

RESEARCH ARTICLE

Deer density drives habitat use of establishing wolves in the Western European Alps

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Abstract

1. The return of top carnivores to their historical range triggers conflicts with the interests of different stakeholder groups. Anticipating such conflicts is key to appropriate conservation management, which calls for reliable spatial predictions of future carnivore occurrence. Previous models have assessed general habitat suitability for wolves, but the factors driving the settlement of dispersing individuals remain ill-understood. In particular, little attention has been paid to the role of prey availability in the recolonization process.
2. High spatial resolution and area-wide relative densities of the wolf's main ungulate prey species (red deer, roe deer and chamois) were assessed from snow-track surveys and modelled along with wolf presence data and other environmental descriptors to identify the main drivers of habitat selection of re-establishing wolves in the Western European Alps.
3. Prey species abundance was estimated from the minimum number of individuals recorded from snow-tracks along two hundred and eighteen 1-km transects surveyed twice a year during four successive winters (2012/2013–2015/2016). Abundance estimates per transect, corrected for species-specific detection probabilities and averaged across winters, were used to model area-wide relative prey density and biomass.
4. Confirmed wolf observations during the same four winters were used to develop a spatially explicit habitat selection model for establishing wolves, based on our estimates of prey supply and other environmental descriptors of topography, land-use and climate.
5. Detection-corrected ungulate prey abundances and modelled relative densities varied considerably in space (0–2.8, 1.3–4.5 and 0–6.3 per 50 ha in red deer, roe deer and chamois respectively; 1.3–11.65 pooled), while total predicted prey biomass ranged from 23 to 304 kg per 50 ha.
6. Red deer density was the most important factor explaining wolf occurrence (31% contribution), followed by roe deer density (22%), winter precipitation (19%) and presence of game reserves (16%), showing that food supply, especially red deer as

the most profitable prey in the Western Alps, was the main driver of winter habitat selection during the settlement phase.

7. *Synthesis and applications.* We demonstrate the crucial importance of including accurate, fine-grained information about prey supply for predicting recolonization patterns of carnivores and thus anticipating areas with potential human–wildlife conflicts where preventive measures should be prioritized.

KEYWORDS

Canis lupus, habitat modelling, human–wildlife interactions, Maxent, predator–prey relationships, recolonization patterns, ungulate density, wolf

1 | INTRODUCTION

During the last centuries many once widespread species, especially long-lived species such as large carnivores and raptors, were extirpated from the Western world, by direct human persecution and, indirectly, following habitat destruction and massive declines in their prey supply due to overhunting (Breitenmoser, 1998). Superstitious conceptions and unfounded fears as well as increasing depredation upon livestock due to the decline of wild ungulate prey led to merciless persecution until total eradication of top predators and scavengers from most of their historical range (Eiberle, 1972; Fritts et al., 1997; Hirzel et al., 2004). Yet, in the 20th century, public awareness for nature and wildlife protection increased. Changes in legislation were instrumental in the progressive recovery of forests and ungulate populations, while species that were once extirpated recolonized their former range, either by natural dispersal from relict populations (Boyd & Pletscher, 1999; Fabbri et al., 2007; Rice, Ballard, Fish, McIntyre, & Holdermann, 2009; Valière et al., 2003) or by targeted reintroductions (Breitenmoser, Breitenmoser-Würsten, & Capt, 1998; Hirzel et al., 2004). As a result, top predators are on the rise in North America and Europe, even in densely populated areas, which demonstrates that large-bodied wildlife can thrive also in human-dominated landscapes (Chapron et al., 2014; Kaczensky et al., 2013).

Despite their important role in predator–prey co-evolutionary processes and ecosystem functioning (McLaren & Peterson, 1994; Ripple & Beschta, 2012; but see Allen et al., 2017), and despite their presence in a given area being frequently perceived as an added value to nature experience and nature-based tourism (Ednarsson, 2006), the return of wolves generates considerable conflicts, especially with farmers and hunters. This has resulted in hot debates about the role and acceptance of top predators in the modern world, often dominated by emotional rather than rational arguments (Breitenmoser, 1998; Sillero-Zubiri & Laurenson, 2001). A commonly heard claim is that there is not enough natural space left for large carnivores in our densely populated landscapes (Carter & Linnell, 2016; Lute, Carte, López-Bao, & Linnell, 2015), despite the fact that wolves now reproduce in many newly recolonized areas

which are sometimes densely populated by humans. A recent inquiry has shown that deficiencies in the education of people about the virtually zero-threat that wolves represent for our human physical integrity is one of the root causes of the scepticism towards wolves that is observed locally (Behr, Ozgul, & Cozzi, 2017). In this tense socio-economic and cultural context, outreach activities can help resolving this educational problem by a progressive shift in mentalities. To efficiently focus such activities, understanding the main drivers of wolf re-establishment in its former range is needed to accurately predict spatial recolonization patterns in order to anticipate potential future conflicts.

