

ZÜRICH UNIVERSITY OF APPLIED SCIENCES  
DEPARTEMENT LIFE SCIENCES AND FACILITY MANAGEMENT  
INSTITUTE OF NATURAL RESOURCE SCIENCES

# Bed site selection analysis of roe deer fawns in the open land of Switzerland

A step towards alternative mowing regimes with reduced fawn-mortality

## MASTER THESIS

by

**Ninetta Graf**

Master of Science in Environment and Natural Resources  
Institute of Natural Resource Sciences  
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### **Supervised by:**

Prof. Dr. Roland Felix Graf  
ZHAW Life Sciences and Facility Management  
Institute of Natural Resource Sciences  
Grüental, Postfach 335  
CH-8820 Wädenswil

Dr. Benedikt Gehr  
Wildtier Schweiz  
Winterthurerstrasse 92  
CH-8006 Zürich

**Author:**

Ninetta Graf

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**Institute:**

ZHAW Life Sciences and Facility Management  
Institute of Natural Resource Sciences  
Grüntalstrasse 14, Postfach  
8820 Wädenswil

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## Zusammenfassung

Die Intensivierung der Landwirtschaft und die damit einhergehende frühere und häufigere Mahd wird vielen Tieren zum Verhängnis. Betroffen ist auch das Reh (*Capreolus capreolus*), welches die Wiese als Setzstandort nutzt. Rehkitze, die in Wiesen geboren werden, liegen in den ersten Wochen ihres Lebens im Gras versteckt. Da sich diese Phase stark mit der Mähseason überschneidet, sterben jedes Jahr Tausende von Kitzen bei der Mahd. Eine mögliche Massnahme zur Minimierung dieses Risikos wäre der Verzicht auf die Mahd während der Hauptsetzzeit, besonders in Gebieten, in denen das Risiko hoch ist, dass Rehkitze in einer Wiese liegen. Ziel dieser Studie war es daher, die Schlafplatzwahl von Rehkitzen zu untersuchen, um solche Risikozonen zu identifizieren. Mit den Daten von 13'112 Rehkitzen aus dem Langzeitprojekt "Rehkitzmarkierung Schweiz" wurde eine Analyse der Schlafplatzwahl auf der Basis eines Use-Availability-Designs durchgeführt. Mittels konditionaler logistischer Regression wurden fünf Habitatsvariablen an Rehkitzmarkierungsstandorten mit jenen an zufällig verteilten Standorten in einer gepaarten Fall-Kontroll-Studie verglichen. Die Analyse wurde auf einer kleinen (Radius = 100 m) und auf einer grossen räumlichen Skala (Radius = 400 m) durchgeführt. Die Wahl des Schlafplatzes wurde am stärksten durch die Entfernung zum Wald und die Entfernung zur Strasse beeinflusst. Im Allgemeinen wählten Rehkitze Schlafplätze, die nahe am Waldrand lagen und mieden Plätze in der Nähe von Strassen, wobei ersteres auf der grossen Skala und letzteres auf der kleinen Skala wichtiger war. Wir erstellten Risikokarten für zwei exemplarische Schweizer Gemeinden, die das Schweizer Mittelland und die Voralpen repräsentieren. Wir schlagen verschiedene Schwellenwerte vor, um Zonen zu identifizieren, in denen ein angepasstes Mähregime die Kitzsterblichkeit wirksam reduzieren könnte. Mit solchen raum-zeitlichen Anpassungen von Mähregimen zur Rettung von Rehkitzen, könnten auch Synergien mit anderen Massnahmen zur Förderung der Biodiversität in Wiesen geschaffen werden.

## Abstract

Intensified agriculture leads to earlier and more frequent mowing. This has a detrimental impact on many animal species, including the roe deer (*Capreolus capreolus*), which uses meadows as birthing site. Fawns that are born in meadows lie hidden in the grass for the first weeks of their life. Because this phase highly overlaps with the mowing season, thousands of fawns die every year due to mowing. This is not only problematic from an animal welfare point of view, but it can also lead to yield losses for farmers due to the contamination of the harvest. One possible measure that could be taken to minimise this risk would be to refrain from mowing during the peak of the birthing season. Since an adapted mowing regime may involve financial losses for farmers, it would be advisable to do this only in areas where the chance of a fawn lying in the meadow is high. The aim of this study was therefore to examine the bed site selection behaviour of roe deer fawns in order to identify such zones of high risk. We conducted a habitat selection analysis based on a use-availability design with data on bed site locations of 13'112 roe deer fawns from the long-term project "Rehkitzmarkierung Schweiz". Using conditional logistic regression, we contrasted five habitat variables at roe deer fawn marking sites to those at randomly distributed sites in a matched case-control design. We conducted the analysis at the meadow-mosaic scale ( $r = 400$  m) and the within-meadow scale ( $r = 100$  m). We found that the two most important factors influencing bed site selection were distance to forest and distance to road. Generally, roe deer fawns selected for bed sites that were close to the forest edge and avoided sites that were close to roads. Most interestingly, the magnitude of these two influences was different at the two spatial scales. At the meadow-mosaic scale, proximity to the forest was much more important than at the within-meadow scale, where distance to the road was more important. We produced spatially explicit risk maps of two exemplary municipalities of Switzerland, representing the Swiss Plateau and the Prealps and we propose different thresholds to identify zones where an adapted mowing regime could reduce fawn-mortality effectively. Such spatio-temporal adaptations of mowing regimes to save fawns may also produce synergies with other efforts to promote or restore biodiversity in meadows.

**Keywords:** bed site selection, fawn mortality, habitat selection function, mowing regime, human disturbance, mowing restriction zone, roe deer (*Capreolus capreolus*), risk map, roe deer fawn, spatial scale, use-availability design

## Introduction

In the course of agricultural intensification, grasslands are mown increasingly earlier and more frequently (Müller et al., 2005). This has a detrimental impact on the grassland fauna. It leads to a decrease in the abundance of many insect species, especially specialised and rare ones (Di Giulio et al., 2001). It lowers the breeding success of meadow-breeding birds such as the whinchat (*Saxicola rubetra*), the skylark (*Alauda arvensis*) and the corncrake (*Crex crex*) (Green et al., 1997; Jenny, 1990; Müller et al., 2005). Overall, it increases the direct mortality of arthropods, amphibians, reptiles, birds and mammals (Deák et al., 2021; Humbert et al., 2009). The European roe deer (*Capreolus capreolus*) is one of the victims. A large part of roe deer fawns are born in meadows where they spend the first weeks of their life (Linnell et al., 2004; Stubbe, 1997). As roe deer are “hidiers”, their strategy to avoid predators, is to hide from them (Lent, 1974). Therefore, during the first three weeks, they lie hidden and inactive in the tall grass of the meadow to protect themselves from predators such as the red fox (*Vulpes vulpes*) (Kurt, 1991). Most of the fawns are born between May and June (Linnell & Andersen, 1998; Raganella-Pelliccioni et al., 2007; Stubbe, 1997), but births also occur in April and July (Jarnemo, 2004). The birth dates highly overlap with the mowing season (Herren, 2021). From a farmer’s perspective, the first cut should be done in the period of maximum plant growth, if the goal is to reach maximum fodder quality (Bossuyt et al., 2018; Čop et al., 2009). Therefore, harvesting in conventionally used meadows can start as early as at end of April (MeteoSchweiz, 2018). In Switzerland, the date of the first cut is only regularized for extensively and less intensively used meadows, which are bound to subsidies (FOAG, 2014). They cannot be harvested until June 15<sup>th</sup> in the plain zone, July 1<sup>st</sup> in lower mountain zones (1 & 2) and July 15<sup>th</sup> in the higher mountain zones (3 & 4).

