

# WILDLIFE BIOLOGY

## Research

### Hunting suitability model: a new tool for managing wild ungulates

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Rising numbers of wild ungulates in human-dominated landscapes of Europe can induce negative effects like damages to forests. Therefore, effective wildlife management, including harvesting through hunting is becoming increasingly important. However, current hunting practices often fail to diminish those negative effects, as many ungulate species retreat to areas unsuitable for hunting. This predator–avoidance behaviour makes it difficult to fulfill the demand of reducing population numbers. Thus, there is an urgent need for innovative and effective wildlife management tools to counteract this problem. Here we provide for the first time a hunting suitability model for wild ungulate management in mountainous landscapes to visualise hunting suitability objectively and realistically. Using red deer as a model species, we modelled hunting suitability with high spatial resolution ( $10 \times 10$  m), based on remote sensing information, field surveys and expert knowledge of professional hunters. We analysed spatio-temporal habitat selection by radio-collared deer in relation to locations of varying hunting suitability. The suitability of various locations regarding hunting influenced the spatio-temporal habitat selection by this species, consistent with our hypothesis. Red deer avoided areas suitable for hunting during daylight hours in the hunting season, but not during the night. This species seems to perceive a landscape of heterogeneous anthropogenic predation risk, shaped by locations of various hunting suitability, as we modelled it. This confirms the empirical realism of the model. Concerning wild ungulate management, our hunting suitability model provides high-resolution predictions of where species like red deer will retreat when perceived anthropogenic predation risk increases. The model also yields useful insights regarding the hunting suitability of particular locations, which is valuable information especially for non-locals. Furthermore, the model can serve as planning tool to inform decisions about where particular hunting strategies can be performed most efficiently to manage wild ungulates and therefore minimize human–wildlife conflicts.

**Keywords:** accessibility, GPS telemetry, landscape of fear (LOF), red deer, spatio-temporal habitat use, transportability, ungulate management, visibility



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## Introduction

In many regions worldwide, effective wildlife management in human-dominated landscapes is important due to increasing numbers of wild ungulates (Apollonio et al. 2010, Putman et al. 2011, Cromsigt et al. 2013). This is especially true in mountain ranges like the European Alps, where damages to forests caused by wild ungulates not only lead to economic losses but also threaten the integrity and functionality of other forest functions (Gerhardt et al. 2013), like the protection against landslides and avalanches. The ungulate species of highest concern in this regard across many parts of Europe is the red deer *Cervus elaphus* (Gerhardt et al. 2013, Coppes et al. 2017). To diminish damages like browsing or bark stripping and thus mitigate human–wildlife conflicts while ensuring viable deer populations (Putman et al. 2011), sustainable management is required. Concerning this matter, hunting can play an important role by altering the spatial distribution of red deer in the landscape and reducing their numbers through harvesting (Heurich et al. 2015) to reach a population size with favourable sex and age structure. Current hunting practices often fail in this context, however, as many ungulate species like red deer, roe deer *Capreolus capreolus* (Padié et al. 2015) or white-tailed deer *Odocoileus virginianus* (Little et al. 2016) respond to the presence of humans through an avoidance behaviour to reduce the probability of being harvested (Cromsigt et al. 2013). To counteract this phenomenon, tools to inform sustainable management of these species are urgently needed.

When choosing a habitat animals must consider several factors, such as forage quality and availability, shelter and potential threats (Godvik et al. 2009). Likewise, habitat selection by red deer is strongly determined by the presence of food and cover provided by vegetation or topography (Mysterud and Østbye 1999, Heurich et al. 2015). To optimise a forage versus safety tradeoff, this species employs tactics to modulate habitat selection (Zweifel-Schielly et al. 2009, Fattebert et al. 2019). For instance, it is common for red deer to use open forage habitats during darkness and covered habitats during daylight (Godvik et al. 2009) to counter certain effects like temperature, precipitation, wind and potential lethal risks.

To describe the spatial variation in risk, perception and response of prey, Laundré et al. (2010) developed the ‘landscape of fear’ (LOF) concept. Based on this concept, landscapes consist of peaks and valleys reflecting the level of fear of predation that a prey animal experiences. Predator–prey interactions include direct predation (lethal or consumptive effects) and modifications to prey behaviour in response to the anticipation or risk of possible attacks (Bonnot et al. 2013, Say-Sallaz et al. 2019). The mere presence of predators can be perceived as a threat, eliciting various anti-predation responses (Prokopenko et al. 2017, Say-Sallaz et al. 2019). This is referred to as non-lethal, risk or non-consumptive effects of predators on prey populations (Padié et al. 2015, Gaynor et al. 2019, Say-Sallaz et al. 2019).

Humans have replaced large carnivores as apex predators in numerous landscapes and now represent the

most important source of mortality for wild ungulates (Little et al. 2014, Apollonio et al. 2017). Thus, hunting can create non-consumptive effects and alter spatio-temporal distribution of game (Cromsigt et al. 2013). Consequently, wild ungulates may retreat to areas unsuitable for hunting, including areas with limited visibility or access for humans (Apollonio et al. 2010, Gehr et al. 2018). This phenomenon is common in mountainous regions, where areas of low risk are unsuitable for hunting due to their remoteness, steepness or roughness (Apollonio et al. 2010). In summary, Hunting can induce a LOF (Gaynor et al. 2019), which makes it difficult to fulfil the demand of reducing certain ungulate species.

To better understand animals’ spatio-temporal behaviour, habitat suitability models (HSMs) are used to predict species occurrence through the modelling of environmental variables (Ottaviani et al. 2004). HSMs are usually composed of cells with values range from zero (low suitability) to one (high suitability), indicating how close the local environment is to the species’ optimal habitat (Hirzel et al. 2006). Similar to HSMs, a visualisation of hunting suitability from a human perspective could be essential to understand wild ungulate behavioural responses to hunters and changes in levels of perceived anthropogenic predation risk.

Several studies (Lebel et al. 2012, Lone et al. 2014, Plante et al. 2016) have addressed aspects surrounding the hunting suitability of ungulates. However, to our best knowledge no model exists, that generates spatially explicit predictions and visualisations of hunting suitability in mountainous landscapes. Therefore, we develop for the first time a high-resolution hunting suitability model, focusing on hide hunting and stalking, that enables a precise delimitation of locations according to variability in hunting suitability. This model can serve as new management tool to reduce negative effects of increasing numbers of wild ungulates by providing means to understand how species perceive anthropogenic predation risk. Based on this knowledge, hunting strategies can be adapted to increase harvest efficiency by altering the spatial distribution and behaviour of these species.

