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Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges

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Abstract. Outdoor winter recreation exerts an increasing pressure upon mountain ecosystems, with unpredictable, free-ranging activities (e.g., ski mountaineering, snowboarding, and snowshoeing) representing a major source of stress for wildlife. Mitigating anthropogenic disturbance requires the spatially explicit prediction of the interference between the activities of humans and wildlife. We applied spatial modeling to localize conflict zones between wintering Black Grouse (*Tetrao tetrix*), a declining species of Alpine timberline ecosystems, and two free-ranging winter sports (off-piste skiing [including snow-boarding] and snowshoeing). Track data (snow-sports and birds' traces) obtained from aerial photographs taken over a 585-km transect running along the timberline, implemented within a maximum entropy model, were used to predict the occurrence of snow sports and Black Grouse as a function of landscape characteristics. By modeling Black Grouse presence in the theoretical absence of free-ranging activities and ski infrastructure, we first estimated the amount of habitat reduction caused by these two factors. The models were then extrapolated to the altitudinal range occupied by Black Grouse, while the spatial extent and intensity of potential conflict were assessed by calculating the probability of human–wildlife co-occurrence. The two snow-sports showed different distribution patterns. Skiers' occurrence was mainly determined by ski-lift presence and a smooth terrain, while snowshoers' occurrence was linked to hiking or skiing routes and moderate slopes. Wintering Black Grouse avoided ski lifts and areas frequented by free-ranging snow sports. According to the models, Black Grouse have faced a substantial reduction of suitable wintering habitat along the timberline transect: 12% due to ski infrastructure and another 16% when adding free-ranging activities. Extrapolating the models over the whole study area results in an overall habitat loss due to ski infrastructure of 10%, while there was a >10% probability of human–wildlife encounters on 67% of the remaining area of suitable wintering habitat. Only 23% of the wintering habitat was thus free of anthropogenic disturbance. By identifying zones of potential conflict, while rating its relative intensity, our model provides a powerful tool to delineate and prioritize areas where wildlife winter refuges and visitor steering measures should be implemented.

Key words: Alpine ecosystems; Black Grouse; human disturbance; human–wildlife conflict; Maxent; maximum entropy model; ski tourism; Tetrao tetrix; *wildlife refuge; winter sports.*

Introduction

Human recreation and diversification of outdoor sport activities have become of major conservation concern as tourism expands into pristine landscapes, exerting increasing pressure upon biodiversity (Czech 2000, Watson and Moss 2004, Arlettaz et al. 2007). In addition to habitat loss and degradation resulting from the development of recreational facilities and infrastructure, human disturbance can elicit costly behavioral responses in animals, such as flight (Arlettaz et al. 2007, Thiel 2007, Thiel et al. 2007), feeding disruption (Fernández-Juricic and Telleria 2000) breeding failure (Miller et al. 1998), or the progressive abandonment of suitable habitats (Andersen et al. 1990, Thiel et al. 2008). Even in the absence of behavioral reactions, human presence may evoke a physiological stress response (Stillman and Goss-Custard 2002, Walker et al. 2005, Arlettaz et al. 2007, Thiel et al. 2008), with chronically elevated stress levels affecting metabolism, immune response, reproduction and/or survival (Sapolsky et al. 2000). As both physiological and behavioral responses often entail extra energetic costs (Baltic 2005, Williams et al. 2006), disturbance in temperate and boreal ecosystems is expected to be particularly detrimental in winter, when most wildlife species face an energetic bottleneck.

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Winter recreation, especially ski tourism, has undergone rapid development over the last decades, and plays a major role in the economy of the European Alpine region (Elsasser and Messerli 2001). Rapid development is not only reflected by the expansion of ski resorts, with increasing numbers of visitors, but also by a massive spread of free-ranging snow-sport activities, such as free-ride skiing and snowboarding, backcountry skiing, or snowshoeing (Ingold 2005). For wildlife, these activities are particularly problematic as they mostly occur in an unpredictable manner, with only limited possibilities for adaptation (Miller et al. 2001).

The ongoing expansion of tourism and recreation into wildlife habitats calls for measures to mitigate the negative effects of anthropogenic disturbance (Sutherland 2007). The creation of wildlife refuges, by limiting human access to key habitats of vulnerable or endangered species, has proved to be an effective tool in this context (Knight and Temple 1995, Whitfield et al. 2008). Often limited in size, such refuges are frequently established outside traditional nature protection areas, in sites where species' requirements heavily compete with anthropogenic land use. Refined spatial assessments of human–wildlife conflict zones are thus a prerequisite for the establishment of effective wildlife refuges. However, such assessments represent a major challenge in conservation planning as they require area-wide, spatially explicit information not only about a target species' key habitats, but also about the distribution and intensity of different recreational activities. Contrary to when localizing infrastructure-bound sources of disturbance (e.g., Patthey et al. 2008), there is a lack of applicable methods for assessing spatial interference between sensitive wildlife habitats and unpredictable, free-ranging recreation, especially in more remote, natural habitats situated far from sports infrastructure.

The aim of this study was to address this information gap by providing an applicable planning tool for predicting the spatial pattern of human–wildlife co-occurrence, especially outside designated winter sport areas. As a model species we chose the Black Grouse (*Tetrao tetrix*), which is considered as a key indicator of ecosystem integrity in boreal and mountain timberline habitats. The population of the Black Grouse is declining in most parts of its European range (Storch 2007). In the European Alps, Black Grouse occupies the same narrow altitudinal belt around the timberline as where snow-sports activities are concentrated (Menoni and Magnani 1998, Zeitler and Glanzer 1998, Zeitler 2000). Human disturbance has been hypothesized to be among the main causes for the decline of local populations (Zbinden et al. 2003, Storch 2007). Recent studies have revealed negative effects of ski tourism on Black Grouse, showing elevated stress levels after inadvertent flushing (Arlettaz et al. 2007), which may account for the much lower population densities recorded in the surrounding of ski resorts (Patthey et al. 2008), thereby underpinning the necessity of implementing wintering refuges.

We used track data obtained from aerial photographs in combination with spatial modeling to predict the probability of presence and co-occurrence of wintering Black Grouse on the one hand, and two free-ranging snow-sports on the other, namely off-piste skiing (including snowboarding) and snowshoe walking. By assessing the impact of both infrastructure-bound and free-ranging activities on the species' presence, and localizing zones of potential conflict while rating its relative intensity, we provide an innovative, applicable, and transferable tool for the spatial planning of wildlife refuges and visitor steering measures over wide areas.