Due to this overlap of the birth and the mowing season, combined with the roe deer fawn’s instinct to hide and lay still when danger approaches, every year between 1’000 and 2’000 fawns are mutilated and killed through mowing in Switzerland, which is equivalent to about an 8% death rate (FOEN, 2021). Wildtier Schweiz suspects this figure to be much higher. According to its own estimates, the death rate is 13%, which corresponds to about 20’000 annual deaths (Wildtier Schweiz, pers. Comm.). For comparison, studies conducted in Germany and in Poland have found death rates as high as 14,5% and 26%, respectively (Kałuziński, 1982; Kittler, 1979). Such a large proportion of fawns is killed every year although hundreds of volunteers participate in rescue operations with ever more advanced detection technologies (Steen et al.,

2012) and although farmers use various methods to scare away the animals before mowing (Cukor et al., 2019; Jarnemo, 2002). This is not only a problem from an animal welfare point of view, but it can also lead to yield losses for farmers due to contamination of the mowed material by the bacterium *Clostridium botulinum* (Braun, 2006).

Therefore, adjustments to current mowing practices are required to reduce mowing-related deaths of fawns. In the literature, suggestions for alternative mowing regimes to protect insects and birds have been brought forward (Buri et al., 2013; Humbert et al., 2012, 2018; van de Poel & Zehm, 2015). Measures that dispense with mowing, at least in parts or at certain times, have proven to be particularly effective. Specifically, leaving strips of old grass or fallow land, foregoing one or more cuts per year or postponing cutting are frequently mentioned.

However, to date only few such recommendations with respect to roe deer fawns exist. For instance, a previous study suggested that the risk of death through mowing could be reduced, if the first cut of a meadow was moved forward 14 days at lower altitudes and delayed by 14 days at higher altitudes (Herren, 2021).

In this study we thus aimed at improving available management recommendations by creating risk maps that identify areas of high risk for fawns to be killed by a mowing machine. Such a map could be used by farmers to avoid areas of greatest risk. It can also serve as a basis for the planning of nature conservation measures and possible compensation payments, since such adjustments in mowing practices might come at economic costs for the farmers due to reduced yield.

To reduce the risk of mowing related deaths in roe deer fawns, profound knowledge about their bed site selection is required. The selection of an optimal bed site is subject to several different trade-offs (van Moorter et al., 2009). On one hand, the fawn relies on being able to hide from predators, since in some areas the main cause of death are red foxes (*Vulpes vulpes*) (Aanes & Andersen, 1996; Jarnemo, 2004; Jarnemo & Liberg, 2005). On the other hand, it needs optimal thermal conditions, since also hypo- or hyperthermia are common causes of fawn mortality (Andersen & Linnell, 1998). The doe must be able to hide in proximity, as she needs to suckle the fawn regularly, without revealing its location (Panzacchi et al., 2010). As an income breeder (Andersen et al., 2000), the doe relies on high energy intake during the lactation period and therefore needs good quality food in close proximity to the fawn's bed site (Panzacchi et al., 2010).

Previous studies found, that roe deer and their fawns select for bed sites with a vegetation of medium height, optimal cover and a mean distance to the forest edge of  $91 \pm 3$  m (Christen et al., 2018; Linnell et al., 2004; van Moorter et al., 2009). Adult roe deer tend to select for forest areas, when they are numerous and avoid areas in close proximity to roads and buildings (Bonnot et al., 2012; Coulon et al., 2008; Hewison et al., 2001).

Thus, we wanted to build a predictive model, to identify sites within meadows that are selected by roe deer does and/or fawns during the hider phase, in which most fawns fall victim to mowing machines. We predicted that 1) fawns select for sites close to forest edges away from human disturbance. In accordance with that, we expected 2) that fawns avoid roads and buildings. Furthermore, we expected 3) bed sites to be located at intermediate solar irradiation for optimal thermoregulation and 4) in mostly flat terrain.

## **Materials and methods**

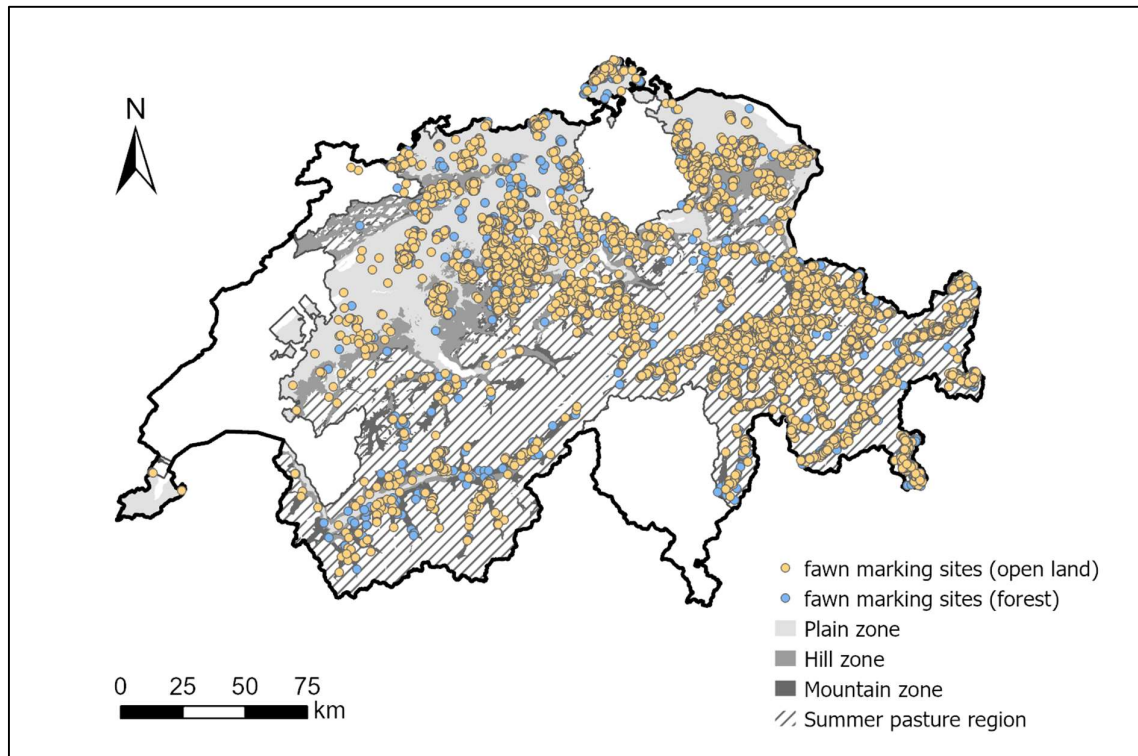
### **Study area**

Data for this study were collected in all the cantons of Switzerland that participate in the project “Rehkitzmarkierung Schweiz” (Figure 1). The Swiss Plateau, the Prealps, the Alps and the Jura are all represented in the study perimeter. We only considered data of the open land, which is defined as the area that is not forested and not populated by humans. Approximately 95% of the open land data were collected in meadows and 5% in other field types. The study perimeter encompasses all six agricultural production zones defined in the “Verordnung über den landwirtschaftlichen Produktionskataster und die Ausscheidung von Zonen” (1999). For this analysis we regrouped these zones into three altitudinal categories: plain zone (plain zone + hill zone), hill zone (mountain zone I and II) and mountain zone (mountain zone III and IV and summer pasture region). The altitudinal gradient of the study perimeter ranged from 250 m.a.s.l. to 4'629 m.a.s.l.

