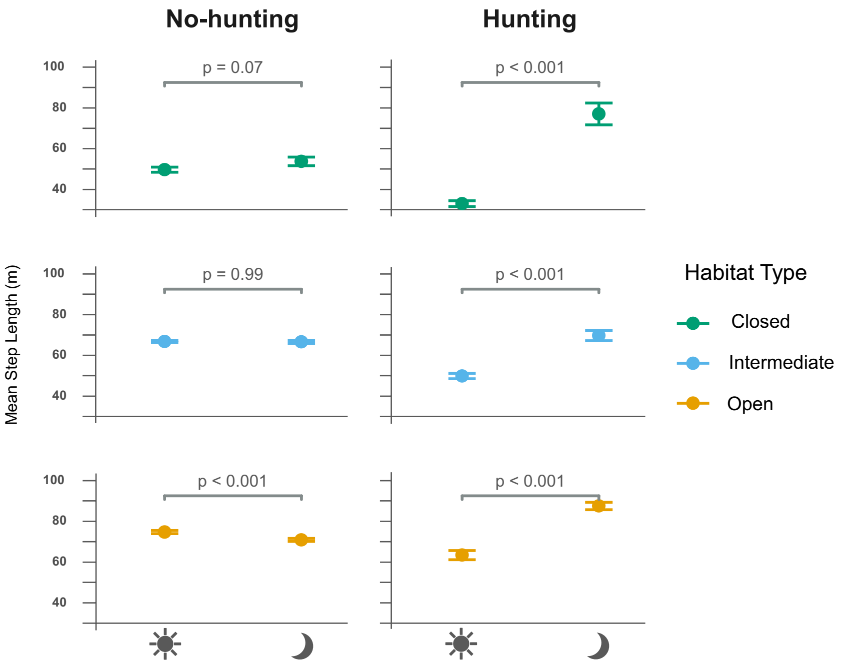

Figure 4. The day-night comparison of mean hourly step length within habitats and hunting regimes.

(Little et al. 2016, Marantz et al. 2016), our analyses revealed that this pattern occurred exclusively within hunting zones, highlighting how varying spatial and temporal risks drive distinct behavioural adaptations in red deer.

The pronounced circadian selection of open and closed habitats in the hunting zone of BGNP is an adaptive response to the experienced risk of being hunted (Richter et al. 2020). The response is particularly strong because hunting is spatially and temporally predictable within the red deer's home ranges (Lima and Bednekoff 1999, Ferrari et al. 2009). The absence of safe resting sites or the concentration of hunting activities mainly in open habitats may drive red deer to preferentially select forested habitats (Cromsigt et al. 2013). This, in turn, can result in increased vegetation impacts (i.e. the opposite of the intended effect of hunting), as they attempt to meet their energy demands within forest stands by browsing and bark stripping (Rajský et al. 2008). This effect may be particularly pronounced in regions where no nearby no-hunting zones are available that red deer can retreat to. In such regions, red deer are likely to further concentrate in dense forests, which often have limited understory vegetation and thus result in increased bark-stripping behaviour, with negative impacts on tree health (Gerhardt et al. 2013). However, similar effects may also arise if wildlife densities are too high or if no-hunting zones too small, as the animals are forced into them by hunting and are then reluctant to leave (Grignolio et al. 2011).

No-hunting zones are essential components of effective and sustainable wildlife management by providing refuges where natural ecological processes and behaviour can be conserved. However, in the absence of apex predators, ungulate populations in many protected areas, including national parks, tend to increase significantly (Cywicka et al. 2019). Consequently, wildlife management is practiced in over 65% of European national parks (van Beeck Calkoen et al. 2020). Our results suggest that hunting in national parks should be confined to designated areas where fostering forest regeneration are paramount, ensuring the presence of sufficiently large no-hunting zones where wildlife can exhibit natural behaviours with minimal human disturbances. This enables ungulates with habitat preferences like red deer to spend more time in open areas, which benefits their fitness (Hanley 1997) and reduces their reliance on forested areas for foraging, thereby decreasing the likelihood of negative vegetation impacts (Gerhardt et al. 2013).

In this study, we equipped solely female red deer with GPS collars, limiting our ability to generalise habitat selection behaviour to the entire population. Female deer likely exhibit more cautious behaviour, especially during periods when they are caring for offspring (Debeffe et al. 2017, Visscher et al. 2017). Future studies that include both sexes, as well as more precise data on factors such as age and maternal status, would provide a more comprehensive understanding of population-wide habitat selection and the differential responses of individuals based on sex and social status. Our analyses focused primarily on the selection of open versus closed habitats, as these provide forage and safety, respectively (Borkowski 2004). However, the relatively high use of intermediate habitats suggests they may offer a compromise between forage availability and safety. This hypothesis cannot be definitively confirmed using GPS data alone. Research incorporating activity data could offer deeper insights into how red deer utilise different habitat types, thereby elucidating the functional role of intermediate habitats in habitat selection and use. Our study analysed hunting pressure at the level of two categorical zones. To obtain a more detailed understanding of red deer responses to hunting, future research should incorporate explicit data on hunting events. This allows for more precise conclusions on how red deer respond to hunting pressure, such as by avoiding areas where recent kills have occurred (Chassagneux et al. 2020, Bojarska et al. 2024). In addition to hunting, other forms of human disturbances may influence the habitat selection of red deer. In our study area, these disturbances primarily include recreational outdoor activities such as hiking and cycling, the presence of mountain huts as well as alpine pasture management. While cycling and alpine pasture management covary with hunting as they are restricted to the hunting zone, the density of hiking trails does not differ between zones, and the number of tourists staying overnight in mountain huts is higher in the no-hunting zone. However, ungulates show stronger responses to any human disturbance in hunted populations than in non-hunted populations (Stankowich 2008, Marchand et al. 2014), so that we are confident that hunting is the dominant factor driving the differences in red deer habitat selection between the hunting and no-hunting zones of BGNP.

Our study found a strong association between hunting and red deer habitat selection. Specifically, we observed that in the hunting zone red deer exhibited a stronger selection for closed forests, particularly during daytime, when the risk of being hunted was highest. Hunting exerts a substantial influence on red deer behaviour, highlighting the need to balance the provision of sufficient undisturbed refuges with the implementation of conservation management plans. Such plans should aim to balance the health of ecosystems by regulating ungulate populations with minimising human-induced disruptions of their natural behaviours.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9ghx3ffw5 (Eggers et al. 2025).

Supporting information

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

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