To generate such a model, we use red deer as a model species and combine information from remote sensing, field surveys and expert knowledge of professional hunters. To quantify habitat selection by this species we employ GPS telemetry. In this context, spatio-temporal habitat use by red deer is analysed in relation to assumed levels of anthropogenic predation risk based on the hunting suitability model.

Regarding the LOF concept, we hypothesise that red deer adapt its habitat use to minimize predation risk. We then predict that within the hunting season and during daylight hours, when humans are frequently active outdoors, red deer avoid areas suitable for hunting. During the night, we expect no avoidance of these areas, due to the behavioural plasticity of this species. Thus, we anticipate that red deer is able to discriminate areas of different hunting suitability and adapt its spatio-temporal behaviour to reduce the risk of being harvested.

## Material and methods

### Study site

The study site of 3367 ha was part of a larger hunting ground (10 203 ha) located in the Austrian province Salzburg (Fig. 1). The area belongs to the Central Alps and altitude ranges between 868 and 2392 m a.s.l. It consisted of 2% anthropogenic infrastructure, 36% woodland, 58% meadows and pastures, 3% rocks and 1% waterbodies (calculated via remote sensing).

Concerning game management, the area can be considered as one unit, in which red deer regulation via hunting is mainly performed by professional hunters. On average 60 red deer are hunted annually, based on harvest quota given by local authorities (for details on hunting management in Austria see Trouwborst and Hackländer 2018). Based on hunting protocols, annual harvest quotas are achieved by hide hunting (80%), stalking (10%) and drive hunting (10%). The hunting season starts on 1 May and lasts until 31 December, depending on sex and age. Meadows, coniferous forests, dominated by Norway spruce *Picea abies* as well as mixed forests, consisting of European larch *Larix decidua*, European beech *Fagus sylvatica*, maple species *Acer* sp., silver fir *Abies alba*, Norway spruce and shrubs characterise the study site. Currently, woodlands cover 1208 ha, consisting of 815 ha protective forest and 393 ha managed forest for timber production. Open areas in the valley and between 1700 and 2300 m a.s.l. are used for livestock farming (mainly cattle and sheep).

### Overview of the hunting suitability model

To determine hunting suitability regarding red deer in mountainous landscapes we defined three indices (Fig. 2): 1) *accessibility* of an area from a hunters' perspective, 2) *visibility* of red deer and 3) *transportability* of shot red deer. We selected these indices using data from literature (Lebel et al. 2012, Lone et al. 2015, Plante et al. 2016) and knowledge of professional hunters.

Terrain slope and vegetation density constitute the *accessibility* of an area. *Visibility* is determined by the density of vegetation and terrain roughness (Riley et al. 1999). Suitability concerning the transport of harvested game to the nearest road (*transportability*) is affected by slope and vegetation density as well. Hence, slope and vegetation density were considered multiple times because we supposed diverse influences on hunting suitability indices. For financial and topographic reasons, transport within the study site is usually carried out by hunters' own physical strength. Thus, *transportability* refers to the transport of shot deer by hunters themselves. Furthermore, we included hiking times between hunting sites and nearest roads or hunting huts in our calculations. We did not incorporate snow cover in late autumn–winter in the model, as this variable can vary considerably depending on the year and region (e.g. due to spatio-temporal variation in the amount of snow or timing of snowfall). However, and to ensure that the model can be adapted and transferred to other study sites we developed it in a way that additional variables can be included, if necessary.

We built and visualised the model using ArcGIS® and ArcMap™ (ESRI, Redlands, CA, USA), following a structure similar to HSMs (U.S. Fish and Wildlife Service 1981). We digitally transformed our study site into a mesh of 10 m and measured terrain slope, vegetation density, terrain roughness and hiking times via remote sensing and field surveys. Based on the knowledge of professional hunters we transformed characteristics of these variables into suitability values regarding the three indices. We calculated *accessibility*, *visibility* and *transportability* for each square and finally combined these indices to predict overall hunting suitability (Fig. 2).

We implemented the model for the whole hunting season, divided into two periods (May–October and November–December).

### Remote sensing

We determined slope, roughness and vegetation types in the study site with a resolution of 1 m by airborne laser-scanning data and digital orthophotos, provided by the geographical

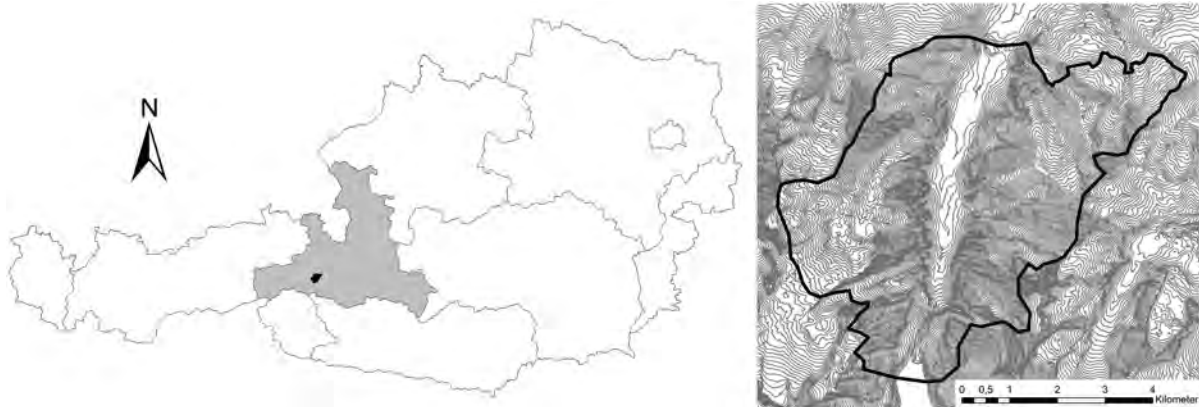


Figure 1. Study site (left: black area, right: black line) of 3367 ha located in the Central Alps in the Austrian province Salzburg (left: grey area). Grey lines in the right picture symbolise 25 m contour lines.