### **Roe deer fawn data**

The roe deer fawn data originated from the long-term data collection “Rehkitzmarkierung Schweiz”. Since 1971 hunters and gamekeepers, in most Swiss cantons, have located and uniquely marked roe deer fawns for this project. Together with the location, they noted the date, the age, number of siblings, bed site (field, meadow or forest), vegetation height (<20 cm, 20-50 cm and >50 cm), distance to next forest edge and vegetation types in a radius of 100 m. When dead roe deer with tags were reported back, the location and cause of death were





**Figure 1** Distribution of the roe deer fawns’ marking sites. No data were available for the cantons displayed in white, as they did not participate in the project “Rehkitzmarkierung Schweiz”.

recorded. The data was not collected systematically, as fawn marking was done on a voluntary basis, often prior to a mowing event. Therefore, roe deer fawns in the forest are generally not found. Due to this opportunistic sampling regime, we cannot draw conclusion about the general habitat selection of fawns.

At the time of the data analysis for this study, data of 19’683 marked roe deer fawns were available. We cleaned the data by deleting data points that missed information on the tag number, the fawn’s age and the marking site’s geographic coordinates, as well as data points with coordinates that lied outside of Switzerland. After data cleaning, 18’890 data points remained.

For the analysis, we only included data of roe deer fawns younger than 22 days ( $n = 18’235$ ), as we were interested in this early life stage during which fawns engage in a hider strategy. To gain additional bed sites, we also considered locations as marking sites at which roe deer fawns were killed by mowing ( $n = 316$ ). Since we were interested in bed site selection in the open, we excluded roe deer fawns that were marked in forests. We did the exclusion in ArcGIS Pro (Esri Inc., 2021) with the land cover layer of swissTLM3D (swisstopo, 2021a). In total, we used 13’428 marking sites for the analysis. Estimated birth dates ranged from day of year (DOY) 109 to DOY

212. 21% of the data stem from the plain zone, 20% from the hill zone and 59% from the mountain zone.

### Habitat variables

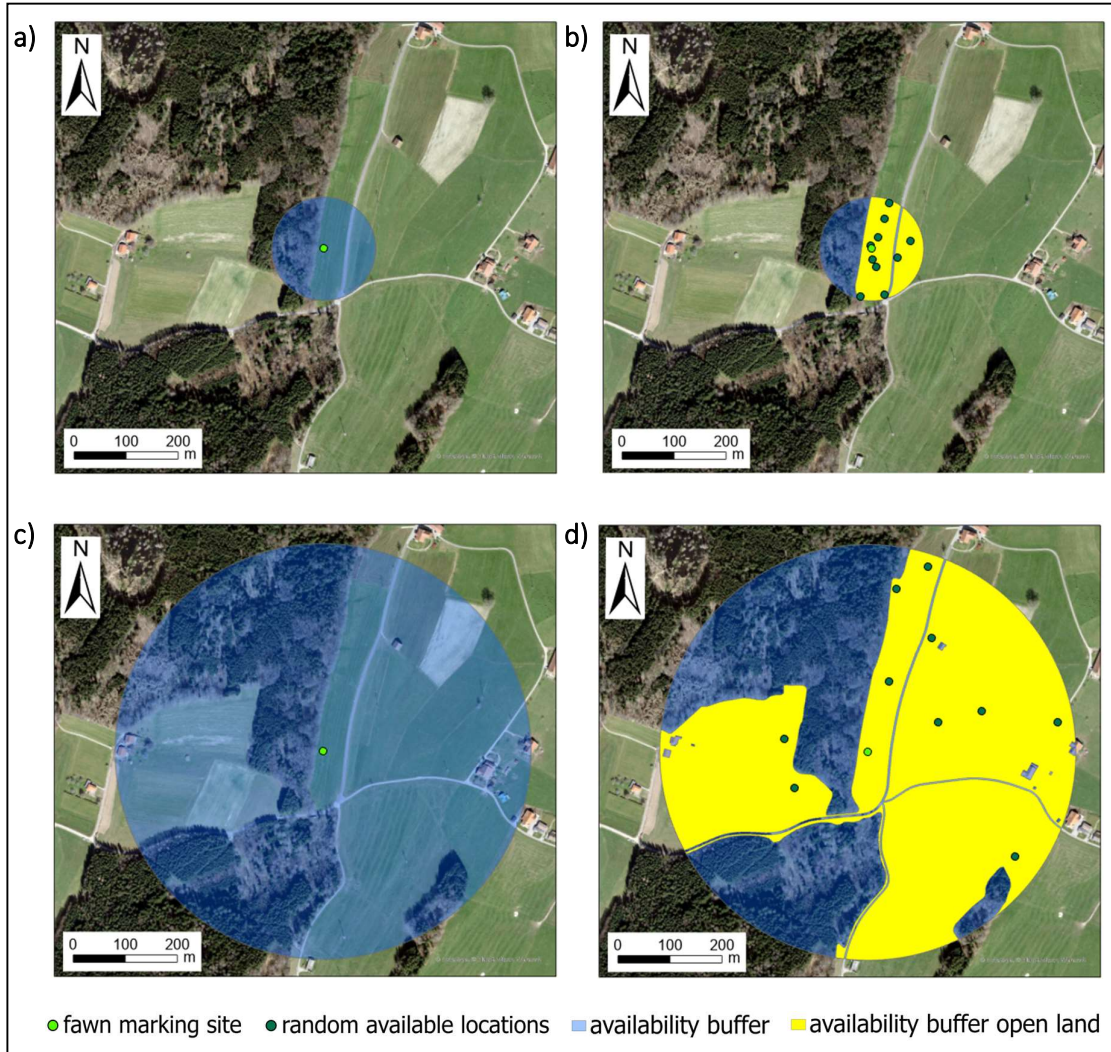
For each roe deer fawn location, we determined the values of the five habitat variables, listed in Table 1, which we expect to be relevant for bed site selection. These values were extracted from ArcGIS Pro (Esri Inc., 2021) using the vector layers of forest cover, buildings, roads and pathways of the topographic landscape model of Switzerland swissTLM3D (swisstopo, 2021a) and the digital height model DHM25 (swisstopo, 2021b).