Habitat models calibrated in areas with wolf occurrence have commonly been used to predict its future spatial expansion (Ahmadi, Kaboli, Nourani, Shabani, & Ashrafi, 2013; Alexander, Paquet, Logan, & Saher, 2005; Corsi, Duprè, & Boitani, 1999; Gehring & Potter, 2005; Glenz, Massolo, Kuonen, & Schlaepfer, 2001; Hebblewhite & Merrill, 2008; Houts, 2003; Jedrzejewski et al., 2008; Kabir et al., 2017; Mladenoff, Sickley, Haight, & Wydeven, 1995; Subba et al., 2017). Yet, the predictive power of such models may be questionable. First, the wolf has proven to be an extremely adaptable species that can colonize a vast range of habitat types (Mech, 1970), which represents a serious challenge for model transferability. Second, according to earlier wolf habitat models, the main key habitat features for wolves in Europe would be a wide forest coverage and limited human infrastructure (Ciucci, Masi, & Boitani, 2003; Falcucci, Maiorano, Tempio, Boitani, & Ciucci, 2013; Jedrzejewski et al., 2008; Karlsson, Broseth, Sand, & Andren, 2007; Massolo & Meriggi, 1998). Prey abundance—although intuitively a key factor—is often ignored in these models (Gehring & Potter, 2005; Hebblewhite & Merrill, 2008; Jedrzejewski, Niedzialkowska, Nowak, & Jedrzejewska, 2004; Kabir et al., 2017), probably due to the lack of data. In some cases, prey abundance is approximated by prey species diversity (Ciucci et al., 2003; Falcucci et al., 2013) or abundance estimates derived from hunting bag statistics (Karlsson et al., 2007), although the latter tends to provide distorted estimates of actual prey supply (Kilpatrick, LaBonte, & Barclay, 2005; Ranta, Lindstrom, Linden, & Helle, 2008). Few studies have used meaningful and credible prey estimates (Massolo & Meriggi, 1998; Potvin et al., 2005; Jedrzejewski et al., 2008; but see Mladenoff et al., 1995); so, clearly, there is an urgent

need for better integrating the prey availability into predictive models of wolf occurrence, which is the aim of our study.

After complete eradication from the European Alps in the early 1930s (Breitenmoser, 1998; Dufresnes, Miquel, Taberlet, & Fumagalli, 2019), wolves have progressively recolonized this range from the Italian Apennine starting in the late 1980s (Dufresnes et al., 2019; Valière et al., 2003). The first indices of wolf presence in our Swiss study area date back to 1995, with a first ascertained reproduction in 2016 (Augstbord, KORA, 2016). Establishment is now in full swing and conflicts are increasing (Behr et al., 2017). We gathered reliable, area-wide density estimates of wolf prey and modelled wolf occurrence during the population installation phase, in relation to both spatial abundance of prey and other environmental descriptors. More specifically, we predicted that wild prey supply operates as a major driver of wolf establishment, especially red deer, which may occur at high density locally and generally belong to the most profitable prey for wolf packs in temperate Europe (Jedrzejewski et al., 2012).

1.1 | STUDY AREA

The study was conducted in the Western Alps (Valais, SW Switzerland, 5,224 km²), a mountainous area flanked in the West and South by France and Italy (Figure 1). Valais consists of a deep, East-West valley (Rhône river) and its tributaries, with elevation ranging from 372 m (Lake of Geneva) to 4,634 m a.s.l. (Dufourspitze) and a fairly continental climate. Forest covers 22% of Valais, with an average human population density of 52 km⁻², but locally up to 500 inhabitants/km² in the highly anthropized valley bottoms. Six species of wild ungulates occur in the area: red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, chamois *Rupicapra rupicapra* and ibex *Capra ibex* are abundant and distributed over most of Valais, while wild boar

Sus scrofa and non-native mouflon *Ovis orientalis musimon* occur only locally, especially in the milder western part of the study area. We restricted our study to an elevational range from the lowest foothills at 500 m up to 2,000 m a.s.l. (3,700 km²), that is, excluding the densely populated valleys and the mountain peaks. This allowed focusing on the main wolf habitat in Switzerland, while avoiding legal constraints for trail camera placement in populated areas as well as access limitations to the mountain peaks in winter.

2 | MATERIALS AND METHODS

2.1 | Species data

2.1.1 | Ungulate data: Snow-tracking

Ungulate data were collected by means of snow-tracking along two hundred and eighteen 1-km long transects, during four subsequent winters starting in 2012/2013. In order to distribute transects in a stratified manner, the study area was first divided into thirty-four 15 km × 15 km squares (Figure 1). In each square, an average of six transects (range: 1–10) were then placed so as to cover the elevational (Figure S1) and environmental gradients present in the study area as representatively as possible, while accounting for accessibility, topography and safety (avalanches). The transects were surveyed twice per winter (December to March). To reduce observer effects, each transect was visited by the same person during the whole study period, and the entire fieldwork was conducted by two experienced wildlife biologists, who trained and standardized their methods for one full season (2011/2012) prior to the start of this study. Tracks found in the snow were recorded for the main potential wolf prey: roe deer, red deer, chamois, ibex, mouflon and wild boar. Based on imprint size and track distribution, we

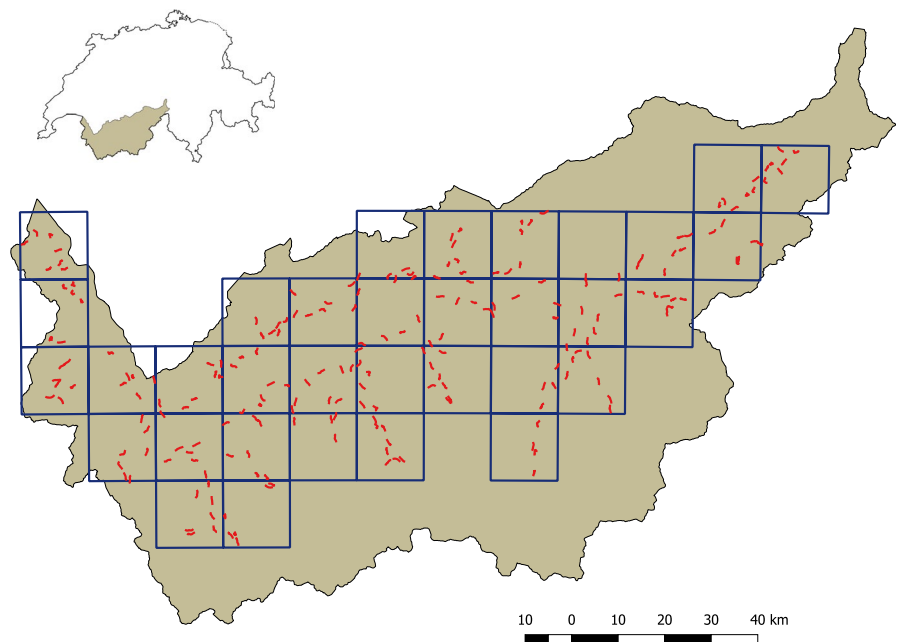


FIGURE 1 Location of the study area (Canton of Valais; lower map) within Switzerland (upper map). Blue squares (15 km × 15 km) indicate the raster used for stratifying the snow-track surveys that were conducted along the two hundred and eighteen 1-km transects (red segments)

estimated the minimal number of individuals present at each visit to a given transect. Multiple individuals were counted if tracks of different size (e.g. from different sexes or age classes) or individuals travelling together in a group could be distinguished. We used a conservative approach: when in doubt we always recorded the lower number.