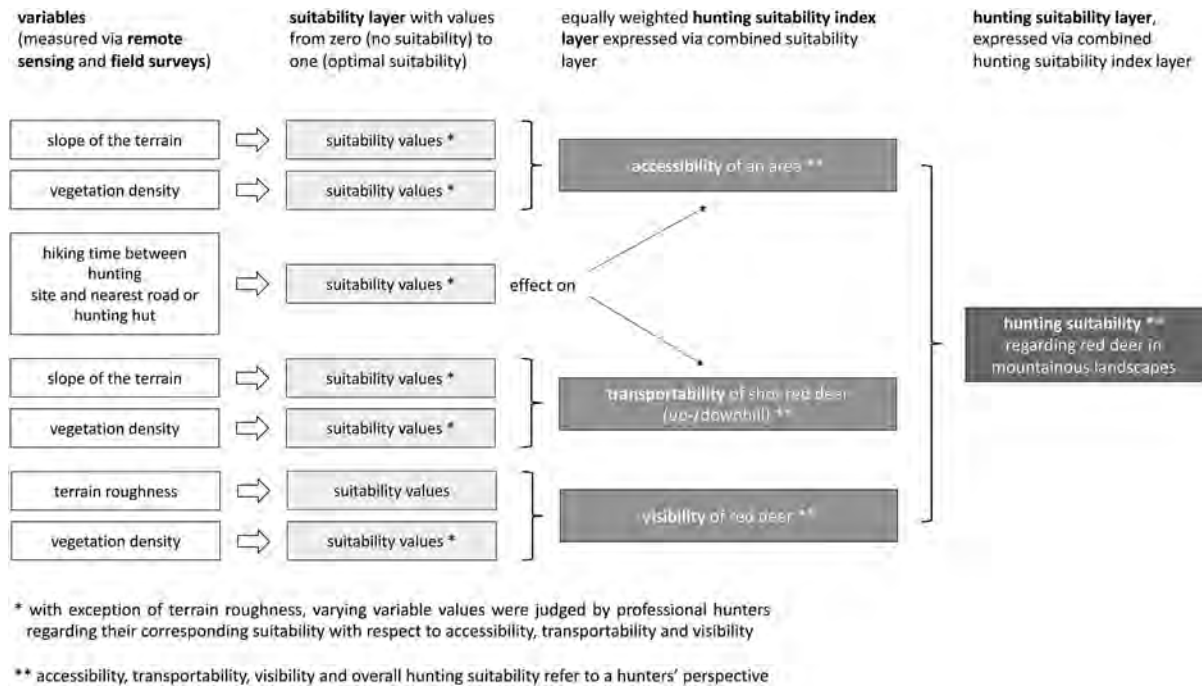


Figure 2. Conceptual diagram of the hunting suitability model.

information system of the province Salzburg. We further digitised roads, trails, hunting huts and meadows.

Based on a digital terrain model (DTM) we calculated slope using the tool Slope in the Surface toolset within the ArcGIS Spatial Analyst toolbox. The computation of roughness was performed according to Riley et al. (1999) to display terrain ruggedness indices (TRIs). TRIs were transformed into five categories with equal intervals (Supporting information).

To classify vegetation within the study site into several types (Table 1) we used Orthophotos with a near infrared channel to discriminate deciduous, coniferous and mixed forests. Differences in altitude between the DTM and a digital surface model (DSM) were used to differentiate vegetation

heights. Vegetation densities were estimated by the DSM. If there were uncertainties during the classification process (e.g. vegetation type assignments were not possible), particular locations were visited on foot and categorised directly in the field. In total 31 locations were inspected and seven of these were reclassified.

### Field surveys to determine vegetation density

For all vegetation types listed in Table 1, we determined vegetation density standardised in the field. For each type, up to seven representative plots within the study site were selected. In total 95 plots were visited on foot. To link vegetation types with corresponding densities, we used a 100 × 50 cm panel

Table 1. Characterisation of vegetation types within the study site. Pole and tree forests were additionally subdivided into deciduous, mixed and coniferous forests.

| Vegetation type                  | Description                                                                                         |
|----------------------------------|-----------------------------------------------------------------------------------------------------|
| No vegetation                    | 0% ground cover, without any trees                                                                  |
| Low vegetation                   | Ground cover less than 30%, without any trees                                                       |
| Meadow                           | More than 30% ground cover, without any trees, farmed                                               |
| Unused grassland                 | More than 30% ground cover, without any trees                                                       |
| Young stands                     | Young trees up to heights of 70 cm                                                                  |
| Between young stands and thicket | Young trees with heights from 70 to 130 cm on up to half of the area                                |
| Thicket                          | Very dense stand of young trees with heights from 130 cm to 5 m covering more than half of the area |
| Pole forest 1 – low density      | Tree heights from 5 to 10 m and ground vegetation on more than 50% of the area                      |
| Pole forest 1 – high density     | Tree heights from 5 to 10 m and ground vegetation on less than 50% of the area                      |
| Pole forest 2 – low density      | Tree heights from 10 to 20 m and ground vegetation on more than 50% of the area                     |
| Pole forest 2 – high density     | Tree heights from 10 to 20 m and ground vegetation on less than 50% of the area                     |
| Tree forest – low density        | Trees higher than 20 m and ground vegetation on more than 50% of the area                           |
| Tree forest – high density       | Trees higher than 20 m and ground vegetation on less than 50% of the area                           |

Vegetation types were classified according to Reimoser et al. (2006).

(comparable in height and length to the body of a female red deer), equally divided into 32 squares (Supporting information). At each plot we took photographs of the panel from distances of 10, 20 and 30 m, respectively. The direction towards the panel was chosen randomly. We measured distances using a Haglöf Vertex Ultrasonic Rangefinder.

Based on these photographs, we calculated the average number of visible squares per vegetation type for all three distances. According to Griffith and Youtie (1988), one square counted as visible, if less than 50% of it was covered by vegetation. Next, we determined the distance up to which at least 50% of the panel was visible and used this metric as reference for vegetation density. Far distances referred to low densities and therefore high visibilities and conversely. We set areas where a visibility of 50% was not reached at any distance to zero and summarised them into the category 'maximal density' (visibility completely blocked). Areas with 50% visibility at distances up to 300 m, as well as roads and trails were categorised as 'minimal density'. Based on knowledge of professional hunters, 300 m referred to the average maximum shooting distance.