Methods

Study area

The study was conducted in the Swiss Alps of the cantons of Valais and Vaud (southwestern Switzerland, around 46°10′ N, 7°20′ E) within an altitudinal belt of 1600–2500 m above sea level along the flanks of the Rhône valley and its main tributaries. The study area encompasses the timberline zone around the upper limit of the subalpine forests, with larch *Larix decidua* being the dominant tree species, locally intermixed with arolla pine *Pinus cembra* or spruce *Picea abies*. The ground vegetation mainly consists of dwarf shrubs (*Rhododendron ferrugineum, Juniperus communis*, and *Calluna vulgaris*) as well as grasses (*Nardus Stricta*, *Calamagrostis villosa*). The study area actually includes two topographic and bioclimatic regions: the Pre-Alps and the Central Alps (Gonseth et al. 2001), both characterized by subcontinental to continental climate conditions with warm and dry summers, and cold, relatively wet winters. The region is popular for winter sports, particularly skiing, snowboarding and ski-mountaineering, harboring several of the largest ski resorts in the Alps (e.g., Portes du Soleil, Verbier-Quatre Vallées, Montana-Crans, Zermatt, Saas Fee).

Black Grouse and snow-sport data

Data on Black Grouse and snow-sport occurrences were retrieved from photographs we took from an airplane over-flying a continuous transect along the timberline throughout the study area (see Appendix A). Flights took place on two days in early spring 2007, three days after a sunny weekend with preceding snowfall (10–25 cm), with the aim to obtain the best conditions for detecting snow-sport activity and grouse tracks. In addition, we chose weekends with a moderate danger of avalanches (level II, Swiss national avalanche bulletin) in order to capture a representative picture of snow-sport activities outside the safeguarded ski pistes.

Due to variations in the plane flight height, in the angle between flight route and aspect of the transect slope, and finally in the timberline vegetation structure itself, the transect covered by aerial photographs was fragmented into horizontal segments of varying length and elevation passing through the timberline (Fig. A1). First, we digitized the part of the timberline transect shown on the photographs. Subsequently, tracks of Black Grouse and people engaging in snow sports were rendered visible by using Photoshop (Adobe, San Jose, California, USA) to accentuate the contrast. We distinguished between tracks of off-piste skiers (including snowboarders) and snowshoers, mapping each of the crossing points with the transect line. Evidence of Black Grouse (i.e., tracks and snow burrows) was registered when occurring up to a distance of 100 m from the transect, assigning the trace to the closest point on the transect line. For each "species" (Black Grouse, skiers, snowshoers) the transect information was converted to a 25×25 m raster map, assigning "presence" to all grid cells that contained at least one track. For validation of the extrapolated Black Grouse model (see *Modeling presence of Black Grouse and free-ranging snow sports*), we used an independent sample of Black Grouse wintering locations taken from previous field work (Arlettaz et al. 2007, Patthey et al. 2008), and casual observations by knowledgeable birdwatchers collected between 2003 and 2008 (archive of the Swiss Ornithological Institute, Sempach, Switzerland).

Environmental predictors

As potential predictors we used characteristics of topography, land cover, human infrastructure, and site accessibility as well as surrogates for snow condition (Table 1). In addition, the observed frequency of free-ranging snow-sport activities was included in the Black Grouse model.

Topography variables contained slope, northing (cosine of aspect), easting (sine of aspect) and different indices of terrain roughness such as the mean curvature and the standard deviation of altitude within different radii (Dirnböck et al. 2003) calculated from the digital elevation model (DEM). Land cover and vegetation characteristics included rocks, open and closed forest, isolated trees and bushes, obtained from the digital landscape model of Switzerland (Vektor 25 as per 2007; precision: 8 m; Swisstopo, Wabern, Switzerland). In addition, we calculated the normalized difference vegetation index (NDVI) for vegetation productivity (Petorelli et al. 2005) based on a Landsat-5 satellite image taken in April. This index, a correlate of photosynthetic activity, was used to localize sites where the vegetation is snow-free at this time of the year, offering foraging opportunities for Black Grouse. As an indicator for the condition of the snow surface we calculated the spectral radiance from each of the six reflectance bands in the visible (blue, green, red), near-infrared, shortwave, and thermal infrared portions of the electromagnetic spectrum using the same Landsat-5 image of April. As no usable satellite image (i.e., without clouds) of the flight date was available, an image from 1998 was employed. Consequently, both Landsat-derived variables do not reflect actual conditions, but only general spatial differences in vegetation productivity and snow condition. In addition, we calculated the mean amount of incoming solar energy per square meter and the mean sunshine duration in winter (January–March), according to Fu and Rich (2002), and based on the DEM. Human infrastructure and site accessibility were described by the distance to, and the density of forest tracks, roads, ski lifts (Vektor 25), and designated routes for ski mountaineering provided by the Swiss Alpine Club (SAC). The frequency of free-ranging snow-sport activities was defined as the number of tracks of all types of snow-sportspeople along the transect (skiers, snowboarders, and snowshoers) and was obtained from the aerial photographs.

Variables were prepared as raster maps (cell size: 25×25 m). To account for the conditions in the surrounding area, vegetation, infrastructure characteristics, and free-ranging snow-sport activities were measured within circular moving windows with a radius of 50, 100, 250, 500, and 1000 m, calculating the mean (continuous variables), proportion (Boolean variables) or density (line and point features) according to variable type. For topographic predictors we calculated the mean values within radii of 250 and 500 m around each grid cell. Slope and snow conditions were only considered at the cell size scale, as they are a direct prerequisite both for skiing and Black Grouse snow-burrowing.

To reduce both the number of variables and problems generated by variable colinearity, we performed a principal-component analysis (PCA) on groups of related variables, as defined in Table 1. For each group, the principal component(s) (PC) that encompassed a significant amount of the information according to the broken-stick heuristics (MacArthur 1960) were retained (Table 1) and used as summary predictors for subsequent modeling.

Modeling presence of Black Grouse and free-ranging snow sports

Statistical approach.—As sampling was conducted only once and, consequently, grid cells without snow sports or Black Grouse signs could not reliably be classified as "absence," we chose a modeling approach for "presence-only" data. Maxent is a machine-learning technique based on the principle of maximum entropy (Jaynes 1957), that was recently adapted for predictive species distribution modeling (Phillips et al. 2004, 2006). In brief, the method's aim is to find the probability distribution of species presence, over all cells of the study area, that best fits the constraints given by the environmental conditions at the species locations, while at the same time remaining as close as possible to a uniform distribution (principle of maximum entropy). As predictors, features (i.e., the environmental variables and functions thereof) are used which can include linear, quadratic and product terms, as well as hinge or threshold functions (Phillips et al. 2006). As in logistic regression, each of these features is weighted by a

Table 1. Predictor variables included in the models.