2.1.2 | Wolf data

Wolf presence locations were obtained from systematic camera trapping and complemented with data from the opportunistic monitoring of wolves in Switzerland (Weber, 2004). Trail camera traps were distributed in a stratified manner, placing three camera traps (Reconyx PC900 Hyperfire Professional, Inc.) in each of the thirty-four 10 km × 10 km squares (Figure 1; for details see Biollaz, Mettaz, Zimmermann, Braunisch, & Arlettaz, 2016). In the winter of 2013/2014, an additional survey scheme was implemented by the KORA foundation (Swiss Carnivore Ecology and Wildlife Management) in the Northern part of the study area, placing one site with two traps in every second grid cell of a 2.5 km × 2.5 km grid (Zimmermann, Dulex, Foresti, Breitenmoser-Würsten, & Breitenmoser, 2014).

Through the opportunistic wolf monitoring, every piece of evidence of wolf presence in Valais since the first proven observations in 1996 has been recorded and categorized by the KORA foundation according to the three SCALP-categories (Molinari-Jobin et al., 2012): C1 = hard fact data such as dead wolf, picture or genetic identification; C2 = verified report of kill (livestock and wild prey) or track; C3 = unverified wild prey remains or track and unverifiable sign like scat, acoustic or visual observation. For our analyses, we used data from the winter months (October to April) of the years 2012/2013 to 2015/2016, that is, matching the period of ungulate sampling. Only data of the categories C1 and C2 recorded in these months were retained. To avoid double-counting of animals, for example when passing in front of a camera trap several times in one night, only one record per day and location was retained, with the exception of records of two wolves following each other within short distance. This resulted in 213 points of confirmed wolf presence (84 camera trap pictures, 56 genetic samples, 73 verified kills and tracks).

2.2 | Snow conditions

To model the detection probability of ungulates in relation to the conditions during sampling, we recorded covariates of snow conditions (Table 1) during the transect surveys: average snow height, quality and percentage of snow cover. In addition, the daily amount of fresh snow recorded at all 56 weather stations across the study area was obtained (MeteoSwiss, 2016), assigning each transect to the nearest weather station. For each transect walk, we calculated the number of days since the last snowfall. We also transformed this continuous variable into a categorical variable describing snow age. Finally, we recorded the amount of fresh snow that had fallen on the last day with snowfall previous to each survey.

2.3 | Environmental predictors

The environmental variables used for predicting relative ungulate densities and wolf occurrence in a spatially explicit way (Table 2) were extracted from existing digital information, from which we produced basic raster layers with a 25 m × 25 m cell size. We obtained data on topography (altitude, slope, terrain roughness and topographic position) from the digital elevation model (DEM) of Switzerland *swissALTI*^{3D}. Roughness was calculated as the standard deviation of elevation of all cells within a predefined radius (564 m), which corresponds to an area of 1 km². The topographic position index (TPI) represents the position of a focal cell relative to the surrounding terrain and is calculated as the sum of angles to the ground measured in all eight cardinal directions (Gallant & Wilson, 2000). Land use and land cover (forest, rock, scree, water bodies, anthropogenic areas, roads and railways, ski lifts) were derived from *vector25*, a digital vector map produced and regularly updated by the Swiss Federal Office for Topography *swisstopo* (<https://www.swisstopo.admin.ch>), with the exception of grassland cover and forest type information, which were derived from the area statistics data set of Switzerland and *Landsat5* data respectively, both provided by the Swiss Federal office of statistics (<https://www.bfs.admin.ch>). Winter temperature and precipitation stemmed from the *Worldclim* dataset (<http://www.worldclim.org>), which was downscaled from a 1-km² raster to a resolution of 100 m × 100 m based on the *SRTM-V4* DEM

Variable	Type	Description	Source
Snow height	Continuous	Height in cm	Snow-tracking
Snow quality	Categorical	old ≥5 days, fresh <5 days	Snow-tracking
Snow cover	Continuous	Covered area in %	Snow-tracking
Snow age	Categorical	1: 0–1 day, 2: 2–4 days, 3: ≥5 days	MeteoSwiss
Days since last snowfall (>10 cm)	Continuous	Days	MeteoSwiss
Amount of fresh snow	Continuous	Height in cm	MeteoSwiss

TABLE 1 Snow variables used for predicting the detection probability of ungulates whose presence was assessed via snow-tracking. Variables were recorded directly in the field or derived from the Swiss weather station network (MeteoSwiss, 2016)

TABLE 2 Environmental variables used to predict relative ungulate densities and wolf occurrence, extracted from buffer zones delineated around the transects or circular moving windows with a size corresponding to winter home range size of the modelled species (see Section 3 for details). Continuous variables were averaged, while percentage of cover was calculated for Boolean variables