**Table 1** Definitions of model variables used for the bed site selection analysis of roe deer fawns.

Variable	Description	Unit	Source
distance_forest	Distance from the fawn’s marking site to the nearest forest	meter	TLM3D swisstopo
distance_building	Distance from the fawn’s marking site to the nearest building	meter	TLM3D swisstopo
distance_road	Distance from the fawn’s marking site to the nearest road	meter	TLM3D swisstopo
slope	Slope at raster cell associated with the fawn’s marking site	degree	DHM swisstopo (Raster size = 25 m)
solar_radiation	Solar irradiation at the raster cell associated with the fawn’s marking site at the DOY that lies midway between the first DOY and the last DOY of all fawn findings	WH/m <sup>2</sup>	DHM swisstopo (Raster size = 25 m)
location_type	Binary numeric variable (1/0) denoting whether the roe deer fawn was found alive or dead		Rehkitzmarkierung Schweiz

### Bed site selection analysis

To understand the selection process by which roe deer fawns choose their bed site, we conducted a habitat selection analysis (HSA) based on a use-availability design (Fieberg et al., 2021; Manly, 2002). We used conditional logistic regression to contrast habitat variables at locations selected by fawns (“used locations”) with habitat variables at random locations assumed to be equally available (“available locations”) in a matched case-control design. For this, we randomly generated 10 available locations around each marking site (Figure 2) at two spatial scales (Boyce et al., 2002; Johnson, 1980). An “availability radius” of  $r_a = 400$  m around a roe deer fawn marking site represented the scale at which the doe choose a meadow within the landscape (“meadow-mosaic scale”) and an “availability radius” of  $r_a = 100$  m around a fawn marking site the scale at which the fawns choose a bed site within a meadow (“within-meadow scale”). We estimated the same habitat variables for the available locations as for the used locations.



**Figure 2** Example of the generation of random available locations around a fawn marking site at two spatial scales (a-b: within-meadow scale, availability radius  $r_a = 100$  m; c-d: meadow-mosaic scale, availability radius  $r_a = 400$  m). *Background map: © swisstopo.*

For the habitat selection analysis, we used the exponential form

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i),$$

where  $w(x)$  is the habitat selection value,  $x_1$  to  $x_i$  are the habitat variables and  $\beta_1$  to  $\beta_i$  are the corresponding regression coefficients (Boyce et al., 2002; Fieberg et al., 2021; Manly, 2002). For a habitat variable  $x_i$  with a positive regression coefficient ( $\beta_i > 0$ ), a one unit increase in  $x_i$  (for continuous habitat variables) or the change from a reference category  $j$  to category  $i$  (for categorical habitat variables) results in enhanced selection whereas in the case of a negative regression coefficient ( $\beta_i < 0$ ) this results in enhanced avoidance. To estimate the regression

coefficients, we fitted a conditional logistic regression of used versus available locations in R (Avgar et al., 2017; RStudio Team, 2000). We declared each used location and its corresponding 10 available locations as stratum (`id_animal`), so that only habitat variables within a stratum were compared to each other. Siblings were treated as clusters (`id_family`), to correct for non-independence. The model predictors are listed in Table 1. To define the variable `distance_road`, we checked whether different types of roads, with various levels of human presence, influenced the selection behaviour of the fawns differently. To this end we fitted three separate univariate models for the three different definitions of this variable as shown in Table 2 and compared them using Akaike’s Information Criterion (AIC) (Burnham & Anderson, 1998). The definition of the `distance_road` variable used in the final model was then selected based on the univariate model with the lowest AIC score.

**Table 2** Definitions of different road variables that were compared to find the one that leads to the best model.

Univariate model	Definition of variable <code>distance_road</code>	swissTLM3D Object
<code>use_availability ~ distance_road_small</code>	Nearest distance to paths or small roads	1-2 m paths, 3 m road
<code>use_availability ~ distance_road_large</code>	Nearest distance to large roads	4-10 m roads, motorway, highway
<code>use_availability ~ distance_road_mixed</code>	Nearest distance to any type of road	1-2 m paths, 3-10 m roads, motorway, highway

We tested for collinearity between habitat variables by calculating Kendall rank correlation coefficients of all pairwise combinations. All habitat variables were centred (except for `location_type`).

We fitted two models, one without interaction and one with interactions between each variable and `location_type`. We chose the most suitable model based on the Akaike’s Information Criterion (Burnham & Anderson, 1998). Model fitting was done in R (RStudio Team, 2000) using the `coxph` function of the R-package `survival` (Therneau, 2020). To evaluate the goodness of fit of the model we used k-fold cross validation (Boyce et al., 2002; Gehr et al., 2017). We repeatedly used 20% of the data as test data set and 80% as training data set. For that we randomly partitioned the used locations into 5 subsamples and then added the corresponding available locations to the respective subsamples. Each of these 5 subsamples was once considered as test data set and the remaining 4 subsamples as corresponding training data sets, resulting in 5 test and training data sets. With the training datasets we fitted a conditional logistic regression model. With the regression coefficients we estimated the habitat selection

function of used and available locations of the corresponding test data set (Gehr et al., 2017). We then divided the habitat selection values of the available locations into ten equal sized bins and filled the habitat selection values of the used locations in the bins with the corresponding bin rank. We calculated the Spearman rank correlation between the bin rank and the frequency of used locations within each bin. Large correlations indicate a good model fit (Wiens et al., 2008). These steps were repeated 100 times, with each time using different test and training data sets. In the end, the average correlation value was used (Gehr et al., 2017). We applied the k-fold cross validation separately for both spatial scales.

### **Relative importance of the habitat variables**

We derived the relative importance of each habitat variable according to Ewald *et al.* (2014), by first successively fitting models with always one of the variables arranged in a random order. Second, we calculated the correlation between the predictions of the “true” model and the models with one of the variables randomly arranged. The higher this correlation was, the less important the randomly arranged variable was. We then subtracted the correlations from 1 and divided the correlations of all habitat variables by the sum of them to get the relative importance of each. We repeated this process 100 times and in the end calculated the mean relative importance for every variable.

### **Visualisation of roe deer fawn bed site selection**

We used the relative selection strength (RSS) as suggested by Avgar *et al.* (2017) to better understand how the different habitat variables relate to fawn bed site selection. The relative selection strength of a location  $l_1$  in relation to a location  $l_2$ , given that these two locations only differ in habitat variable  $x_i$  while all other habitat variables are kept constant, is defined as:

$$RSS(l_1, l_2) = \frac{w(l_1)}{w(l_2)} = \exp(\beta_i \times (x_i(l_1) - x_i(l_2)))$$

Where  $RSS(l_1, l_2)$  is the relative selection strength of the location  $l_1$  in relation to location  $l_2$ ,  $w(.)$  is the habitat selection value,  $x_i$  refers to the one habitat variable that differs between location  $l_1$  and  $l_2$  and  $\beta_i$  is the coefficient of the habitat variable  $x_i$ . To visualize the effect of the two most important variables on the bed site selection, we plotted the RSS for a range of locations that only differed with respect to the variable of interest.

## **Risk maps and mowing restriction zones**

We applied the habitat selection function of the two spatial scales (i.e. meadow-mosaic and within-meadow scale) to habitat data of Einsiedeln (SZ) and Ruswil (LU) to produce spatially explicit maps, that visualize the relative risk of killing a fawn by mowing. We chose Einsiedeln and Ruswil as representative regions of the Prealps and the Swiss Plateau, respectively. All maps were generated using ArcGIS Pro (Esri Inc., 2021). We divided the two communities into raster grids of 1x1 m and multiplied the selection coefficients with the respective habitat variables of each cell and summed and exponentiated them (Signer et al., 2017).