Variable group	Description (units)	Data source	N	PCs retained (variance explained [%])
Human infrastructure and site accessibility				
Ski lifts	density of ski-lift wires (m/ha), distance to ski-lift wires (m)	Vector 25	6	Ski-lift-PC1 (60.7), Ski-lift-PC2 (18.6)
Ski routes	density of ski routes (m/ha), distance to ski routes (m)	Swisstopo	6	SkiR-PC1 (59.1), SkiR-PC2 (19.9)
Pedestrian roads and walking trails	density of pedestrian roads (m/ha), distance to pedestrian roads (m)	Vector 25	6	PedR-PC1 (65.6), PedR-PC2 (17.8)
Roads	density of roads (m/ha), distance to roads (m)	Vector 25	6	Road-PC1 (72.1)
Settlements	proportion of settlements (%), distance to settlements (m)	Vector 25	6	Settll-PC1 (73.1)
Land cover and vegetation				
Rocks	proportion of rocks (%)	Vector 25	5	Rock-PC1 (85.0)
Single trees	number of single trees (trees/ha)	Vector 25	5	Tree-PC1 (73.6)
Bushes	proportion of area with bushes (%)	Vector 25	5	Bush-PC1 (78.4)
Open forest	proportion of open forest (%)	Vector 25	5	Oforest-PC1 (68.4), Oforest-PC2 (24.5)
Dense forest	proportion of dense forest (%)	Vector 25	5	Dforest-PC1 (90.7)
Vegetation index	index of vegetation growth	Landsat 5	5	NDVI-PC1 (96.9)
Surrogates for snow condition				
Radiance†	spectral radiance April (six reflectance bands) ($W \cdot sr^{-1} \cdot m^{-2}$)	Landsat 5	6	Rad-PC1 (66.9), Rad-PC2 (28.8)
Solar energy†	mean solar energy per area and month (kwh/m^2), mean monthly sunshine duration (h)	DEM	2	Sun-PC1 (96.7)
Topography				
Relief roughness‡	SD of altitude (m), SD of curvature (index)	DEM	6	Rough-PC1 (77.6)
Slope†	slope (degrees)	DEM	1	Slope (100)
Northing§	cosine aspect	DEM	3	North-PC1 (90.4)
Easting§	sine aspect	DEM	3	East-PC1 (91.5)
Off-piste activities	number of tracks, distance to next track (m)	Aerial photographs	6	Offp-PC1 (48.7), Offp-PC2 (21.2)

Notes: A principal-components analysis (PCA) was performed on each group of collinear variables. The components that accounted for a significant amount of the explained variance were retained as predictors for the subsequent models. All variables were considered at radii of 50, 100, 250, 500, and 1000 m unless noted otherwise.

† Radius was not considered for these variables.

† Variables were considered at radii of 100, 250, and 500 m.

§ Variables were considered at radii of 0, 250, and 500 m.

coefficient. Starting with a uniform probability distribution, the coefficients are iteratively changed to converge to the probability distribution that maximizes the likelihood of the occurrence data. The algorithm stops after a predetermined maximum number of iterations or when the increase in log likelihood falls below a minimum value. To avoid overfitting, a smoothing algorithm (regularization) is employed, that constrains the average value for a given feature so as to be close (i.e., within the confidence intervals) to its empirical average (for detailed information see Phillips et al. 2004, 2006, Elith et al. 2006, Phillips and Dudik 2008).

Following the recommendations by Phillips and Dudik (2008) we chose the feature types and regularization values (β) according to the number of presence data used for model calibration. Linear ($\beta = 0.25$), quadratic ($\beta = 0.25$), and hinge ($\beta = 0.5$) features were employed for the snowshoers (<80 presence points). Product ($\beta = 0.05$) and threshold ($\beta = 0.1$) features were additionally included for Black Grouse and skiers (>80 presence points). We ran the models with a maximum of 500 iterations and a convergence threshold of 1×10^{-5}. Maxent assigns to each grid cell (x) a sample-likelihood $q(x)$ that sums up to 1 over the study area. We used the logistic output (Phillips and Dudik 2008) that provides the probability of species observation $p(x)$, given a sampling intensity similar to that used for collecting the species data for model calibration.

Model generation.—The models were calibrated for the transect (i.e., all segments covered by the aerial photographs) using a random 70% of the presence data, with the remaining 30% retained for evaluation. First we ran a model including all predictors. Subsequently, to reduce and optimize the predictor set, we conducted a leave-one-out, stepwise, jack-knife procedure by systematically excluding one predictor at a time, thereby discarding all predictors that reduced the models' accuracy to predict the test data (Hastie et al. 2001, Parolo et al. 2008). Model accuracy was determined by the area under the receiver operating characteristics curve (AUC; Hanley and McNeil 1982, Zweig and Campbell 1993), with confidence intervals calculated according to DeLong et al. (1988: Eq. 2). We used the 30% evaluation data for testing the models' predictive power within the calibration area (transect).

Models were produced for skiers, snowshoers, and Black Grouse. In addition, to estimate the effect of both ski infrastructure and free-ranging snow sports on Black Grouse distribution and determine potentially suitable habitats in theoretical absence of winter sports, we recalculated Black Grouse presence simulating two scenarios: (1) theoretical absence of free-ranging snow sports and (2) additional absence of ski lifts. In both cases the values of the respective predictors (Offp-PC1/2 and Ski-lift-PC1/2, Table 1) were set to zero.

The resulting models were then extrapolated to the altitudinal range of Black Grouse occurrence. As this range differs between the two bioclimatic regions (Gonseth et al. 2001), we determined the 99% confidence interval of the altitudinal distribution of Black Grouse wintering sites in both regions, using the independently collected field and survey data (total $N = 372$; pre-Alps $N = 63$, central Alps $N = 309$). In addition, these data were employed for a second evaluation of the two extrapolated Black Grouse models (1 and 2). As data of off-piste activities were only available along the transect, the model predicting Black Grouse presence under the influence of both off-piste activities and ski infrastructure could not be extrapolated.

Probability of co-occurrence and conflict potential between Black Grouse and winter recreation

As Maxent provides the probability of species' observation given a similar sampling intensity, and the sampling strategy was the same for all three species (off-piste skiers, snowshoers, and Black Grouse), the respective probabilities of occurrence could be multiplied to calculate the probability of co-occurrence p_c between Black Grouse and each of the two snow-sport types, respectively. The p_c were added and capped at 1, thereby obtaining a map that quantifies the probability of Black Grouse being confronted with either one or both types of snow sportspeople. Probability of co-occurrence was calculated using Black Grouse presence unaffected by free-ranging snow-sports (model 1) and, in order to exclude areas insignificant for Black Grouse, was only considered within suitable Black Grouse wintering habitat, i.e., where the Black Grouse model predicted a higher probability of Black Grouse presence than expected when assuming a random species distribution. The cutoff value between positive and random prediction was determined according to Hirzel et al. (2006) by calculating the continuous Boyce curve (Boyce et al. 2002, Hirzel et al. 2006) from the independently sampled Black Grouse data set.