Furthermore, we used these photographs to predict altered vegetation densities at the end of the year, by virtually excluding leaves and ground vegetation like raspberry *Rubus idaeus*, nettle *Urtica dioica* and ferns. These species can be found mostly in montane regions (Lauber et al. 2012), at altitudes between 868 and 1200 m a.s.l. within our study site. Therefore, we considered areas higher than montane regions and meadows used for livestock farming free from these species.

### Hunter judgements

To link varying terrain slopes and vegetation densities with suitability values regarding *accessibility*, *visibility* and *transportability*, we again selected representative plots within the study site via remote sensing. At the centre of each plot, we took a 360° photograph using a Ricoh Theta S camera. In total 14 photographs that represented the range of slope (3–140%, divided into intervals of approximately 10%) and 11 that represented vegetation densities from minimum to maximum (based on vegetation types listed in Table 1) were taken (Supporting information). We then presented these 25 photographs to 20 selectively chosen male professional hunters. The hunter's age ranged from 23 to 62 years with a mean age of 42 years. We selected them based on their experience (several years at least) regarding the management of red deer in mountainous landscapes. Eight of them hunted in the study site before. We presented all 360° photographs to each hunter in a random order via an Ipad mini 4 using the Ricoh Theta S App. This provided them the possibility to rotate, pan and zoom within each photograph. With this approach we simulated the experience of standing on the ground where the photograph was taken.

Based on the 360° photographs, the hunters separately evaluated *accessibility* and *transportability* (up- and downhill),

by linking varying slopes and vegetation densities with suitability values. Regarding these values a continuous scale with two decimal points from zero (no suitability) to one (optimal suitability) was used. *Visibility* based on vegetation densities was evaluated in the same way. Apart from the photographs, hunters received no additional information regarding the plots.

To incorporate the influence of distance between hunting site and nearest road or hunting hut on hunting suitability, we asked questions about hunters' preferred hiking time (optimal condition), average hiking time based on their experience (normal condition), and maximum hiking time they would invest (worst condition) to reach a hunting spot. We advised the participating hunters to consider that they theoretically must transport harvested game back to the nearest road. Thus, hiking time is not only shaped by the path chosen for approaching the hunting spot, but also by the way back, including the transport of red deer.

### Model building

Initially, we generated a 10 × 10 m grid cell layer covering the whole study site. We deleted cells intersecting waterbodies or buildings. We used remote sensing to determine slope and vegetation density (based on vegetation types listed in Table 1) for each cell. Based on hunter judgements we created scatter plots with polynomial regression lines via Microsoft Excel, ver. 15.36 illustrating how *accessibility*, *visibility* and *transportability* were shaped by slope and vegetation density (Supporting information). Using formulas of these polynomial regression lines, we converted slope and vegetation density values within each grid cell into suitability values from zero (no suitability) to one (optimal suitability) regarding each hunting suitability index. As a result, five out of seven suitability layers were generated, accounting for the effects of slope on *accessibility* and *transportability* and vegetation density on *accessibility*, *transportability* and *visibility* (Fig. 2).

Further, we estimated the average time needed for crossing each grid cell by foot with a formula of Alpine Associations in Austria (VAVÖ, Vienna, Austria) to calculate hiking times in mountainous landscapes:

$$T = \text{greater time value}(t_1 \text{ or } t_2) + \frac{1}{2} \times \text{smaller time value}(t_1 \text{ or } t_2)$$

$T$  ... total hiking time to cross a given grid cell

$t_1$  ... hiking time based on width of grid cell (width [m] × 0.015)

$t_2$  ... hiking time based on difference in altitude per grid cell (calculated via the DTM) (uphill: difference [m] × 0.2; downhill: difference [m] × 0.12). We designated each grid cell as 'up'- or 'downhill' with respect to the nearest road or hunting hut.

Based on these calculations, we determined hiking times between each cell and the nearest road or hunting hut. Next, we determine via remote sensing which grid cells can be reached under optimal, normal and worst conditions (see hunter judgements). We transformed the outcome into a sixth suitability layer with values from zero to 0.75 (zero = not reachable, 0.25 = reachable under worst conditions, 0.5 = reachable under normal conditions, 0.75 = reachable under optimal conditions). This layer accounted for the effect of hiking time on *accessibility* and *transportability*.

As indicated in Fig. 2, corresponding suitability layers (slope, vegetation density and hiking time) were combined by summation to model *accessibility* and *transportability*. Recognising that costs like physical effort increase with distance walking we included cost- and path-distance computations in our calculations by using the tools Cost Distance and Path Distance in the Distance toolset within the ArcGIS Spatial Analyst toolbox. For these calculations, roads and hunting huts were used as starting points. Regarding the transport of shot deer, roads serve as end points. We did not consider hunting huts as suitable end points, since the lack of refrigeration preventing meeting hygiene standards for storing game (Paulsen et al. 2011).

To model *visibility*, we connected the corresponding vegetation density suitability layer with calculated ruggedness indices (seventh suitability layer). Particular we used the tool Viewshed in the Surface toolset within the ArcGIS Spatial Analyst toolbox to calculate the influence of each TRI category on visibility.

To visualize hunting suitability for the part of the hunting season with growing vegetation (May–October), we merged the modelled hunting suitability index layers (*accessibility*, *transportability* and *visibility*) by summation. Based on input from the professional hunters, we assumed equal weights of importance among these layers. To predict hunting suitability outside of the vegetation period from November to December, we used calculated vegetation densities at the end of the year within the described calculations. In the study site, red deer regulation usually takes place at the end of the year. We therefore used the second period (November–December) as basis for determining hunting suitability classes. Based on quantiles of the final hunting suitability layer values (high values = high suitability, low values = low suitability), we generated five suitability classes (very suitable, suitable, moderate, poor, not suitable).

To account for how much variation in hunting suitability is due to *accessibility*, *visibility* and *transportability* we performed commonality analyses (CA) similar to Ray-Mukherjee et al. (2014). We used CA to investigate unique and common effects of these three indices on hunting suitability during May to October and November to December by decomposing  $R^2$  from multiple regressions. Unique effects display the amount of variance independently shaped by *accessibility*, *visibility* or *transportability*. Common effects reveal how much variance is common to a set of these indices. The total variance explained is calculated by a summation of unique and common effects.