### **Meadow-mosaic scale**

With the habitat selection function of the meadow-mosaic scale we produced risk maps that show a risk spectrum from areas with a low risk to areas with a high risk of a fawn lying in a meadow within the community. These could be used to designate meadows within the landscape that should be taken into consideration for an adapted mowing regime.

### **Within-meadow scale**

We used the habitat selection function of the within-meadow scale to produce maps that designate zones within meadows, where it would make sense to adapt the mowing regime (which will hereinafter be referred to as "mowing restriction zones"). A possible approach to designate such zones is to employ a simple threshold criterion, based on a quantile of the habitat selection values (HSV) of the used locations (i.e. the observed fawn bed sites). We therefore calculated the HSV of all 13'428 used locations and chose the 25%, 50% and 75% quantiles as potential target thresholds for the respective mowing restriction zones. We then designated three exemplary mowing restriction zones according to these three target thresholds for Ruswil and Einsiedeln, respectively (i.e. all pixels of the municipalities that had an HSV above the respective threshold were assigned to the mowing restriction zones). We calculated the area for each of the three mowing restriction zones and estimated the mean distance between the forest edge and the boundary of the mowing restriction zone. Finally, to get an impression of what proportion of fawns was exposed to the danger of being mown within these three mowing restriction zones, we calculated the percentage of all fawns marked in Ruswil that were reported in these zones. The last analysis was done only for Ruswil since this was the only municipality where enough data (n = 735) was available.

Using the habitat selection function of the within-meadow scale, we also produced a similar risk map for one exemplary meadow as we did for the meadow-mosaic scale. This map could be used to prioritize zones when searching the meadow prior to a mowing event.

## Results

Distances to forest at all marking sites ( $n = 13'428$ ) ranged from 0 to 1820 m (mean  $\pm$  SD =  $66 \pm 102$  m). Marking sites were on average at a distance of  $133 \pm 117$  m and  $65 \pm 56$  m from buildings and roads, respectively. Maximal slope at a marking site was 75 degrees (mean  $\pm$  SD =  $15 \pm 8$  degrees). Mean solar radiation was  $5935 \pm 414$  WH/m<sup>2</sup>. The lowest marking site was at 301 m.a.s.l., the highest at 2718 m.a.s.l.

### Model selection

The comparison of the different road types showed that considering the distance to all types of roads results in the best model. We therefore defined the variable `distance_road` as the distance of the marking sites to any type of road, independent of their size. But interestingly, defining `distance_road` as the distance to paths and small roads resulted in a more accurate model ( $\Delta\text{AIC}(r_a = 100) = 104.3$ ;  $\Delta\text{AIC}(r_a = 400) = 125$ ) than when defining it as the distance to large roads ( $\Delta\text{AIC}(r_a = 100) = 563.6$ ;  $\Delta\text{AIC}(r_a = 400) = 559.8$ ).

All Kendall rank correlation coefficients between habitat variables were below 0.5, with the highest being -0.26 between `slope` and `distance_forest`. We therefore included all variables in the conditional logistic regression analysis.

For the bed-site selection analysis, we selected the model without interactions between the habitat variables and `location_type` based on the Akaike's Information Criterion (Table 3).

**Table 3** Conditional logistic regression models with  $\Delta\text{AIC}$  at two spatial scales.

Model	$\Delta\text{AIC}$	
	Within-meadow scale	Meadow-mosaic scale
<code>use_availability ~ distance_forest + distance_building + distance_road + slope + solar_radiation + strata(id_animal), cluster = id_family</code>	0.00	0.00
<code>use_availability ~ distance_forest x location_type + distance_building x location_type + distance_road x location_type + slope x location_type + solar_radiation x location_type + strata(id_animal), cluster = id_family</code>	3.1	3.3

## Bed site selection analysis

From the best model (Table 3,  $\Delta AIC = 0$ ), all habitat variables had a significant effect on the bed site selection of roe deer fawns (Table 4). Fawns selected sites that were close to the forest and avoided sites that were close to buildings or roads. With increasing slope, the chance to find a roe deer fawn in a meadow decreased. The direction of these four effects was the same for both spatial scales of availability locations. The solar irradiation only influenced the bed site selection at the meadow-mosaic scale ( $r_a = 400$  m), where the fawns selected for sites with higher solar irradiation.

K-fold cross validation indicated a good model fit of the data ( $r_{cv}(r_a=100) = 0.90$ ,  $SD = 0.05$ ;  $r_{cv}(r_a=400) = 0.99$ ,  $SD = 0.009$ ).

**Table 4** Coefficients of the final conditional logistic regression model and relative importance of each variable at two spatial scales.

Variable	Coef.	SE	Z	P	Relative importance
<b>Within-meadow scale</b>					
distance_forest	-0.004	<0.001	-17.47	<0.001	0.21
distance_building	0.002	<0.001	7.41	<0.001	0.03
distance_road	0.008	<0.001	27.10	<0.001	<u>0.66</u>
slope	-0.027	0.003	-10.04	<0.001	0.10
solar_radiation	-0.00003	<0.001	-0.52	0.607	0.001
<b>Meadow-mosaic scale</b>					
distance_forest	-0.006	<0.001	-31.26	<0.001	<u>0.68</u>
distance_building	0.0007	<0.001	5.01	<0.001	0.009
distance_road	0.005	<0.001	23.61	<0.001	0.21
slope	-0.03	0.002	-17.00	<0.001	0.10
solar_radiation	0.00009	<0.001	2.30	0.021	0.002

From the model with interactions (Table 3), the only significant interaction (slope x type\_location) showed that less roe deer fawns were killed through mowing with increasing slope of a meadow ( $r_a = 400$  m; Coef. = -0.023;  $p = 0.029$ ). Otherwise, we found no significant interactions.