Variable	Source	Description
Topography		
Altitude (m)	DEM ^a	
Roughness (m)	DEM	Standard deviation of altitude
Slope (°)	DEM	Angle
Topographic position index (TPI) ^b (index value)	DEM	Relative position to surrounding terrain
Landuse		
Proportion of forest (%)	Vector25 ^c	
Proportion of and distance to anthropogenic areas (% , m)	Vector25	
Proportion of rock and scree (%)	Vector25	
Proportion of grassland (%)	Arealstatistics	Pastures, meadows
Length of main and secondary roads (m)	Vector25	Main roads = categories 1–3, small roads = categories 4–6
Distance to roads/rails (m)	Vector25	
Forest type (coniferous, deciduous, mixed) (%)	BFS ^d	
Forest type (dense, open) (%)	Vector25	
Forest edge (inner, outer) (%)	Calculated	Calculated from the vector25 forest layer
Distance to rivers/creeks and lakes (m)	Vector25	
Proportion of rivers/creeks (%)	Vector25	
Distance to skilifts and cableways (m)	Vector25	
Sheep and goat density (N/ha)	Agricultural statistics	
Proportion of game reserves (%)	FOEN ^e	Federal and cantonal game reserves
Climate		
Mean precipitation in winter (mm)	Worldclim	December to February
Mean temperature in winter (mm)	Worldclim	December to February

^aDEM: Digital Elevation Model *swissALTI*^{3D}, produced by Federal Office for Topography *swisstopo*.

^bSee Gallant and Wilson (2000).

^cVector25: Digital vector map produced by Federal Office for Topography *swisstopo*.

^dBFS: Swiss Federal office of statistics.

^eFOEN: Swiss Federal office for the Environment.

and the method described in Zimmermann and Roberts (2001). Estimates of livestock (sheep and goat) densities were obtained by relating the number of livestock per community (as obtained from the Agricultural statistics of Switzerland) to the amount of pastures present in that community. Finally, spatial data on the location of game reserves was obtained from the Federal Office for the Environment (FOEN).

2.4 | Statistical analysis

2.4.1 | Ungulate abundance on the transects

Abundance was modelled for the three main ungulate prey species (roe deer, red deer, chamois), as the other three species (ibex, wild

boar and mouflon), with only marginal occurrence on few transects, did not produce enough detections for model calibration. To obtain annual, detection-corrected abundance estimates, N-mixture models were fitted with the R-package *UNMARKED* (Fiske et al., 2017), taking into account sampling occasion and snow conditions (Table 1). For red deer and roe deer, Poisson-N-mixture models were applied, while for chamois we used a zero-inflated Poisson distribution. First, variables were tested for collinearity. Of pairs or groups of correlated variables (Spearman's correlation coefficient $|r_s| > 0.5$), we retained the one that performed best in univariate N-mixture models, according to Akaike's information criterion corrected for small sample sizes (AICc, Akaike, 1974). Finally, models including all possible combinations of variables significantly affecting detection probability in univariate models were tested and ranked according to their AICc using the *dredge* function of the R-package *MuMIn* (Bartón, 2014). The resulting best model

was used to predict the detection-corrected minimum numbers of individuals per transect and winter, for each species. After evaluating between-winter variance, these values were averaged over the four winters and rounded to integer numbers to obtain one single value of estimated prey abundance per transect.

2.4.2 | Relative ungulate densities

For extrapolating relative densities of the three ungulate species across the study area, we related the average ungulate abundance per transect to the environmental conditions within an area corresponding to what might be considered as a winter home range size of the respective prey species. For roe deer and chamois, variables were calculated within a 200-m buffer around the transect, resulting in a reference area of 50 ha (Hamr, 1985; Mysterud, 1999). For red deer we considered an area of 100 ha (350 m buffer, Luccarini, Mauri, Ciuti, Lamberti, & Apollonio, 2006).

For modelling relative ungulate densities, we used generalized linear models with a Poisson (red and roe deer) or zero-inflated negative binomial (chamois) distribution (R-package *PSCL* for the latter species: Jackman, Tahk, Zeileis, Maimone, & Fearon, 2015). We first tested each of the environmental variables in a univariate model and retained the ones statistically related to relative ungulate density, then discarded the less-performing of pairs or groups of correlated variables ($|r_s| > 0.5$), based on AICc. From all possible combinations of the retained variables, the best model was then determined.

The best model for each species was used to predict the relative abundance (number of individuals per 50 or 100 ha, see above) across the whole study area. For this purpose, the proportion (for binary variables) or average (for continuous variables) of the environmental variables (Table 2) was calculated within circular moving windows of 100 ha (radius = 564 m, red deer) and 50 ha (399 m, roe deer and chamois), respectively, around each cell of the study area. We restricted the extrapolations to the areas within the same elevational range (387–2,193 m a.s.l.) and with a similar amount of forest cover (>14%) as found in the 350 m buffer zones around the transects. Additionally, we predicted overall ungulate densities (N/50 ha) and overall prey biomass (kg/50 ha) from the species-specific average emptied body masses, assuming 79 kg for red deer (Blankenhorn, Buchli, Voser, & Berger, 1979), 17.5 kg for roe deer and 21.5 kg for chamois, as given by the Valais hunting statistics during the study period.

2.4.3 | Wolf habitat selection

We modelled the relative probability of wolf presence as a function of the ungulate variables and other environmental variables using a presence-only model implemented in the software *Maxent* (Phillips, Anderson, & Schapire, 2006). *Maxent* compares the environmental conditions at the observed species locations with locations randomly sampled across the study area (in this case 10,000 random points). It

allows to fit complex nonlinear models by using the environmental variables as well as different functions thereof (in the following termed 'feature classes', FCs) as predictors, including linear (L), quadratic (Q) and product (P) terms as well as threshold (T) and hinge (H) features (Phillips et al., 2006; Phillips & Dudík, 2008; Phillips, Dudík, & Schapire, 2004). To avoid overfitting and limit model complexity, an L_1 regularization procedure is commonly applied (Phillips et al., 2006; Warren & Seifert, 2011), which constrains the average predicted value for a given feature to be close (i.e. within the confidence intervals) but not exactly similar to the empirical value measured at the presence locations.