## Red deer telemetry

To analyse spatio-temporal behaviour of red deer in relation to assumed levels of anthropogenic predation risk as indicated by the hunting suitability model, we equipped 20 adult deer (10 females, 10 males) with GPS collars (GPS PLUS collar, Vectronic Aerospace, Berlin, Germany) from 2015 to 2018 (Supporting information). We either captured deer in wooden box-traps (length 3.3 m, width 1.3 m, height 2 m) or freely darted them at feeding sites. We anaesthetized the captured or free-ranging animals by remote injection using a filled dart (3 ml air pressurised dart DAN-INJECT Smith) containing a combination of 2.5 mg kg<sup>-1</sup> ketamine and 3 mg kg<sup>-1</sup> xylazine per estimated body mass. The dart was projected into the muscles of the pelvic girdle via a carbon dioxide powered rifle (Dan-Inject Smith; Model JM) or carbon dioxide powered pistol (PL4 anaesthesia pistol, Telinject GmbH, Dudenhofen/Pfalz, Germany). To reverse the xylazine-component of the anaesthesia combination the animals were antagonised by intramuscular injection of atipamezole. All animals were observed until recovery.

To retrieve collars, deer were harvested (8 individuals), or an integrated drop-off unit was used (12 individuals). The tracking period of individual deer ranged between 6 and 29 months. Position recordings were taken in general every 2 h and 15 min, saved on the collar and transmitted to a ground station once a day per SMS.

## Quantifying landscape of fear effects

For testing our hypothesis, we analysed spatio-temporal behaviour of red deer within the hunting season using R ver. 3.6.1 (<www.r-project.org>) and RStudio ver. 1.2.5019 (<www.r-project.org>). See the Supporting information regarding all packages used.

In this assessment, we only included validated GPS points (five or more satellites were used to calculate positions) with a dilution of precision value smaller than 10. We calculated home ranges for each individual using enhanced local convex hulls (T-LoCoHs, Lyons et al. 2013). With this approach we balanced the temporal autocorrelation of GPS data by incorporating the time stamp of each location. Previous to analyses, we checked our data for possible gaps (missing positions) and bursts of locations that are closely spaced in time due to changes in sampling frequency (recording interval) during data collection. By plotting the cumulative percentage across sampling frequencies, we detected bursts of points in our data. We thinned out those bursts to avoid bias by using the package tlocoh ver. 1.40.07 (Lyons et al. 2019). Through this process and regarding a sampling frequency of 2 h and 15 min, we had a good temporal consistency in our data and an average fix rate success of 93%. Based on Godvik et al. (2009) we considered this rate as sufficient for our analyses. Finally, approximately 4500 GPS positions per individual were used for home range and selection indices calculations.

By using the hunting suitability model, each home range was divided into areas of different suitability classes for July to October and November to December, respectively. These areas represented the available habitat for each collared deer during these periods, measured in m<sup>2</sup>. We did not include the months January to June in the analyses, as hunting of red deer in the study site usually starts with July.

To each GPS point collected during either period, we assigned the corresponding hunting suitability class. Based on Manly et al. (2002) we linked available and used habitats, where the latter was expressed as the number of GPS locations within each class. To test habitat selection by red deer, we calculated Manly selectivity measures (selection ratios = used/available) and analysed preference or avoidance of areas with varying hunting suitability. We used our hunting suitability model and not actual culling locations as a spatial indicator of perceived human threat, as the association between single hunting sites and predation risk within our study site is shaped by several unquantified factors (e.g. hunters' behaviour, number of red deer witnessing the death of a conspecific, wind).

By measuring used and available habitat for individuals separately, we considered that the proportions of different categories of available habitat and the use of those varied between each collared deer. Thus, we treated the selection of single animals as independent events and estimated selection ratios for each animal using a type III log-likelihood test statistic (Khi2L) approach. We used  $\chi^2$  tests to examine habitat selection for all animals and for each individual animal.

We calculated selectivity measures for day and night for each sex to consider temporal changes of preferences and sexual differences. We defined one hour before sunrise until one hour after sunset as 'day' (daylight hours). We included only those individuals in the analyses for which sufficient data were available ( $n_{\text{(July–October)}} = 9$  females, 9 males;  $n_{\text{(November–December)}} = 8$  females, 7 males).

## Results

### Hunter judgements

Professional hunters assigned steep areas and higher vegetation density with low suitability values, whereas flat areas and low vegetation density were linked with high suitability values. Thus, *accessibility* and *transportability* (up- and down-hill) decreased with increasing slope. Declining vegetation density was linked with increasing *accessibility*, *visibility* and *transportability*. All mentioned relationships were non-linear (Supporting information). Areas steeper than 140% (54.46 degrees) were judged by hunters as not suitable, due to a lack of *accessibility* and impossibility to transport deer without technical devices.

Concerning hiking times, 12.5 min ( $\pm 2.75$  min) were estimated by professional hunters to cover an optimal distance (optimal condition) between the hunting place and nearest road or hunting hut. They noted one reason for having some hiking was to avoid shooting next to infrastructure. Average hiking time (normal condition) was estimated as 30 min ( $\pm 4.45$  min). Regarding maximum hiking time (worst condition), they would invest 90 min ( $\pm 8.04$  min) to reach a hunting spot.

### Hunting suitability model

The model indicated better hunting suitability from November to December compared to May to October (Fig. 3), which illustrates the influence of vegetation.

In general, open as well as flat areas with low vegetation density and regions close to roads or hunting huts were characterised by good suitability (Fig. 4a). A low suitability was linked to steep or rough areas, high vegetation densities and regions far away from infrastructure. The CA highlighted the unique influence of *visibility* on hunting suitability during May to October and November to December (Table 2). Effects of vegetation density on hunting suitability shown