Finally, based on these data, we distinguished two types of conflict between wintering Black Grouse and snow sports. First, within the currently suitable Black Grouse habitat (as we defined), we used the co-occurrence probabilities p_c rounded to the first decimal to scale the potential of conflict with free-ranging snow-sports activities, ranging from null ($p_c = 0$) to very high ($p_c = 1$). Second, we subtracted the current Black Grouse distribution (model 1) from the distribution in theoretical absence of ski lifts (model 2). The result showed the zones where Black Grouse are now predicted to be absent due to excessive disturbance by ski facilities and infrastructure-bound snow-sport activities (Patthey et al. 2008), and this despite the fact that the natural habitat conditions would otherwise be suitable for them. In contrast to the first category, where conflict could be mitigated or rescinded by visitor management, the latter areas, hereafter termed "unsuitable due to ski infrastructure," are permanently lost as wintering habitat.

Results

Transect data

The exploitable photographs, i.e., pictures with sufficient quality, covered 71% of the timberline transect (585 km of a total of 824 km), with a mean elevation 2047 m above sea level (range = 1600–2500, SD = 256; Appendix A: Fig. A1). Along this transect, we recorded 305 signs of Black Grouse occurrence distributed over 214 grid cells (assigned "Black Grouse presence"), 6945 tracks of off-piste skiers and snowboarders ($n = 3367$ grid cells) and 174 tracks of snowshoers ($n = 91$ grid cells).

Predictor ranking

The principal-component analysis allowed us to reduce the number of predictors from 87 raw environmental variables to 24 principal components that will be our subsequent summary predictors (PCs; Table 1). The correlations of the original environmental variables with the most important PCs are shown in Appendix B. In most groups of variables, only the first PC (PC1) was retained; PC1 either correlated positively with the respective variables in its group (e.g., density of ski lifts for group 1) or, where applicable, negatively with the distance to it (e.g., distance to ski lifts). As the groups contained the same environmental attribute at different spatial scales, the PC1 of each group can be interpreted as a composite spatial index for this feature (e.g., ski lift abundance; Appendix A: Table A1). In some groups also the PC2 was retained, which always correlated positively with the variable-measures obtained for the small radii (50 up to 250 m) and negatively with those of

TABLE 2. Predictor importance, given as percentage contribution to the total increase in regularized log likelihood of the maximum entropy model compared to a uniform distribution.

Predictor type	PC	Skiers	Snowshoers	Black Grouse
Ski lifts	Ski-lift-PC1	**45.2 (±)**	4.1 (±)	**8.7 (–)**
Ski lifts	Ski-lift-PC2	0.1 (±)	···	0.1 (–)
Ski routes	SkiR-PC1	···	**12.8 (+)**	1.7 (–)
Ski routes	SkiR-PC2	0.7 (±)	···	···
Pedestrian roads	PedR-PC1	1.2 (+)	**28.2 (+)**	1.8 (–)
Pedestrian roads	PedR-PC2	0.1 (–)	···	1.3 (±)
Roads	Road-PC1	8.9 (±)	···	4.1 (–)
Settlements	Settl-PC1	1.3 (±)	6.8 (±)	1.4 (±)
Rocks	Rock-PC1	1.9 (–)	10.4 (–)	**7.3 (–)**
Single trees	Tree-PC1	2.4 (–)	8.6 (±)	3.0 (+)
Bushes	Bush-PC1	0.9 (–)	···	2.0 (±)
Open forest	Oforest-PC1	0.1 (+)	4.2 (+)	2.9 (+)
Open forest	Oforest-PC2	0.1 (±)	1.0 (–)	0.2 (±)
Dense forest	Dforest-PC1	0.7 (–)	2.0 (+)	**10.7 (±)**
Vegetation index	NDVI-PC1	2.9 (–)	···	1.5 (±)
Radiance	Rad-PC1	5.9 (+)	···	4.7 (±)
Radiance	Rad-PC2	1.0 (–)	0.2 (±)	2.4 (±)
Solar energy	Sun-PC1	2.0 (±)	6.6 (±)	4.9 (±)
Relief roughness	Rough-PC1	**20.4 (±)**	···	···
Slope	SLOPE	1.5 (±)	**15.1 (±)**	···
Northing	North-PC1	1.1 (±)	···	**30.5 (+)**
Easting	East-PC1	1.6 (+)	···	3.5 (+)
Off-piste activities	Offp-PC1			6.1 (–)
Off-piste activities	Offp-PC2			1.2 (–)
Total increase in regularized log likelihood†		0.481	1.304	1.382

Notes: At each iteration of the training algorithm, this increase (gain) was added to the value of the corresponding predictor, or subtracted from it if the gain was negative. The most important predictors that conjointly contributed to at least 50% of the gain are shown in boldface type. The signs in brackets indicate how the probability of presence is related to an increase in predictor values when holding all other predictors constant at their mean value: "(+)" indicates a positive, "(–)" a negative, and "(±)" a unimodal or multimodal response type. As the response curves are very complex, only the rough trend is indicated here.

† A total increase in regularized log likelihood of x means that the average likelihood of the presence samples used for training is $\exp(x)$ times higher than that of a random cell in the calibration area.

the large radii (500 or 1000 m), thus indicating the local-scale importance of a variable.

Out of a total of 22 summary predictors (the 24 PCs above minus two predictors for off-piste activities included only in the Black Grouse model), 21 were retained in the skiers' model and 12 in the model for the snowshoers. Among the 24 PCs used for the Black Grouse model, 21 were retained (see *Methods* and Table 2). The summary predictors' contributions to the overall increase in regularized log likelihood of the three models are shown in Table 2. Off-piste skiers' presence was mainly associated with the presence of ski lifts (Ski-lift-PC1) and a smooth terrain (Rough-PC1). The presence of snowshoers was best explained by a moderate slope (Slope) and the presence of pedestrian roads (PedR-PC1) and designated ski routes (SkiR-PC1). Black Grouse presence was mostly determined by northern expositions (North-PC1), which offer the best snow conditions for digging snow burrows, and an intermediate proportion of forest (Dforest-PC1), and was negatively related to ski lifts (Ski-lift-PC1) and rocky sites (Rock-PC1). In addition, there was a considerable negative effect of free-ranging snow-sport activities (Offp-PC1). The predicted probability of Black Grouse presence decreased almost exponentially with the increase of ski infrastructure or off-piste activities, respectively (Fig. 1). Comparing the predicted area of Black Grouse presence when modeled (0) with all types of snow-sports, (1) without off-piste activities, and (2) without any snow-sports, a habitat reduction along the transect of 15.6% could be attributed to free-ranging activities, and another 11.9% to ski infrastructure.

Model accuracy

According to the classification of Hosmer and Lemeshow (2000) we obtained an excellent model fit for the models of Black Grouse and snowshoers (AUC > 0.9) and a good fit for the skiers' model (AUC > 0.8). The accuracy in predicting the 30% evaluation data along the transect was good in all three "species" models (AUC > 0.8) (Table 3).