## Relative importance of the habitat variables

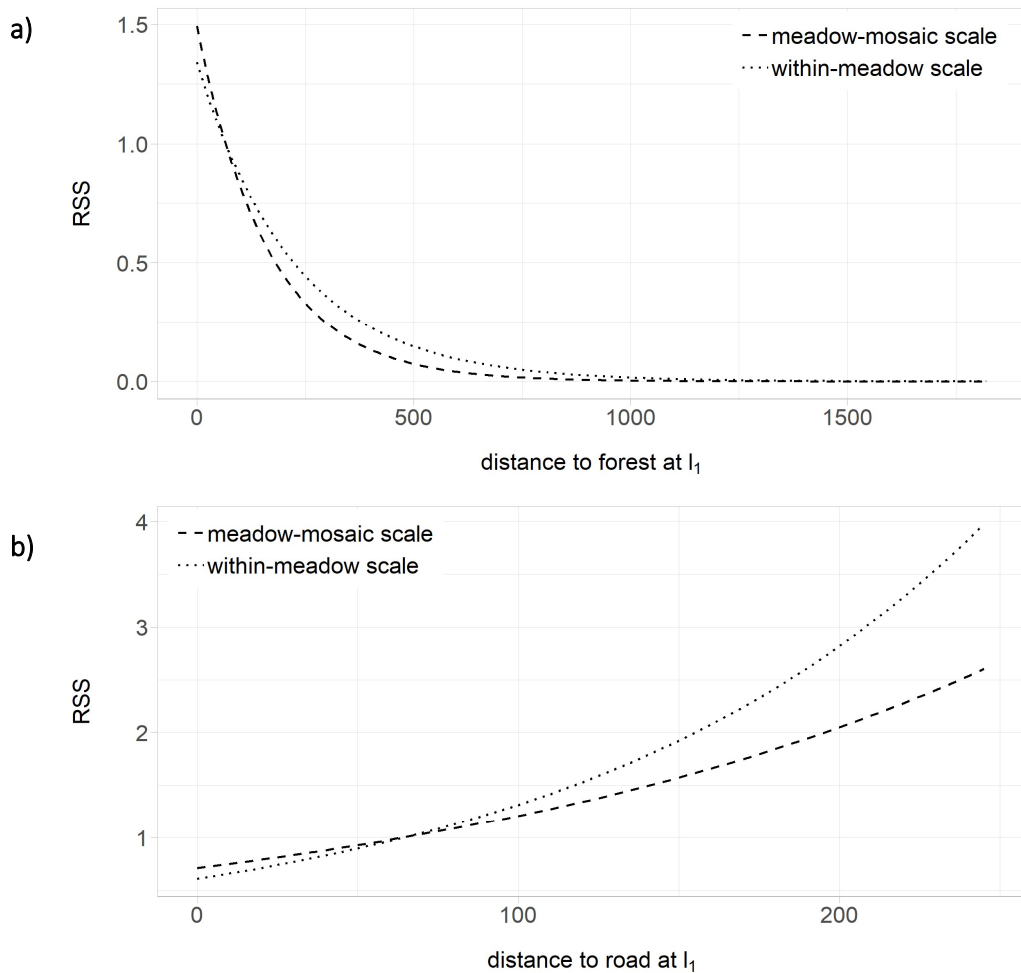
Considering the model of the within-meadow scale, the most important variable explaining bed site selection of roe deer fawns was distance to road (relative importance: 0.66), followed by distance to forest (relative importance: 0.21) (Table 4). In contrast, the most important variable



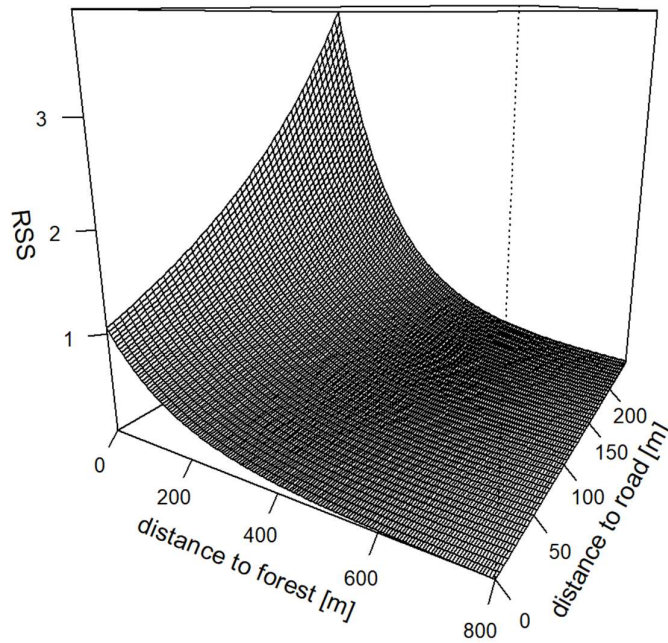
on the meadow-mosaic scale was distance to forest (relative importance: 0.68), followed by distance to road (relative importance: 0.21) (Table 4).

### Visualisation of roe deer fawn bed site selection

Distance to forest mainly influenced the bed site selection of roe deer fawns within the first 500 m (Figure 3a). At the meadow-mosaic scale, the selection of a bed site at a distance of 500 m was almost 14 times less likely than at the mean distance (66 m) of all marking sites, assuming all other variables remain constant. When all variables are held constant except distance to road, it is 4 times more likely that a roe deer fawn selects a bed site 450 m away from the road than at the mean distance to road (65 m) of all marking sites (Figure 3b). In general, the further away from the road and the closer to the forest, the more likely it was that a site was selected by a roe deer fawn (Figure 4).



**Figure 3** Relative selection strength of a location  $l_1$  over location  $l_{\bar{x}_i}$  as a function of a) distance to forest and b) distance to road at  $l_1$ .  $\bar{x}_i$ : mean distance of all marking sites to a) forest: 66 m and b) road: 65 m.  $RSS(l_1, l_{\bar{x}_i}) = \exp(\beta_i \times (x_i(l_1) - x_i(l_{\bar{x}_i})))$



**Figure 4** Relative selection strength of the two most important habitat variables distance to forest and distance to road combined at the meadow-mosaic scale. RSS was calculated as described in Figure 3.

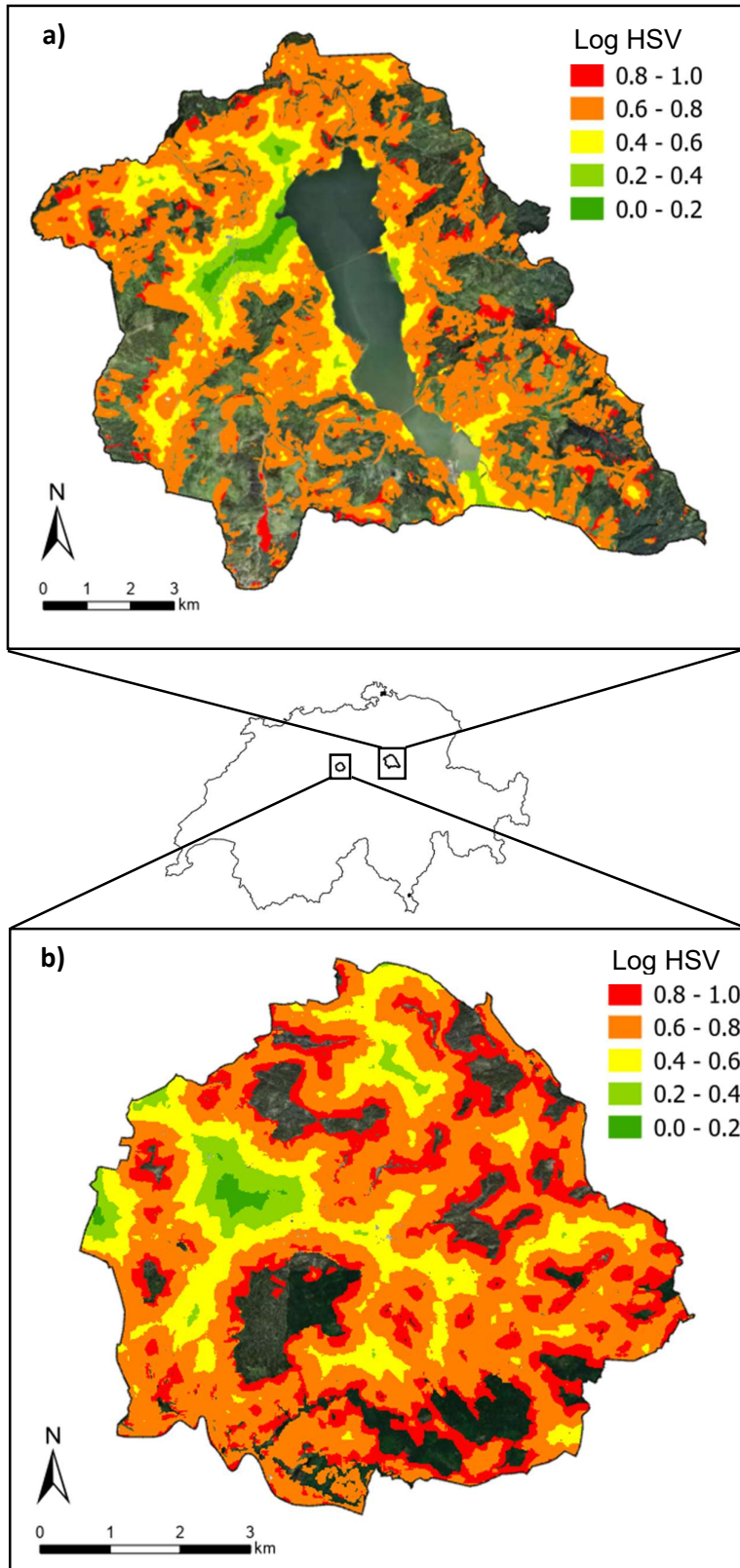
## Risk maps and mowing restriction zones