The default value of the regularization multiplier (RM; default = 1.0; Phillips & Dudík, 2008) is not necessarily optimal for all specific data sets (Radosavljevic & Anderson, 2014; Warren, Wright, Seifert, & Shaffer, 2014) and can result in poorly performing models (Radosavljevic & Anderson, 2014; Shcheglovitova & Anderson, 2013). Hence, we adopted a stepwise procedure to tune model complexity (i.e. trade it off against performance) in order to choose an optimal set of predictors: from the initial set of predictors we generated a set of models using six different FC combinations (L, LQ, H, LQH, LQHP, LQHPT). Each combination was tested using different RM values, ranging from 0.5 to 10.0, with increments of 0.5, which resulted in 120 different models (Warren et al., 2014; Wright, Hijmans, Schwartz, & Shaffer, 2015). We then selected the settings that provided the most parsimonious model based on the AICc which were used for further variable selection.

First, of pairs or groups of correlated variables (Pearson's product moment correlation coefficient $|R| > 0.7$), we retained only those that achieved the highest gain (i.e. increased in regularized log-likelihood) in univariate models. With the resulting variable set, the 120 FC-RM-combinations were run again and all variables contributing <2% to the overall model gain were excluded. Finally, the 120 FC-RM-combinations were run a third time with the remaining variables and the best model was selected based on AICc. The best model was used to predict relative probability of wolf occurrence over the whole study area. The predictive performance of the final model was assessed using a fivefold cross validation, calculating the area under the receiver operating characteristics curve (AUC) on the test data of each replicate.

All analyses were conducted in R version 3.4.1 (R Core Team, 2017) and with *Maxent* version 3.2.3 (Phillips, Dudík, & Schapire, 2010). AICc's were computed using package *ENMEVAL* (Muscarella et al., 2014). Variable preparation and extrapolations were performed in QGIS version 2.18.9 (QGIS Development Team, 2017) and ArcGIS Release 10.

3 | RESULTS

3.1 | Ungulate abundance on the transects

The individual detection probability of the three prey species was affected by snow properties and sampling occasion, but the variables that yielded the best model fit differed considerably between sampling winters and species (Table 3). Detection probabilities, averaged

TABLE 3 Best models for estimating ungulate detection probability from snow-track surveys, per species and winter. Estimates (and *p*-values) are given for the variables retained. For categorical variables, the reference category is given in parentheses. All candidate models can be found in Table S5

Variable	Categories	Red deer			Roe deer			Chamois		
		2012	2013	2014	2015	2012	2013	2014	2015	2015
Snow height			-0.030 (<0.001)	-0.010 (0.108)	-0.023 (<0.001)	-0.005 (0.058)	-0.009 (<0.001)			-0.010 (0.022)
Snow height squared				1.41e-4 (0.309)						
Snow quality	(or: ≥ 5 days) <i>y</i> : <5 days	<i>y</i> : -0.116 (0.632)		<i>y</i> : -0.519 (0.007)					<i>y</i> : -0.620 (<0.001)	<i>y</i> : 0.205 (0.359)
Snow cover			-0.013 (0.234)	-0.009 (0.398)					0.015 (0.009)	
Sampling occasion	(1: first) 2: second		2: 0.612 (<0.001)		2: -0.267 (0.058)					2: -0.286 (0.073)
Days since last snowfall		0.032 (0.004)	-0.024 (0.597)		0.037 (0.107)				0.039 (<0.001)	
Days since last snowfall squared			0.004 (0.064)							
Height of fresh snow				0.005 (0.505)					-0.015 (0.016)	
Snow age category	(1: 0–1 days) 2: 2–4 days 3: 5 days and more						2: 0.375 (0.074) 3: 0.576 (0.005)			
Detection probability		81%	88%	79%	68%	86%	82%	84%	63%	55%
Average detection probability across years		80%				85%			59%	

across all winters, were 0.80, 0.85 and 0.59 for red deer, roe deer and chamois respectively.

Resulting detection-corrected predictions of red deer abundance per transect and winter ranged from 0.07 to 10.68 individuals. After averaging across the winters, estimated prey abundance ranged from 0.30 to 7.23 individuals per transect. Predictions of roe deer abundance ranged from 0.23 to 6.46 individuals in a given winter, and from 0.40 to 4.93 after averaging between winters. In chamois, the respective abundance values were 0.07–7.65 and 0.11–6.45 individuals. Transects with high or low individual numbers in one winter tended to rank similarly in the other winters, which suggests that averages across winters appropriately reflected general density patterns of the prey species (Figure S2).

3.2 | Relative ungulate densities

High red deer winter densities were found typically in areas with higher ambient winter temperature and lower precipitation, as well as a low proportion of screes in the wider landscape (Table 4a). Predicted relative densities ranged from 0 to 5.49 individuals per 100 ha (Figure 2a). Winter roe deer densities were highest in areas

TABLE 4 Best models for predicting relative densities of red deer (a), roe deer (b) and chamois (c), with estimates, standard errors (SE) and *p*-values. For red deer and roe deer, we assumed a Poisson and for chamois a zero-inflated negative binomial distribution. For chamois, only the count part of the zero-inflated negative binomial model is shown (the binomial part is provided in Table S3)

Variable	Estimate	SE	<i>p</i> value
(a) Red deer			
Intercept	1.556	0.239	<0.001
Grassland	0.523	0.307	0.089
Scree	-6.131	2.175	0.005
Winter temperature	0.013	0.005	0.004
Winter precipitation	-0.008	0.002	0.002
(b) Roe deer			
Intercept	1.268	0.201	<0.001
Forest	0.435	0.216	0.044
Rivers and Creeks	-1.241	0.814	0.127
Winter precipitation	-0.004	0.002	0.017
(c) Chamois			
Intercept	0.972	0.427	0.023
Coniferous forest	0.165	0.359	0.646
Distance to roads/rails	-9.12e-5	4.69e-4	0.846
Grassland	-1.358	0.489	0.005
Rock	0.160	1.258	0.899
Sheep and goats	-0.291	2.188	0.894
Slope	0.021	0.012	0.083
Winter precipitation	-0.005	0.003	0.079