Referring to the varying altitudinal distribution of Black Grouse wintering sites in the two bioclimatic regions, we extrapolated the models to an altitudinal belt of 1600–2050 m above sea level in the Pre-Alps and 1800–2400 m above sea level in the Central Alps, over a total area of 1872 km^2. Within this extrapolation area, our Black Grouse models (i.e., Black Grouse presence unaffected by free-ranging snow sports [1], and in theoretical additional absence of ski lifts [2]) provided acceptable predictions of the independently collected

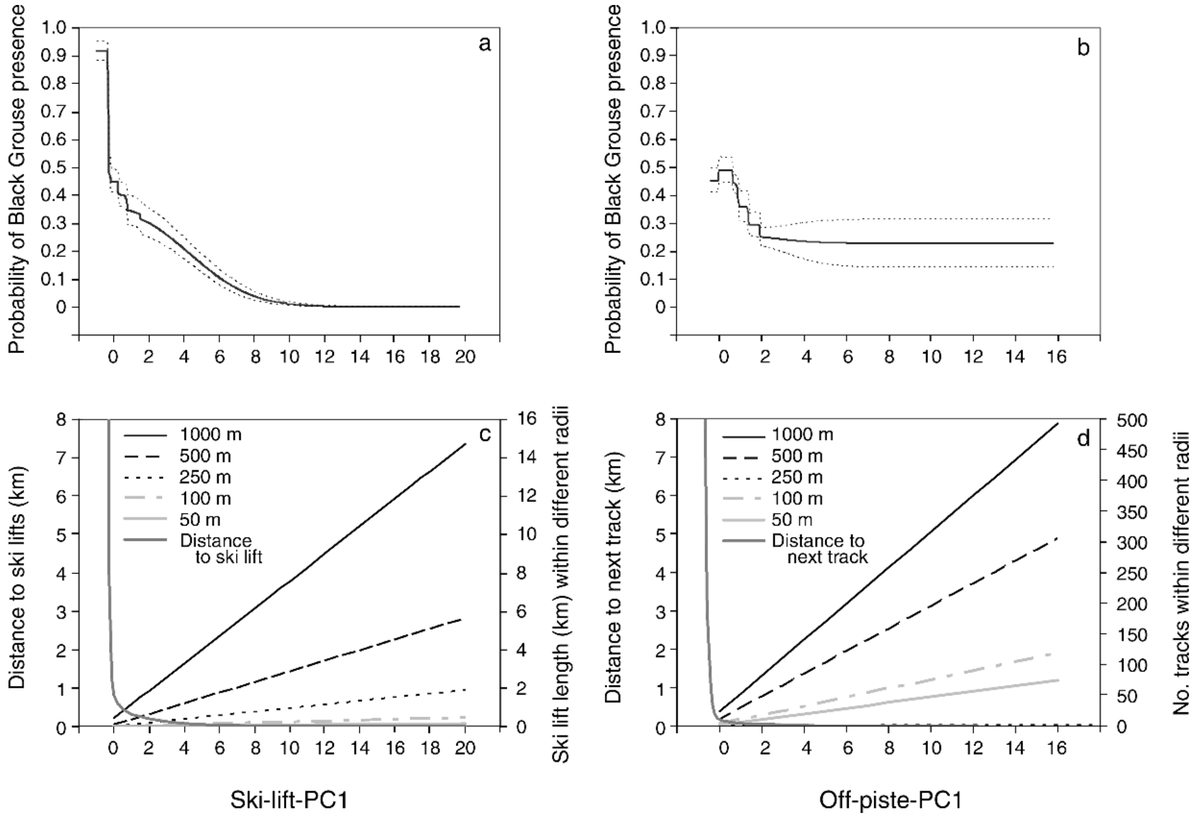

FIG. 1. Predicted probability of Black Grouse presence as a function of (a, c) ski infrastructure (Ski-lift PC1) and (b, d) off-piste activities (Offp-PC1) when holding all other variables at their average sample value. Mean (solid line) and standard deviation (dashed lines) calculated from 10 cross-validation replicates are provided in panels (a) and (b). Panels (c) and (d) show how the principal components (PC) values correspond to the original variables (length of ski lifts and number of skiers' and snowshoers' tracks respectively, measured within radii of 50, 100, 250, 500, and 1000 m and distance to the respective feature).

Black Grouse observation data (AUC = 0.78, and 0.74, respectively).

Predicted presence: maps of wintering Black Grouse and snow-sport activities

The distribution pattern of off-piste skiers, snowshoers, and wintering Black Grouse differed noticeably, as illustrated for a selected region located around two major ski resorts (Verbier and Nendaz, which belong to the Quatre Vallées ski complex; Fig. 2): skiers showed the widest spatial distribution, only really converging around ski lifts, whereas snowshoers were spatially more regrouped, and more frequently predicted at lower altitudes. Black Grouse were clearly confined to a narrow altitudinal belt along the timberline zone and, as derived from the comparison with the potential distribution in theoretical absence of ski lifts (Figs. 1c vs. 1d), showed a discernable avoidance of ski facilities.

Conflict zones between Black Grouse and winter recreation

According to the continuous Boyce curve ($r_s = 0.911$, $P < 0.0001$, see Appendix C), all areas with a probability of Black Grouse presence ($p(x) > 0.12$) were considered as suitable Black Grouse wintering habitat. The resulting habitat area amounted to 55 968

TABLE 3. Model results for Black Grouse, skiers, and snowshoers and the number of presence points (N) used for model calibration (cal) and evaluation (val).

Variable	Presence data, N (cal/val)	Model fit AUC (cal)	Model accuracy AUC (val) (95% CI)
Black Grouse	150/64	0.948	0.862 (0.821–0.903)
Skiers	2293/982	0.854	0.837 (0.825–0.849)
Snowshoers	64/27	0.910	0.848 (0.791–0.905)

Note: The models' fit on the calibration data and the models' accuracy in predicting the evaluation data (including 95% confidence interval, CI) is indicated by the area under the receiver operating characteristics curve (AUC).