### Meadow-mosaic scale

We used the habitat selection function of the meadow-mosaic scale to produce spatially explicit risk maps for Einsiedeln and Ruswil (Figure 5). The maps display five color-coded areas, indicating the relative risk of killing a roe deer fawn by mowing from low (green) to high (red).

### Within-meadow scale

To provide a method for designating mowing restriction zones, we have calculated threshold HSV based on the 25%, 50% and 75% HSV quantiles of all used points (Table 5). The effect of the different threshold criteria on the size of the mowing restriction zones can be seen in Table 5, represented as the mean distance between the zone boundary and the forest edge, and the area of the community that would be affected. Using the 75% quantile as threshold for example would result in mowing restriction zones of totally 550 ha (15% of the open land) in Ruswil and 1019 ha (19% of the open land) in Einsiedeln. To visualise the effect of different thresholds, we have mapped the mowing restriction zones for Ruswil using the 25% and the 75% HSV quantile in Figure 6a and Figure 6b, respectively.

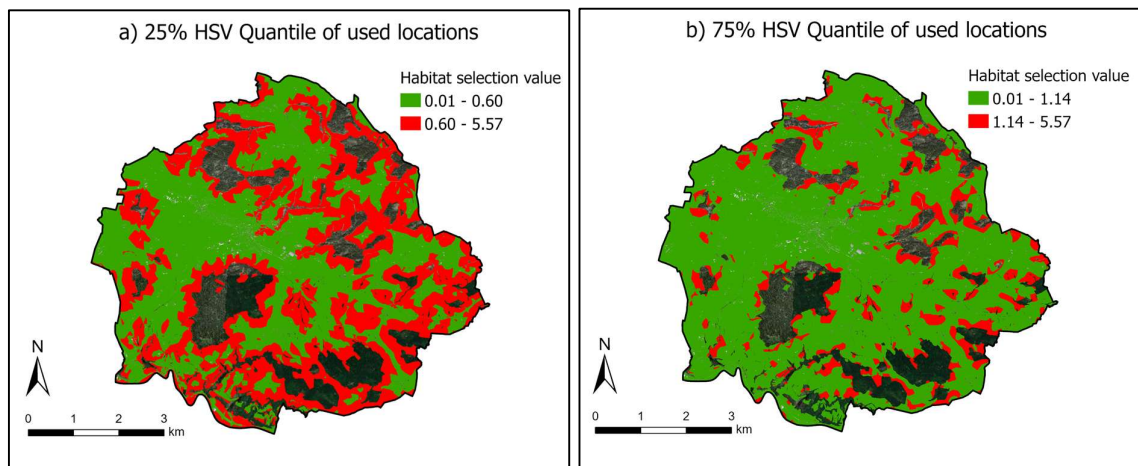


**Figure 5** Risk maps of a) Einsiedeln and b) Ruswil. For each 1x1 m pixel the habitat selection function  $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i)$  was evaluated based on the estimated model coefficients. Habitat selection values are displayed at the logarithmic scale. *Background map: © swisstopo.*

Of all roe deer fawns that were marked in Ruswil, the majority (54%) was found within the designated zone based on the 75% HSV quantile threshold (Table 5).

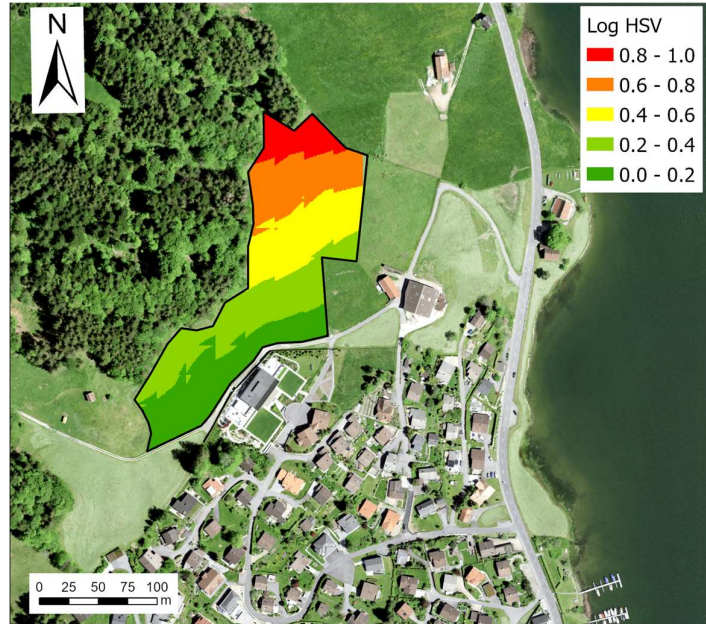
**Table 5** Threshold HSV to designate “mowing restriction zones” in risk maps. The mowing restriction zone referred to in the last three columns represents the area on the risk map that is composed of pixels with HSV above the threshold HSV, i.e. the designated mowing restriction zone based on the threshold criteria in the first column.

Threshold criteria	Threshold HSV	Mean distance between forest edge and mowing restriction zone boundary [m]		Area of mowing restriction zone (% of open land area)		% Marking sites within mowing restriction zone
		Einsiedeln	Ruswil	Einsiedeln	Ruswil	Ruswil
25 % HSV quantile of all marking sites	0.6	88	142	3030 ha (55%)	1666 ha (47%)	84
50 % HSV quantile of all marking sites	0.8	67	102	1913 ha (35%)	1107 ha (31%)	74
75 % HSV quantile of all marking sites	1.1	52	79	1019 ha (19%)	550 ha (15%)	53



**Figure 6** Mowing restriction zones (red) in Ruswil designated based on the a) threshold HSV = 0.91 (25% HSV quantile) and b) threshold HSV = 1.6 (75% HSV quantile). *Background map: © swisstopo.*

The risk map in Figure 7 illustrates the relative risk of killing a roe deer through mowing in different zones in a meadow in Einsiedeln. To generate this map, we used the habitat selection function of the within-meadow scale.