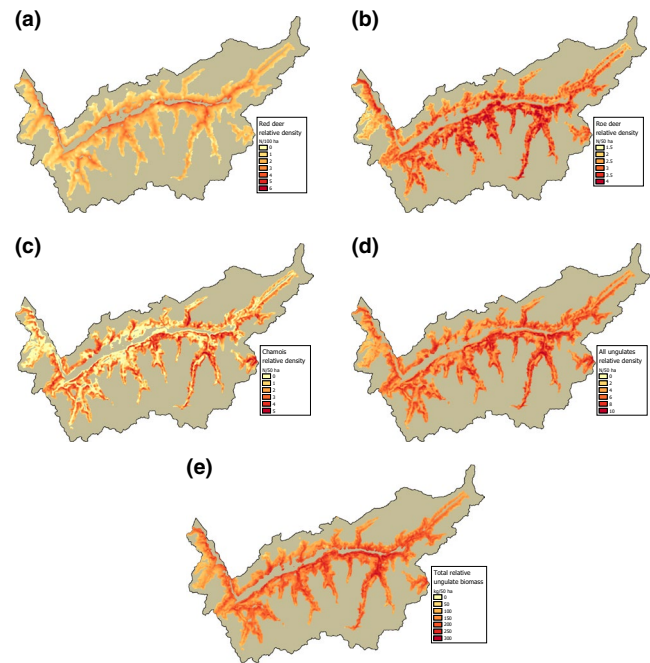


FIGURE 2 Predicted relative densities of (a) red deer (ranging from 0 to 5.5 individuals per 100 ha), (b) roe deer (1.3–4.5 individuals per 50 ha), (c) chamois (0–6.3 individuals per 50 ha), (d) all ungulates grouped (1.34–11.65 individuals per 50 ha) and (e) predicted relative ungulate biomass (23.43–304.01 kg per 50 ha). The shaded area represents the canton of Valais (see Figure 1) while the coloured areas represent the study zone

TABLE 5 Variables best explaining relative wolf occurrence probability, ranked by their per cent contribution to the overall model gain (see Phillips et al., 2006). The permutation importance indicates the drop in the area under the receiver operating characteristics curve (AUC, normalized to percentages) of a model where the values of the respective variable are randomly permuted compared to the final model. Symbols indicate the response type, with + indicating a positive, – a negative and \cap a unimodal response. Average AUC over five cross-validations was 0.83 (SD: 0.02)

Variable	Percent contribution (%)	Permutation importance (%)	Response
Red deer relative density (N/100 ha)	30.6	42.6	\cap
Roe deer relative density (N/50 ha)	21.9	13.2	+
Average winter precipitation (mm)	19.4	30.3	\cap
Proportion of game reserves (%)	15.9	4.9	\cap
Eastness	10.7	4.2	+
Frequency of anthropogenic areas (%)	1.5	4.7	–

with a high proportion of forest within the 50-ha transect buffer, and also under low winter precipitation (Table 4b). Predicted relative roe deer winter densities ranged from 1.33 to 4.48 individuals per 50 ha (Figure 2b). Chamois winter habitat was also mainly characterized by a lower than average winter precipitation and a low proportion of grasslands in the wider landscape. There was some, but no statistically significant, evidence for a preference for steeper slopes (Table 4c). Predicted relative winter densities of chamois ranged from 0 to 6.30 individuals per 50 ha (Figure 2c). Thus, pooled predicted relative densities of all main prey species of the wolf ranged from 1.34 to 11.65 individuals per 50 ha, which gives an overall prey biomass ranging from 23.43 to 304.01 kg per 50 ha (Figure 2d,e).

3.3 | Wolf habitat selection

With an overall contribution of 31% (43% permutation importance, see legend of Table 5), relative density of red deer was the

best predictor of wolf occurrence, followed by relative density of roe deer (22% contribution and 13% permutation importance) and winter precipitation (19% contribution and 30% permutation importance) (Table 5). The relative probability of wolf occurrence increased steeply with increasing red deer density, peaking at a relative density of two individuals per 100 ha, followed by a slight decrease afterwards (see response curve in Figure 3a), while it showed a continuous positive relationship with roe deer relative density (Figure 3b). In contrast, chamois density, overall relative prey density and biomass were not retained in the model, whereas the presence of game reserves had a positive effect (16% contribution; Figure 3d). Areas with high winter precipitation were avoided (Figure 3c). Finally, eastern slopes were preferred (11% contribution). Anthropogenic areas tended to be avoided, but this variable contributed very little (1.5%). Altogether, with an average AUC of 0.83 (SD: 0.02) over the five cross validation replicates, wolf occurrence could be predicted with a high level of accuracy. The relative probability of wolf occurrence across the study area in winter is illustrated in Figure 4.