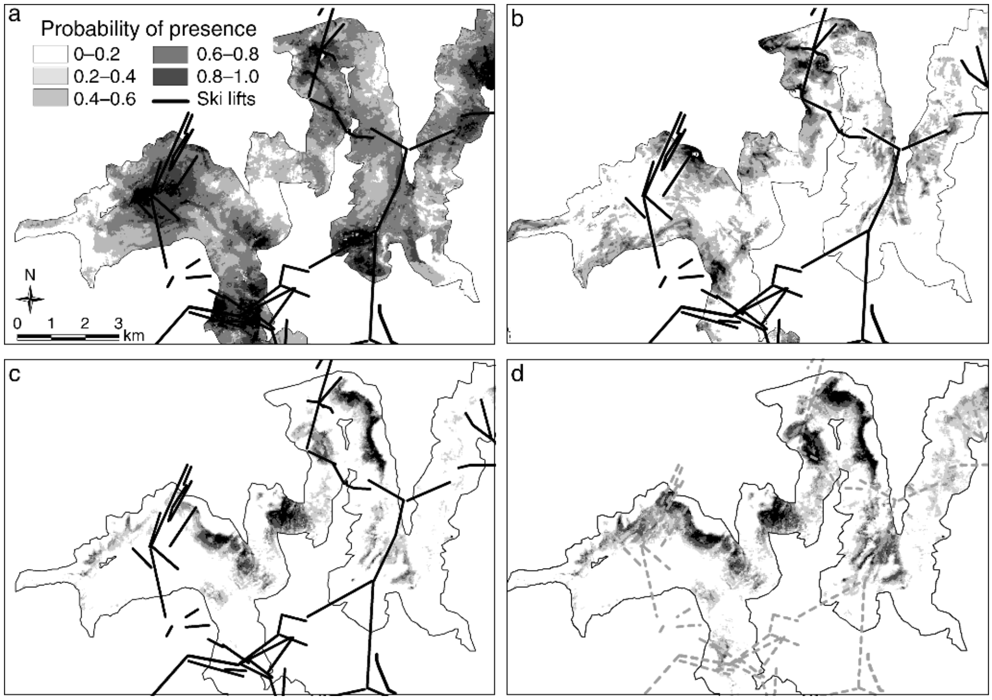

FIG. 2. Predicted spatial distribution of winter recreation and wintering Black Grouse, illustrated for the Quatre Vallées region, Switzerland (including the major ski resort of Verbier and Nendaz, Valais). Gradients of gray indicate the probability of presence of (a) off-piste skiers, (b) snowshoers, (c) Black Grouse (unaffected by off-piste activities), and (d) Black Grouse (in theoretical absence of ski lifts).

ha, which corresponds to 30% of the total extrapolation area. Under a scenario of theoretical absence of ski lifts, 62 095 ha would have been classified as suitable, indicating that over the total extrapolation area the presence of ski facilities is likely to have reduced the area of suitable wintering habitat by 10%. In the remaining wintering area there was a risk of encounter with off-piste skiers on 34 827 ha and with snowshoers on 15 715 ha, when including all areas with a probability of human–Black Grouse co-occurrence of at least 10%. As the areas used for skiing or snowshoeing partly overlapped, the total area of potential conflict with either one or both snow sports amounted to 41 853 ha which corresponds to another 67% of the potentially available wintering habitat (Fig. 3). Within this area, the fractions of habitat affected by different levels of "conflict potential" decreased exponentially with increasing co-occurrence probability (Fig. 4). The remaining 14 115 ha (23%) of Black Grouse wintering habitat did not seem currently affected by winter recreation. Fig. 5 illustrates the spatial pattern of conflict caused by both free-ranging snow sports and ski infrastructure in the aforementioned example region.

DISCUSSION

Modeling human–wildlife conflict

Given the rapid expansion of outdoor recreation, assessing and managing the impact of human disturbance upon biodiversity increasingly gains in importance in conservation planning (Sutherland 2007). Free-ranging activities are considered to be particularly problematic in this context, especially given the current lack of applicable methods to predict their distribution. Generally, visitor interviews are a popular means to collect information about target-group specific preferences (Haider 2002), which, implemented directly or in agent-based models, can be used to reconstruct spatial patterns of recreational behavior (Janowski and Becker 2002, Zhan 2005). However, spatial predictions based upon such information often suffer from subjectivity, as the visitors' self-estimation is frequently biased towards a supposedly environment-friendly behavior (Daniel 2002). Mapping visitor traffic is a more objective way to explore patterns of recreational use (e.g., Kerbiriou et al. 2009), but it requires a huge effort, especially in low-accessibility sites such as mountain ecosystems. From this viewpoint, our approach is innovative, as it provides area-wide information by using a non-disturbing and cost-effective remote technique for collecting unbiased data in combination with spatial modeling. In this context the two snow sports considered were treated like different "species," which enabled the assessment of patterns of preference vs. avoidance, and predicting their distribution in the environmental space, as is usually done in predictive species distribution modeling.

The restriction to a narrow altitudinal transect for data sampling and model calibration brought about