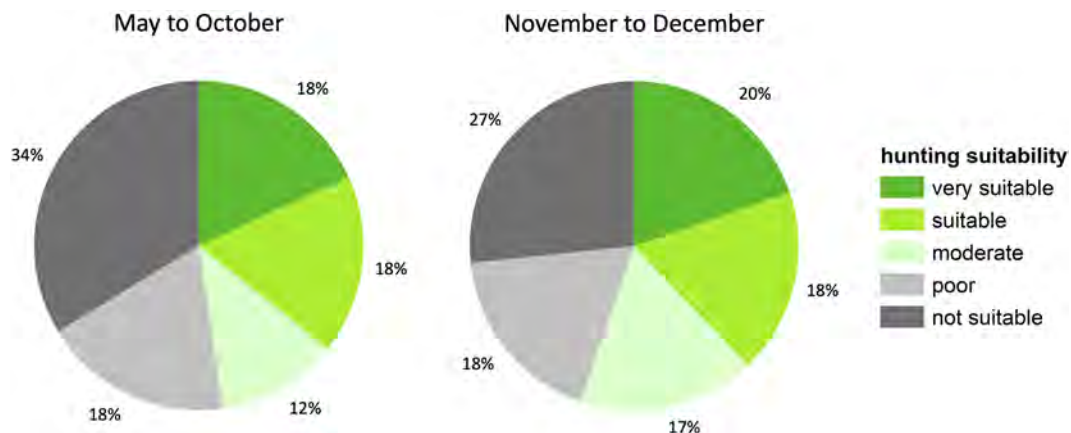


Figure 3. Changes in hunting suitability regarding red deer during the hunting season from May to October (growing vegetation) and November to December (outside of the vegetation period), illustrated in area percent. This figure relates to a study site of 3367 ha in the Central Alps.

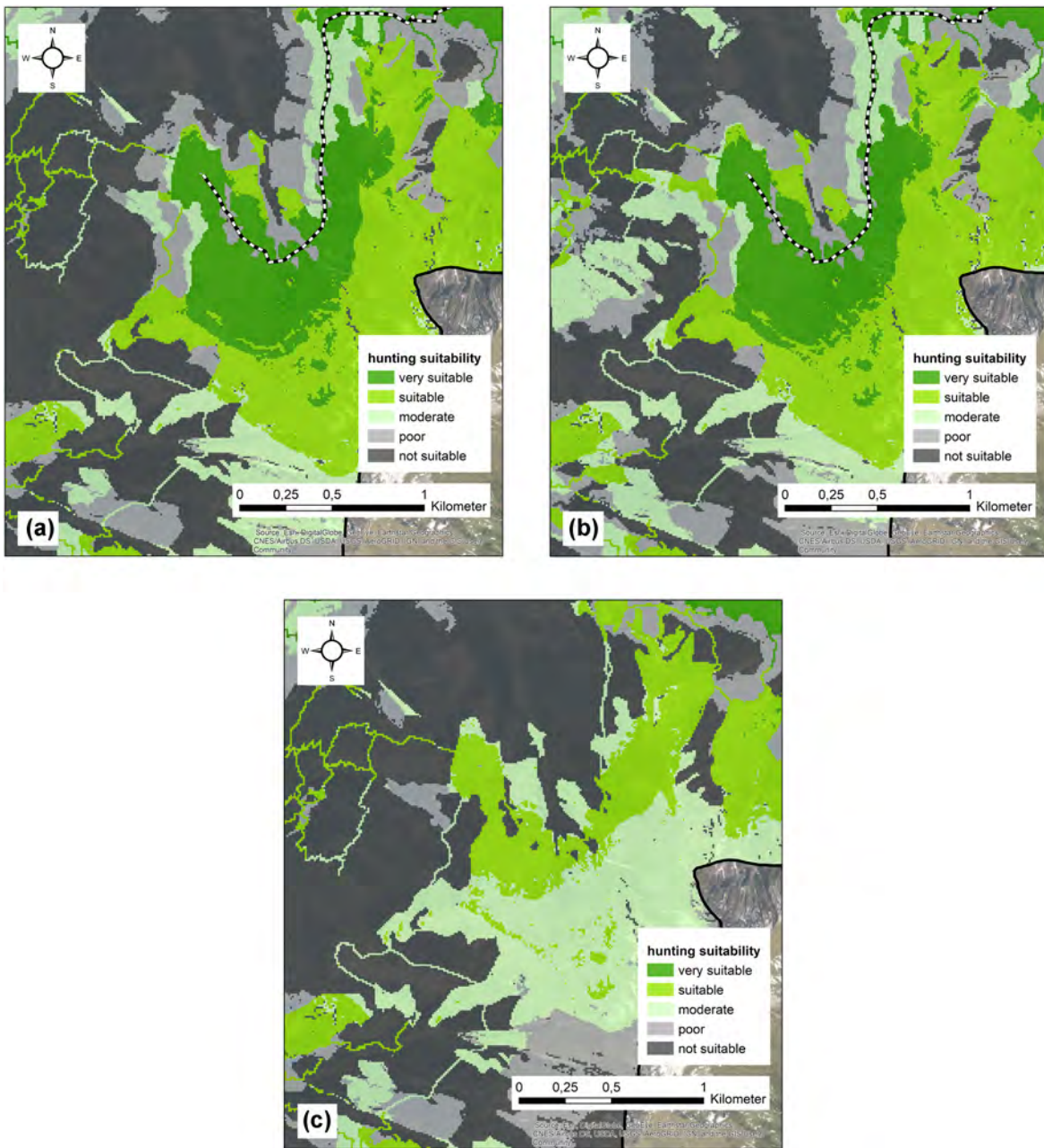


Figure 4. Hunting suitability regarding red deer within a part of the study site with a 10 m resolution from (a) May to October (growing vegetation), (b) November to December (outside of the vegetation period) and (c) May to October, under the assumption that no road (striped line) exists in this area. As trails were linked with minimal vegetation density values, they are also visible. The bold black line marks the border of the study site.

Table 2. Effects of commonality coefficients on hunting suitability regarding red deer in mountainous landscapes during May to October and November to December. Numbers represent the explained variation in percent. <sup>1</sup> Accessibility of an area from a hunters' perspective, <sup>2</sup> visibility of red deer, <sup>3</sup> transportability of shot red deer.

| Coefficients                  | May-Oct |        |       | Nov-Dec |        |       |
|-------------------------------|---------|--------|-------|---------|--------|-------|
|                               | Unique  | Common | Total | Unique  | Common | Total |
| Accessibility <sup>1</sup>    | 2.83    | 32.73  | 35.56 | 2.79    | 38.10  | 40.89 |
| Visibility <sup>2</sup>       | 41.42   | 17.21  | 58.63 | 37.24   | 15.83  | 53.07 |
| Transportability <sup>3</sup> | 5.22    | 53.34  | 58.56 | 5.55    | 57.21  | 62.76 |