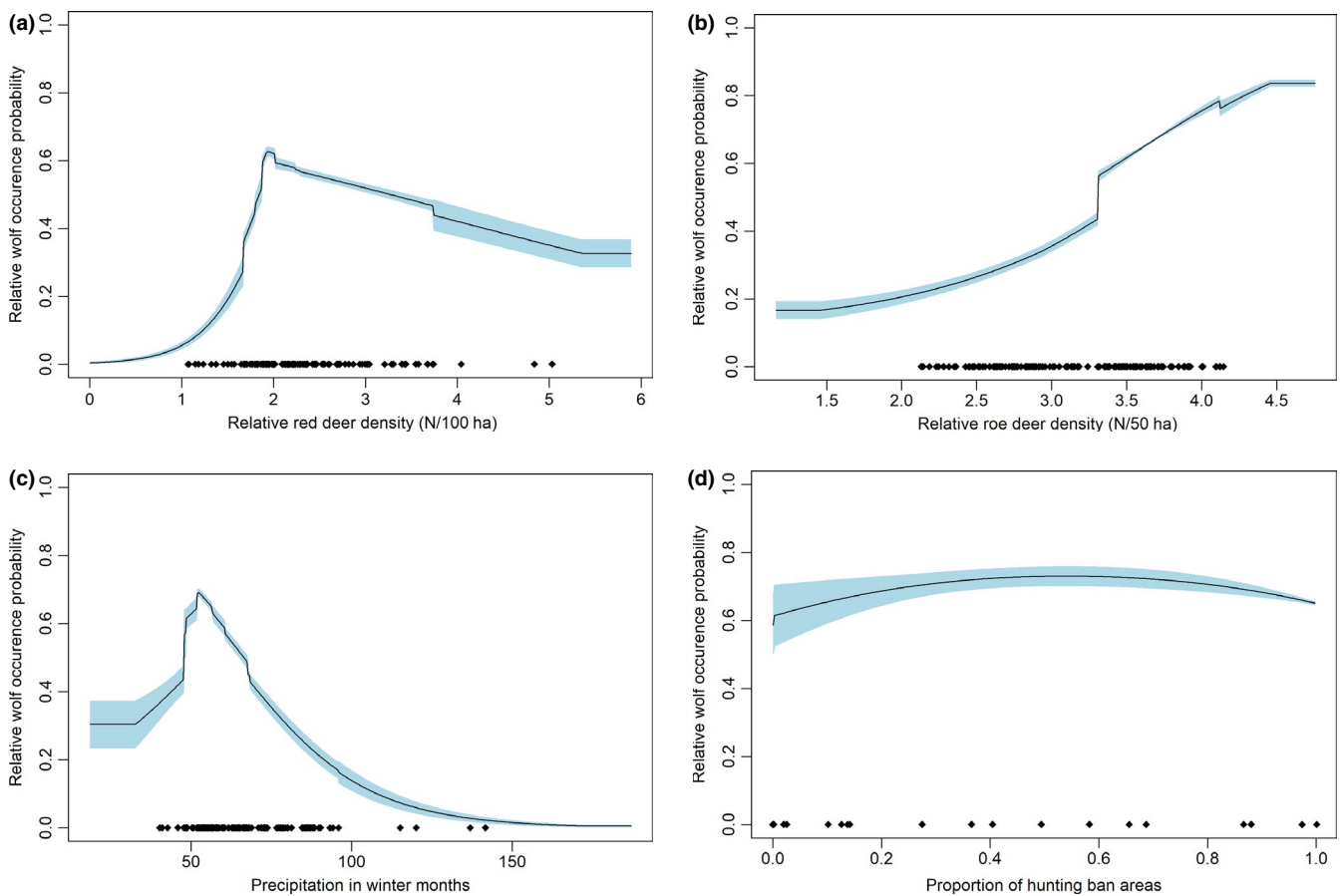


FIGURE 3 Univariate response curves of the four variables contributing most to explaining variation in relative wolf occurrence probability. Relative probability of wolf occurrence is shown in response to (a) relative red deer density per 100 ha, (b) relative roe deer density per 50 ha, (c) precipitation in winter and (d) proportion of game reserves. These four variables combined together contribute to c. 90% of the wolf model (Table 5). Black dots represent wolf presence locations along the variable range. Marginal response curves are provided in Figure S4

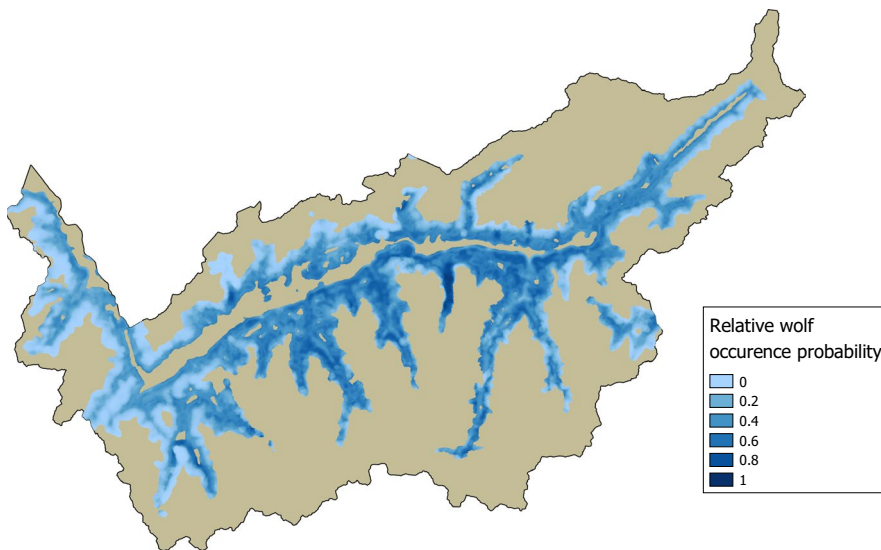


FIGURE 4 Relative wolf occurrence probability (Maxent logistic output) in the study area

4 | DISCUSSION

Our study suggests that the density of red deer, and to a lesser extent of roe deer, is the main driver of wolf establishment in the Western Alps, when considering areas with limited human presence. This illustrates the paramount importance of including accurate estimates of prey abundance in spatially explicit habitat selection models for predators, an aspect which has much too often been neglected (Gehring & Potter, 2005; Hebblewhite & Merrill, 2008; Jedrzejewski et al., 2004; Kabir et al., 2017; but see Hebblewhite et al., 2014; Jedrzejewski et al., 2008; Massolo & Meriggi, 1998; Potvin et al., 2005). In comparison, anthropogenic factors played almost no role in our study area. However, as we focused here on forested areas at intermediate elevation and excluded the densely populated valley bottom, the real importance of human presence on the wolf distribution in our study area cannot be inferred from our data.

The fact that red deer plays a more important role than roe deer furthermore indicates that this large ungulate may well represent the best energetic trade-off for wolf predation in the Western Alps, in line with the predictions of optimal foraging theory (Stephens & Krebs, 1986). This is further corroborated by the fact that, in our model, individual prey species contributed more to spatial occurrence patterns of the wolf than overall, that is, pooled relative prey density and biomass. Spatial models incorporating detailed, high-resolution information on species-specific prey supply are therefore needed to draw reliable predictions about habitat suitability for recolonizing wolves.