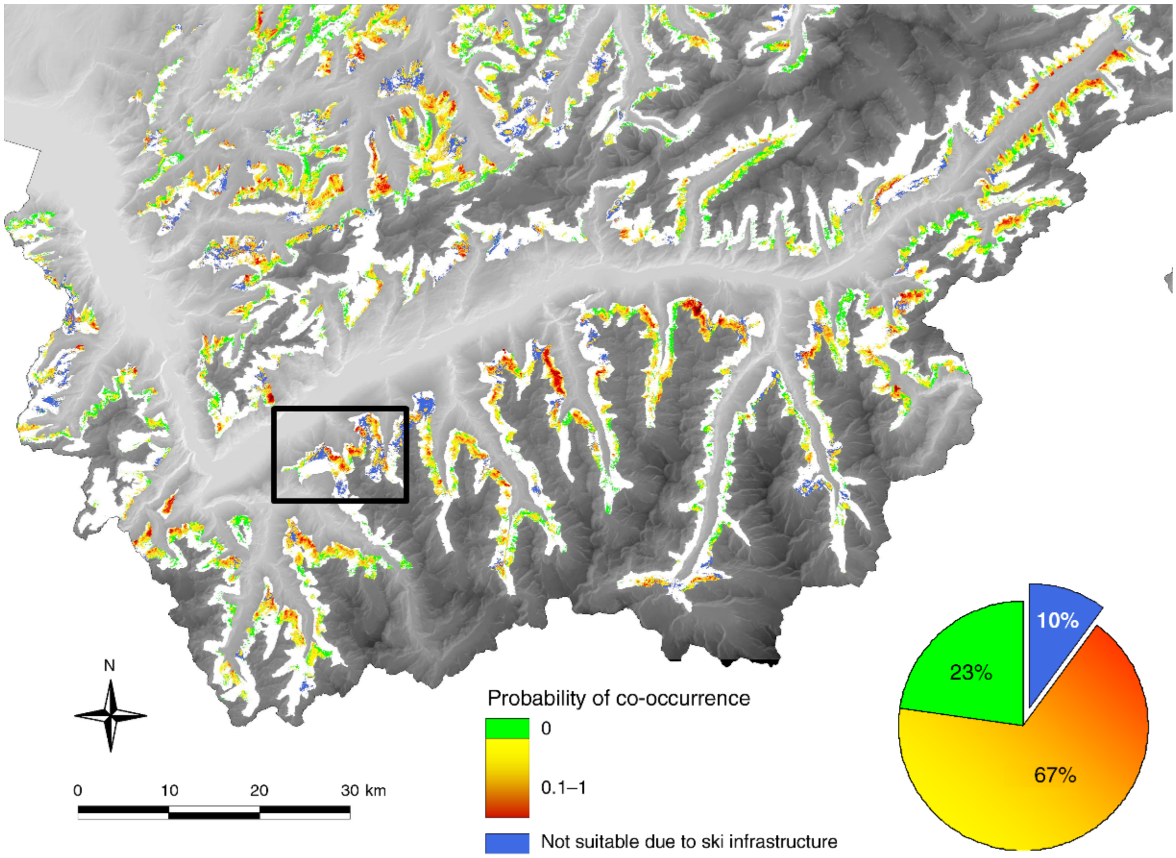

FIG. 3. Conflict zones between wintering Black Grouse and snow-sport activities in the study area. Conflict potential is defined as the probability of co-occurrence of Black Grouse with either one or both of the two investigated snow sports (off-piste skiing and/or snowshoeing). Key: green, Black Grouse wintering habitat currently untouched by snow sports; yellow to red, wintering habitat with increasing probabilities of human–wildlife co-occurrence; blue, wintering habitat unsuitable due to ski infrastructure. The black rectangle indicates the location of the example region illustrated in Figs. 1 and 4.

several challenges. First, data collection was concentrated around the timberline (on average ~2100 m above sea level), which means that elevation could not be included as predictor in the models. As this could have led to severe errors when extrapolating the models beyond the common altitudinal range of Black Grouse occurrence, the extrapolation had to be rigorously restricted to a limited range. Within this range, differences in vegetation and snow conditions, which mainly resulted from differences in altitude and exposition, were directly derived from satellite imagery. Since the images used dated from April 1998, they did not reflect the conditions in the study year but only informed about general differences in snow conditions and melting patterns. We can assume, however, that these patterns remained largely consistent over the years, notwithstanding the potential effects of climate change. Second, species presence usually depends not only on the conditions at the location of observation (i.e., within a 25 $\times$ 25 m grid cell), but also on those of a wider surrounding. Not surprisingly, spatial scale selection, including the use of multiple scales, can strongly improve the accuracy of species distribution models (Graf et al. 2005, Braunisch and Suchant 2007). In the present study, we attempted to integrate the environmental information over multiple spatial scales in the most comprehensive way by relying upon composite factors obtained from multivariate statistics (principal-component analysis, PCA). At the same time we maintained model interpretability as high as possible by performing separate PCAs for each environmental variable measured at different spatial scales without merging them into one single global PCA. The approach was reasonable, as we were not primarily interested in how specific environmental features affect "species" presence, but rather in obtaining the best possible spatial prediction. Moreover it proved beneficial as the resulting models tended to perform better than the corresponding models including all variables at one single scale (mean test-AUC of PCA-based models (see Table 3) vs. single-scale models: Black Grouse, 0.862 vs. 0.842; skiers, 0.837 vs. 0.833; snowshoers, 0.848 vs. 0.733). Finally, as track data of off-piste activities were only available along the transect, the model including their effect on Black

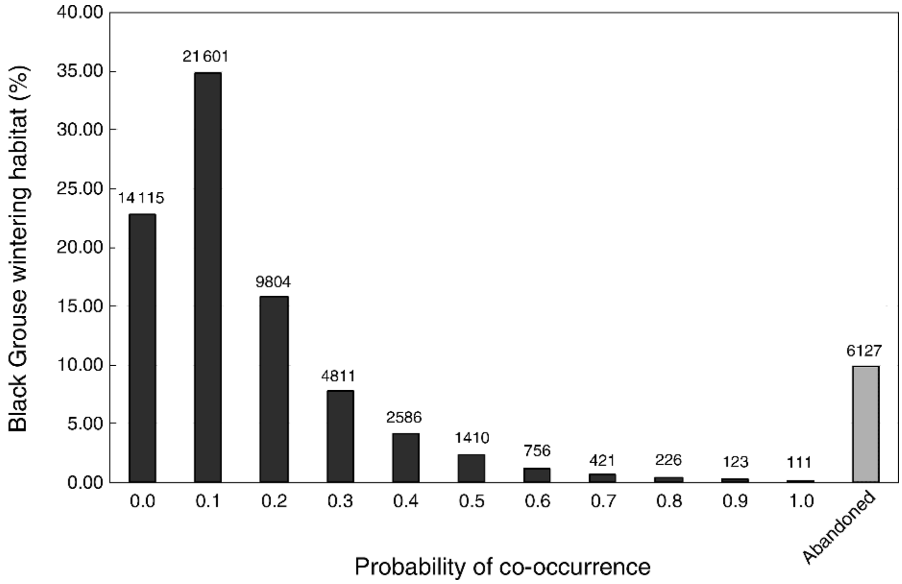

FIG. 4. Percentage of Black Grouse wintering area affected by different probabilities of human–wildlife co-occurrence. The proportion of wintering habitat within ski resorts, currently unsuitable due to ski infrastructure is also shown ("Abandoned"). The numbers above the bars indicate the area (ha) concerned.

Grouse presence could not be extrapolated to the entire study area. We had thus to assume an absence of off-piste activities in our spatial projections. However, this was not problematic, as for determining human–wildlife conflict zones the potential distribution of Black Grouse, unaffected by off-piste activities, was required.

As the data for both the two snow-sports and Black Grouse were sampled simultaneously and with the same sampling intensity, the Maxent models' logistic outputs are directly comparable. This enabled combining them to calculate the probability of human–wildlife co-occurrence as an indicator for relative conflict intensity. Rather than just indicating range-use overlap, this quantitative index can be used directly to rank the areas according to the potential impact of winter recreation upon Black Grouse, i.e., to set spatially explicit priorities for the creation of winter preserves.

Snow sports and Black Grouse

The simultaneous collection of data on both off-piste activities and Black Grouse also enabled us to quantify the direct effect of this unpredictable source of disturbance on the target species. Whereas ski infrastructure has previously been shown to be negatively associated with Black Grouse population densities (Patthey et al. 2008), similar investigations on free-ranging snow sports or comparative studies are still lacking. Our results indicate that free-ranging snow sports can account for even greater habitat reductions than infrastructure-bound activities (16% vs. 12%, determined for the 585-km transect), although the two factors cannot be completely separated. Throughout the entire extrapolation area the model suggests that the development of ski infrastructure and the associated outdoor snow-sport activities have led to the permanent loss of 10% of naturally suitable Black Grouse wintering habitat. Although still suitable in terms of vegetation characteristics, these wintering grounds are no longer used by the birds, probably because of a "too high" risk of conflict with tourists. Since there is an additional risk of encountering free-ranging snow-sportspeople on 67% of the remaining wintering area, the total proportion of wintering habitat affected by different intensities of winter tourism sums up to 77%. Only 23% of the potentially suitable Black Grouse wintering habitats remain currently untouched by snow-sport activities. This estimate is lower than a previous one (56%) by Patthey et al. (2008), although the latter was based on a different methodology (counts of displaying cocks in various habitats with different disturbance intensities) and, above all, did not account for free-ranging winter sport activities that take place far away from ski resorts. Our study was conducted in a popular winter sports region which hosts some of the largest ski-resorts in the European Alps. It is also the area with the highest peaks of Europe, i.e., a hotspot for alpinism. How representative this area is for the situation prevailing in other parts of the Alps remains unknown. It seems that snowshoeing is less widespread in the southwestern part of the Swiss Alps due to the difficult terrain, compared to what is observed in the lower parts of the massif, e.g., in the Pre-Alps. What is sure, however, is that encroachment of free-ranging winter sports into Black Grouse habitat is reported from different regions throughout the Alps (e.g., Zeitler 2000, Ingold 2005),