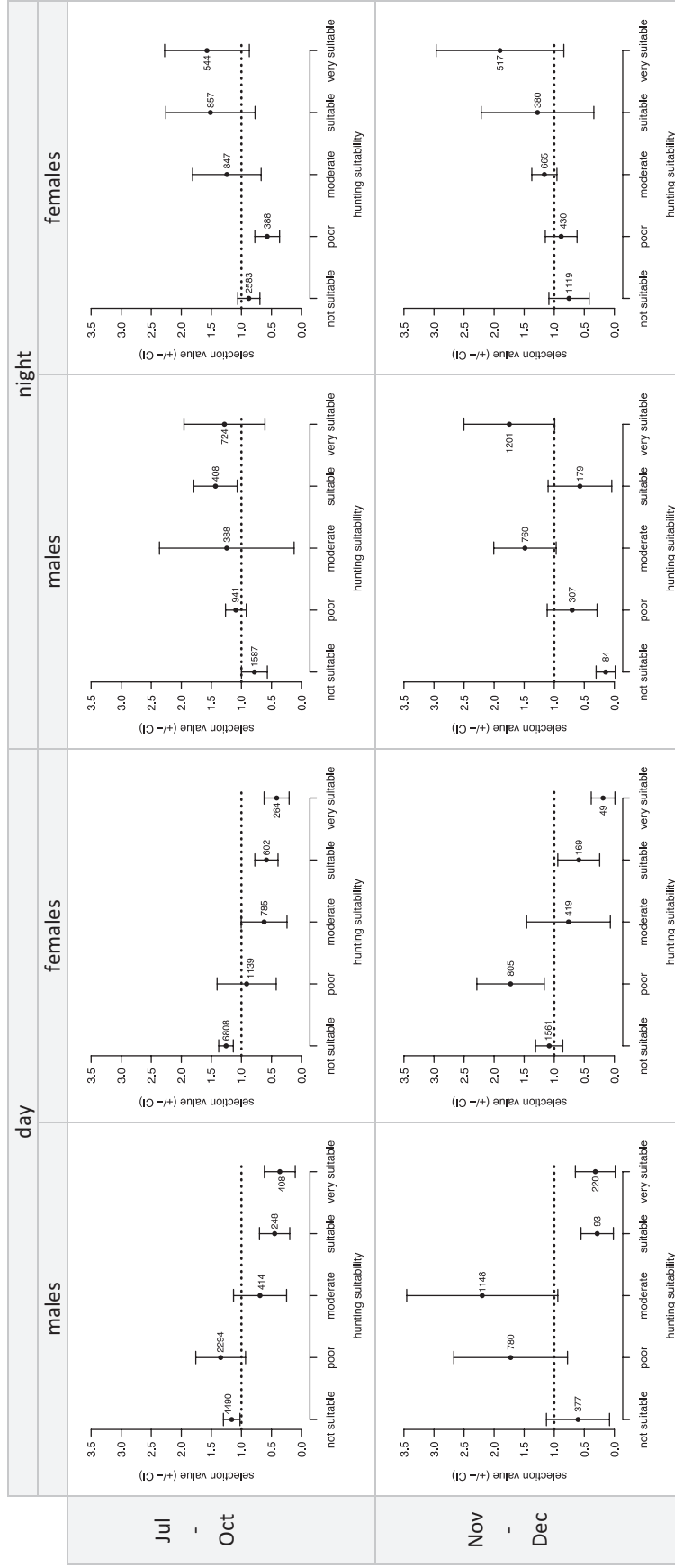


Figure 5. Selection of areas with varying hunting suitability by adult red deer of both sexes within the hunting season from July to October (9 females, 9 males) and November to December (8 females, 7 males) during day and night, respectively. One hour before sunrise until one hour after sunset was defined as 'day'. Points represent mean selection values. Values larger than 1 represent positive selection, whereas values smaller than 1 illustrate negative selection, if the 99% confidence intervals (CI) do not include the value of 1. If a CI overlaps 1, utilisation of areas conforms with their availability. Numbers next to selection values represent the amount of GPS points recorded for each hunting suitability class.

Table 3. Log-likelihood test statistic (Khi2L), degrees of freedom (df) and p-values based on a habitat selection analysis according to Manly et al. (2002). Spatio-temporal habitat use by collared red deer was analysed in relation to assumed levels of anthropogenic predation risk based on areas of different hunting suitability. Selectivity measures were calculated separately for sex, season and time of the day.

|         | Males   |    |         | Females |    |         |
|---------|---------|----|---------|---------|----|---------|
|         | Khi2L   | df | p-value | Khi2L   | df | p-value |
| Jul–Oct |         |    |         |         |    |         |
| Day     | 891.84  | 36 | < 0.001 | 867.37  | 36 | < 0.001 |
| Night   | 322.33  | 36 | < 0.001 | 529.32  | 36 | < 0.001 |
| Nov–Dec |         |    |         |         |    |         |
| Day     | 1232.10 | 28 | < 0.001 | 548.66  | 30 | < 0.001 |
| Night   | 955.23  | 28 | < 0.001 | 413.28  | 30 | < 0.001 |

in Fig. 4b, compared to Fig. 4a were most likely responsible for this strong unique influence of *visibility*. Regarding common effects, *transportability* followed by *accessibility* affected hunting suitability the most during both periods. To demonstrate common effects of *accessibility* and *transportability* we excluded one road in the analysis exemplarily. This exclusion reduced the suitability in surrounding areas visibly (Fig. 4c). Furthermore, *transportability* was strongly affected by its direction (up- or downhill). Uphill areas (transport downhill) resulted in better suitability compared to those downhill the road (transport uphill).

The empirical realism of the model was supported by all professional hunters that were active in the study site ( $n=4$ ). They assessed randomly chosen areas with a diameter of 100 m, six for each hunting suitability class. A Spearman rank correlation showed a highly significant association ( $p < 0.001$ ) and good positive relationship ( $\rho = 0.76$ ) between the model predictions and hunter judgements (Supporting information).

### Landscape of fear effects

The comparison of used and available areas with varying hunting suitability revealed distinct patterns of habitat selection by red deer (Fig. 5). During daylight hours, areas suitable for hunting were avoided. During nighttime, this selection shifted and suitable areas were not avoided anymore. With slight differences, these patterns could be found during July to October and November to December for both sexes. Computed Manly's selectivity measures displayed highly significant overall habitat selection regarding males, females and both periods ( $p < 0.001$ , Table 3). The tested habitat selection for each collared deer was always very significant ( $p < 0.01$ ).