**Figure 7** Risk map of a meadow in Einsiedeln. Pixel values were estimated in the same way as in Figure 5, but with the habitat selection function of the within-meadow scale. Habitat selection values are displayed at a logarithmic scale. *Background map:* © swisstopo.

## Discussion

In agreement with our predictions, roe deer fawns and does did not choose bed sites randomly. The two most influential habitat characteristics were distance to forest and distance to road. As we expected, they generally selected sites in close proximity to forests and avoided roads. However, the magnitude of these two influences was different at the two spatial scales. On the meadow-mosaic scale, proximity to the forest was much more important than on the within-meadow scale, where distance to the road was more important.

This finding is in accordance with Van Moorter *et al.* (2009). They discovered that the distance to edges only influenced the survival of roe deer fawns on the doe's home range scale and not on the bed site scale. One possible explanation could be, that on the meadow-mosaic scale, the mother has a strong influence on the bed site selection, by selecting the meadow in which the fawn is born. For the doe, it is crucial that the fawn's bed site is in close proximity to a forest. On the one hand, this allows the mother to hide in the forest (Panzacchi *et al.*, 2010) and reach good quality food sources at the forest edge (Tufto *et al.*, 1996). On the other hand, the mother can regularly suckle the fawn and protect it from predators, by chasing them away (Jarnemo, 2004). In accordance with our findings, Panzacchi *et al.* (2010) found that fawn bed site

selection decisions at the landscape scale were primarily influenced by maternal energetic constraints and only secondarily by avoidance of predation risk.

We expect that the roads mainly influence the bed site selection through the associated presence of humans. This assumption is supported by the fact that the distance to paths and small roads better explained the data than the distance to large roads. Therefore, we further hypothesize, that once the meadow has been selected, the distance to forest became much less important and the risk from human disturbance was weighed more. It has been observed that if a preferred habitat type is sufficiently present to satisfy the needs of an individual, this may lead to a negative availability-use ratio if the availability of this habitat type is increased (Aarts et al., 2013). This may then lead to negative coefficients in the habitat selection function, indicating an avoidance of said habitat type (Mysterud & Ims, 1998).

Fawns avoid bed sites near buildings. This would be in agreement with the findings of Bonnot *et al.* (2012), which state that during daytime, roe deer used open fields more, the farther away from roads and buildings they were. Coulon *et al.* (2008) found that the avoidance of roads and buildings is stronger when woodland is scarce, indicating that there is an interacting effect of presence of forest, roads and buildings.

In agreement with our expectation, bed sites in steep slopes were avoided at both spatial scales. Canon & Bryant (1997) also found that pronghorn (*Antilocapra americana*) fawns selected for flatter sites, but only at the bed site scale. They had no preference at the landscape scale. They also found that this selection behaviour changed with the fawn's age.

More roe deer fawns were killed through mowing on flat terrain. This could either be explained by roe deer fawns not selecting bed sites in steep slopes or by less mowing activity in these zones.

Solar irradiation only had a significant effect on the bed site selection at the meadow-mosaic scale, where bed sites were in areas with higher solar irradiation than random locations around them. However, this result has to be interpreted with caution, since the irradiation was only estimated for the average DOY over all marking sites and not for the particular DOY corresponding to the marking date, as the latter would have required too much computing power. Huegel *et al.* (1986) showed that the effect of the solar irradiation on the bed site selection works on a very small temporal scale. They found bed sites of white-tailed deer (*Odocoileus virginianus*) fawns more often on slopes facing the sun on cool days and on slopes

facing away from the sun on warmer days. Such small-scale factors were not considered in our model, therefore the coefficients of this variable needs to be interpreted with caution.

In general, the interpretation of bed site selection analyses is complex, mostly because bed site selection is influenced by both the roe deer fawn and its mother and because it is scale dependent. For further investigations in that topic, it might be useful to try disentangling the effects of the doe and the fawn.

The risk maps illustrate in which zones the risk of killing a fawn during mowing is particularly high. The maps show that roe deer fawns in the open land are not generically selecting forest edges, as is often assumed. If the other factors are taken into account, it becomes clear that some forest edges are not selected, because they are also near houses or roads (e.g. Figure 7).

There are some possible constraints of the analysis. When habitat selection analysis is applied to individuals experiencing different habitat availabilities, availability dependence can be an issue (Fieberg et al., 2021). This means that animals switch between selection and avoidance of certain habitats depending on their availability (van Beest et al., 2016). However, with the range of availability locations used in our analysis, we argue that this is not a relevant problem.

A constraint of our analysis is the fact that we used the topographic landscape model swissTLM3D from 2021 to measure the habitat variables of all roe deer finds from 1971 to 2020.

We thereby attributed habitat variables to bed sites that were not recorded in the same decade as the bed site locations themselves. It is therefore possible that at the time a fawn was marked, the distance to the nearest forest was not the same as at the time the forest was mapped. We expect, that this is especially the case in the alpine regions, where the forest-open mosaic has changed and is still changing markedly due to changes in agricultural land use (Brändli et al., 2020). However, we argue that these potential errors were evened out by the large data set as otherwise we would expect more noise in the data and hence a weaker effect size.

We also did not consider phenology in our analysis. Linnell *et al.* (2004) showed that bed site selection behaviour differs among DOY, depending on the vegetation characteristics.

Vegetation height for example has a strong impact on bed site selection (Christen et al., 2018).

When vegetation is low, fawns seem to select bed sites that are closer to the forest than when it is high. It would be interesting if this factor could be included in a continuative study.

Furthermore, the high significance of the model coefficients leads us to believe that our method has led to pseudo replication. Although we corrected for siblings by treating them as a

cluster in the conditional logistic regression analysis, we did not account for spatial correlation among years, which is something that needs to be taken into account in a follow-up study.

The coefficients of the habitat selection analysis of this study and threshold HSV can be used to generate risk maps for regions all over Switzerland. Together with data from previous studies about temporal (Herren, 2021) and phenological aspects (Christen et al., 2018) of bed site selection, they can be used to plan locally adapted mowing regimes with reduced roe deer fawn mortality. The maps are particularly useful in planning the mowing regime so that as many fawns as possible can be spared with as little effort and financial loss for farmers. The last factor is especially important and must always be included in the planning process. Because if mowing is postponed by one day alone, this can already have strong economic consequences for the farmers. To quantify these financial losses, a variety of factors need to be considered. The financial yield of a meadow depends, among other things, on the composition (herb-rich, legume-rich or grass-rich), the main grass species, the stage of development at the time of harvest, the type of conservation (ensiling or hay), the management intensity and the agricultural production zone (AGRIDEA, 2001; Daccord et al., 2007). There is a need for a cost-benefit trade-off analysis from an agronomic perspective. This would provide a clear roadmap how mowing practices can be adapted in order to reduce the number of mowing accidents while minimizing associated costs. In cases where the mowing regime cannot be adapted, the risk maps can help prioritise search efforts prior to mowing.

Furthermore, future studies could investigate to what extent roe deer fawns might act as an umbrella species under which's protection other animals and plants would also benefit. There are various endangered and rare species that would also profit from spatial and temporal mosaic mowing regimes (Buri et al., 2013; Humbert et al., 2012, 2018; van de Poel & Zehm, 2015). Therefore, adapting mowing regimes in a spatiotemporal way to save roe deer fawns may produce synergies with other efforts to promote or restore biodiversity in meadows.



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