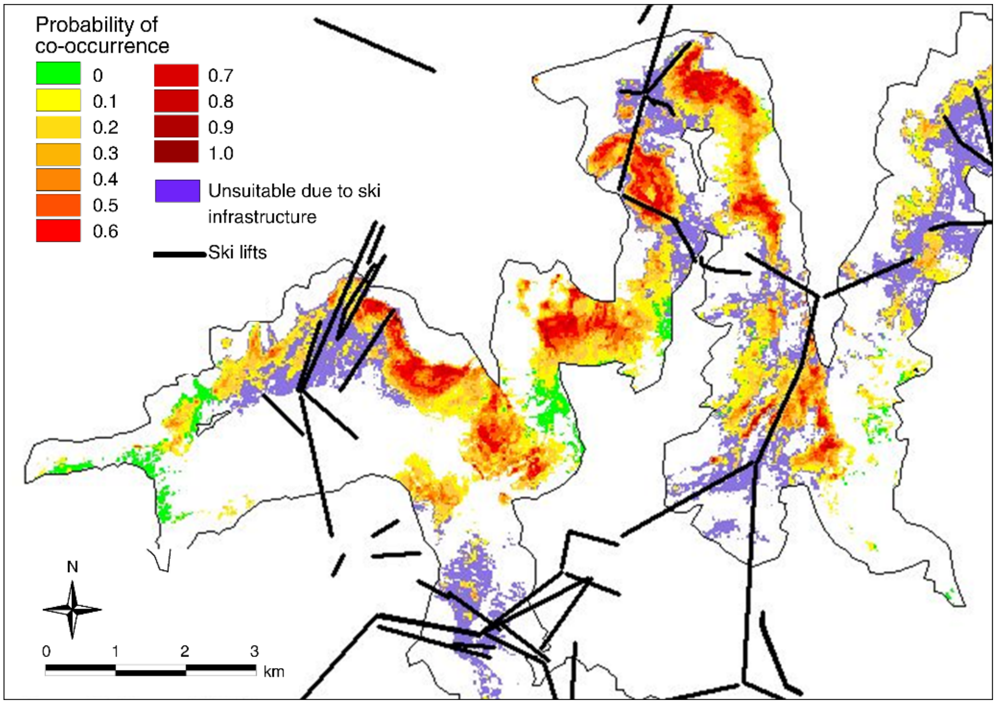

FIG. 5. Predicted levels of conflict potential between wintering Black Grouse and snow-sport activities, illustrated for the Quatre Vallées region (including the major ski resort of Verbier and Nendaz, Valais). Conflict potential corresponds to the probability of co-occurrence of Black Grouse with either one or both of the two investigated free-ranging snow-sport activities (off-piste skiing and/or snowshoe walking). Key: green, Black Grouse wintering sites without snow-sport activities; yellow to red, wintering sites with increasing probabilities of human–wildlife co-occurrence; blue, wintering sites currently unsuitable due to ski infrastructure.

which corroborates a far-reaching need to mitigate impacts of winter sports on Alpine wildlife.

Application and outlook

Spatially explicit modeling of human–wildlife conflict is an essential tool for concrete land-use planning in sensitive wildlife habitats. Based on predictive conflict maps, problematic ski routes or snowshoe trails can be identified and modified, while the designation of new routes can be optimized by virtual evaluation of different alternatives. As conflict maps illustrate both the spatial extent and intensity of human–wildlife conflict, they can directly be used to prioritize areas for the designation of wildlife refuges with restricted or banned human access. For Black Grouse, such winter reserves should be implemented both within and outside ski resorts, where wintering habitat is suitable but conflict potential is particularly high. The approach developed here can be transferred to other species and types of recreational activity, with some potential restrictions. First, the probability of human–wildlife spatial overlap does not necessarily mean conflict: a site with a high probability of spatial co-occurrence, but frequented by humans during the day and by wildlife at night will experience no encounters, i.e., no conflicts. In the case of Black Grouse, both spatial and temporal overlaps with tourists were clear, especially as bird roosts (snow burrows or trees) and feeding places (usually trees) are located in close vicinity to each other (Pauli 1974, Klaus et al. 1990). Second, assessed co-occurrence is not necessarily synonym of ascertained conflict, as the latter implies a negative impact on species' fitness. We used the term "conflict" here, because there is evidence for adverse effects of snow-sport activities on Black Grouse ecophysiology (stress response; Arlettaz et al. 2007), population abundance (Patthey et al. 2008), and habitat use (this study), although the exact fitness consequences at the individual level are still unclear. In the absence of the latter data, we relied on a probability of co-occurrence of $>10\%$, as a precautionary measure, when inferring a "conflict." Finally, after having localized "hot spots" with major human–wildlife conflicts in the landscape, the minimal area for designing effective winter refuges still needs to be determined, i.e., in our case, preserves which can actually guarantee tranquility for wintering Black Grouse. An analysis of flushing distance of birds in different disturbance contexts may serve to that purpose (Arlettaz et al. 2007). Finally, defining tolerance thresholds and even habituation potential in areas subjected to various intensities of recreation disturbance, in the presence or absence of winter refuges *and* hunting, which is another potential source of disturbance, would be a last necessary step to provide a comprehensive guidance for the planning of refuges in the Alps. As Black Grouse is a key indicator species of ecosystem integrity in timberline habitats, all these measures are likely to benefit other flora and fauna elements of the Alpine biocenoses.

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APPENDIX A

Figure of the study area showing the transect used for sampling (*Ecological Archives* A021-043-A1).

APPENDIX B

Table showing the main predictors of Black Grouse and snow-sports occurrence derived from a principal-component analysis, and their correlations with the original variables (*Ecological Archives* A021-043-A2).

APPENDIX C

Figure showing the continuous Boyce curve, calculated from the independently collected Black Grouse data, and the cutoff value for suitable Black Grouse habitat (*Ecological Archives* A021-043-A3).