### Discussion

Increasing population densities of wild ungulates and associated negative effects, such as forest damages (Putman et al. 2011), in combination with inefficient hunting practices, highlight that additional solutions are needed to counteract rising numbers of these species. Thus, the request for science-based methods and tools is on the rise. Although multiple studies (Lebel et al. 2012, Lone et al. 2015, Plante et al.

2016) suggested that hunting suitability regarding ungulate species is shaped by various factors, to our best knowledge there is no published method until now to create a predictive map of hunting suitability. We filled this gap by developing a high-resolution hunting suitability model as an innovative and effective tool to inform wild ungulate management in mountainous landscapes and to objectively determine and visualise hunting suitability. We modelled this suitability regarding hide hunting and stalking. Results concerning drive hunting may be different.

Comparable to ideal HSM (Jedrzejewski et al. 2008) we built the model by using variables that can be readily measured via remote sensing and field surveys, to ensure an easy application to diverse mountainous hunting grounds. By combining three hunting suitability indices (*accessibility*, *visibility* and *transportability*), we were able to model hunting suitability realistically, which was verified by professional hunters that were active in the study site. Further, we were able to display unique and common influences of these indices on overall hunting suitability. The empirical realism of the model was additionally confirmed by red deer in our study site. In particular, we found that habitat selection of red deer followed our assumption that they perceive a landscape of heterogeneous anthropogenic predation risk, like we modelled it.

Cromsigt et al. (2013) highlighted that in hunted ungulates, temporally predictable risk should lead to adjustments of habitat selection. A study by Fattebert et al. (2019) demonstrated that red deer selects risky habitats mostly at night, when hunting risk was low. Our study supports these findings by providing evidence that red deer select habitat relative to overall hunting suitability. Our results illustrate that regions unsuitable for hunting, including areas with steeper slopes, complex topography, high vegetation density and areas far away from roads were used by red deer preferentially during daylight hours. Besides other benefits of using such areas (e.g. the use of forests for thermal cover (Myserud and Østbye 1999, Gerhardt et al. 2013)), the spatio-temporal habitat use by red deer in our study site seems also to be shaped by perceived anthropogenic predation risk. We demonstrated that regions suitable for hunting, including open flat areas or areas close to roads were avoided by red deer during daylight hours. During nighttime, this avoidance behaviour disappeared. We found this pattern of habitat use in both sexes during July to October and November to December, which conforms to our risk-avoidance hypothesis. We thus suggest that red deer are capable to differentiate between areas according to hunting suitability, which corresponds with the level of anthropogenic predation risk. This species then adjusts its spatio-temporal habitat use to reduce the probability of being harvested.

These findings are supported by Wisdom et al. (2018), who demonstrated that wapiti *Cervus canadensis* in north-east Oregon (USA) prefer steep areas, presumably to avoid humans. In line with that, Lone et al. (2015) highlighted, that hunted red deer in central Norway select dense vegetation to

avoid being harvested. Padié et al. (2015) showed that roe deer in the southwest of France avoid risky habitats during the day but selected these habitats at night positively. Other studies especially regarding large mammals (Benítez-López 2018) like mouflon *Ovis gmelini* in France (Marchand et al. 2014), wild boar *Sus scrofa* in Sweden (Thurfjell et al. 2013) or white-tailed deer in Oklahoma (USA) (Little et al. 2016) had similar findings. Thus, wild ungulates of different regions seem to react to human disturbance and anthropogenic predation risk by an avoidance behaviour.

This behaviour can be linked with our model to provide detailed information about locations not suitable for hunting in which wild ungulates will likely retreat when perceived anthropogenic predation risk increases. The results of our study can be used to understand and explain marginal detectability and low harvest rates of ungulate species and associated management problems in regions comparable to our study site. Furthermore, our model can demonstrate how challenging it might be to regulate specific species in certain areas due to insufficient hunting suitability. The model can therefore provide valuable information especially for non-locals along with realistic background information for hunting authorities when setting hunting quotas (Trouwborst and Hackländer 2018). Regarding management recommendations, the verified behavioural plasticity of wild ungulates can be seen as an opportunity. By selectively altering the spatio-temporal distribution of anthropogenic predation risk, the LOF can be modified to increase visibility of species like red deer and therefore hunting success. Our model can serve as planning tool to decide where varying hunting strategies can be performed most efficiently to improve hunting success, reduce ungulate numbers and therefore lower human-wildlife conflicts. Such strategies could include an increase in hunting pressure to concentrate perceived anthropogenic predation risk in specific areas while lowering the risk in other areas to manage the spatial distribution of wild ungulates. Furthermore, in regions suitable for hunting long closed seasons with reduced anthropogenic predation risk can alternate with short open seasons to increase harvest rates by benefiting from reduced predator-avoidance behaviour. Thus, the utilisation of the model can contribute to selectively alter the spatial distribution of ungulate species in the landscape. Further, it can be used to adjust population numbers in relation to resources provided by the habitat and therefore also reduce intraspecific competition. Open foraging sites, which are suitable for hunting can become usable for species like red deer during daylight hours if hunting pressure is selectively reduced in such areas. Regarding sustainable wildlife management, the application of this new model can thus also have positive consequences for wild ungulates in the long term.

To modify a LOF successfully, it is important to be aware that perceived anthropogenic predation risk is not evenly distributed across the landscape. Furthermore, it is essential to know where various hunting strategies can be performed most efficiently. In this context a hunting suitability model can serve as necessary planning tool to alter anthropogenic predation risk across the landscape selectively. For the first time it is now possible to use

such a tool to visualise hunting suitability in mountainous landscapes, objectively and realistically.

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*Permits* – Complied with federal and state laws, collaring and immobilisation of red deer were authorized by the responsible agencies of Salzburg (official notifications: 20401-01072/4/10-2015, 20401-01070/21/10-2015).

## Author contributions

**Paul Griesberger:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (equal); Resources (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Leopold Obermair:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (equal); Supervision (supporting); Validation (supporting); Visualization (supporting); Writing – review and editing (supporting). **Josef Zandl:** Conceptualization (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Validation (supporting); Writing – review and editing (supporting). **Gabrielle Stalder:** Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Writing – review and editing (supporting). **Walter Arnold:** Formal analysis (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Klaus Hackländer:** Conceptualization (equal); Funding acquisition (equal); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.rbnzs7hcp>> (Griesberger et al. 2022).

## Supporting information

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

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