4.1 | Estimating prey abundance under imperfect detection

The main prey of wolves in Valais are forest-dwelling, fairly elusive animals (Coppes, Burghardt, Hagen, Suchant, & Braunisch, 2017) whose abundance is difficult to estimate. Conventional survey

methods of ungulates include direct visual counts, scat and track counts, trail camera trapping and genetic sampling (Ebert, Sandrini, Spielberger, Thiele, & Hohmann, 2012; Forsyth, MacKenzie, & Wright, 2014; Singh & Milner-Gulland, 2011). Widely deployed, they concern mostly monitoring for estimating population trends (Singh & Milner-Gulland, 2011). This study shows that snow-tracking is another valuable method for estimating relative prey abundance. Yet, it requires extended periods of snow cover and is logistically demanding. Moreover, accounting for probability of detection—which is dependent on species, observer and environment—necessitates at least two visits per transect and season. The importance of accounting for detection probability is supported by the fact that different variables related to snow conditions explained detection probability in the different study years, which points to differences in the within-year variance of the snow condition variables. Limiting the sampling to two visits is the approach we had to adopt given the logistic constraints of working in a large area (two hundred and eighteen 1-km transects over approximately 3,700 km²). Not surprisingly, this resulted in fairly large confidence intervals in our estimates.

4.2 | Ungulate densities

Our models revealed different species-specific patterns for relative ungulate densities. For red deer, a transhumant species in the Alps, the highest winter densities were found at low elevation adjacent to valley bottoms, that is, where more accessible grassy foraging grounds occur in winter (Luccarini et al., 2006). Roe deer winter density, in contrast, was much more homogeneous across the study area; this species occupies the same territory year-round. For chamois, the pattern was more complex and predicted areas with high relative densities were much more patchily distributed. This reflects the greater habitat and elevational amplitude of the species, which may also remain above the timberline in winter (Baumann, 2005).

4.3 | Wolf habitat selection

Deer density seemed to drive winter habitat use of wolves in our study region (explanatory contribution of 53.5%). This is in line with the results of Weber and Hofer (2010), who found that red and roe deer make up the majority of wild prey consumed by wolves in Switzerland. The response curve (Figure 3a) further suggests a high relative probability of wolf occurrence in winter as soon as red deer density reaches two individuals per km². The slight decrease in the relative probability of wolf presence above that density, which seems counterintuitive at first glance, could be explained by a mere human shield effect (Kuijper et al., 2016). In effect, in winter red deer concentrate near densely populated valley bottoms, which appear to be avoided by wolves. The valley bottoms themselves however, which consist mostly of settlements, transport infrastructure and intensive agriculture, were excluded from this study.

For roe deer, a comparably high relative probability of wolf occurrence is reached with approximately four individuals per 50 ha (i.e. eight roe deer per km²). Interestingly, this prey density ratio (1:4) matches well the ratio of species-specific emptied body masses (1:4.5; red deer: 79 kg vs. roe deer: 17.5 kg). This finding further highlights the importance of considering not only overall prey abundance but also prey species-specific abundances in range predictions for predators. In two previous wolf habitat suitability models for the Alps as a whole and for the NW Swiss Alps (Glenz et al., 2001; Landry, 1997), habitat was predicted more suitable in the NW part of our study area than in the SE part, a pattern opposite to our findings (Figure 4). Falcucci et al. (2013) predicted greater wolf occurrence at higher elevation, mostly above the treeline, which also contrasts with our model. These discrepancies may stem, on the one hand, from the fact that all three cited models were calibrated outside Switzerland while prey supply was either ignored (Landry, 1997) or estimated based on extremely coarse proxies (Falcucci et al., 2013; Glenz et al., 2001). On the other hand, however, we must recognize that our model is restricted to winter. An appropriate summer model would probably corroborate the findings by Falcucci et al. (2013) because red deer in the study area is an elevational transhumant.

Since the wolf population is establishing and therefore its density is still very low, systematically collected wolf observations were complemented with opportunistically collected data. For the latter we cannot exclude an observer bias, for example, towards more accessible areas. However, we consider this potential bias minute as it would have resulted in a positive effect of anthropogenic areas or infrastructure, whereas we found the opposite. Due to our study design, our findings are only applicable to areas of intermediate elevation and extensive forest cover, that is, excluding densely populated areas and mountain peaks. As this, however, represents the main habitat for wolves in Switzerland, we are still able to make a valuable prediction of future wolf settlement in the country as well as for nearby regions.

The wolf population establishing in the European Alps will be instrumental for the connection of wolf populations throughout Europe (Genovesi, 2002; Randi, 2011). Properly predicting future areas of establishment enables anticipating where forthcoming human–wolf conflicts will arise, and where adaptive or preventive measures should be carried out in priority. This can include educational activities revolving around the danger that wolves represent for our physical integrity, protective measures for livestock, as well as adapting hunting plans for the wolf's main prey species. Accurate information about prey density, especially of red and roe deer as concerns the Alps, will be essential for reliable spatial planning and forecasting, which calls for a systematic monitoring of prey species in areas where wolves are returning or expected to return.

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AUTHORS' CONTRIBUTIONS

R.A. raised the funds; R.A. and V.B. conceived the study and designed methodology; F.B. and S.M. collected the data; S.R. analysed the data; F.Z., R.M. and L.F. provided the wolf data; M.K. and S.V. assisted with modelling; S.R., V.B. and R.A. wrote the manuscript. All authors contributed to the drafts at several stages and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Ungulate and environmental data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.2v6wwpzhx> (Roder et al., 2020). Wolf records used in the present paper are not archived due to the sensitive location data, but are available upon request at KORA (info@kora.ch).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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