

Improved ecological insights commission new conservation targets for a crepuscular bird species

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Keywords

European Nightjar; Switzerland; foraging ecology; spatial use; habitat selection; home range; GPS tracking; landscape heterogeneity.

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Email: ruben.evens@uhasselt.be

Editor: Jeff Johnson

Associate Editor: Viviana Ruiz-Gutierrez

Received 20 January 2020; accepted 09 September 2020

doi:10.1111/acv.12650

Abstract

Knowledge on species' ecological requirements is the key to an effective evidence-based conservation. An adaptive approach can refine management recommendations following the outcomes of previous actions or as improved scientific knowledge about a species' ecology becomes available. Following severe population declines the majority of the Swiss European Nightjar (*Caprimulgus europaeus*) population is now restricted to a small core area in the canton of Valais, despite the local application of evidence-based restoration measures to the breeding habitats. The habitat use of this crepuscular bird species is presumed to be restricted to semi-open oak-pine scrublands and rocky steppe. By deploying miniature GPS loggers we assessed the spatial and habitat selection of 42 individuals (25 individuals in 2018 and 30 individuals in 2019; comprising 13 redeployments between years) in five study sites in the canton Valais. We highlight the importance of using fine-scaled movement data to obtain insight into complex multi-scale habitat requirements of a species. Nightjars used multiple habitats, indicating the importance of complementary resources to breed (e.g. open forest and shrub) and to forage (e.g. semi-extensive grasslands and vineyards). The connectivity between these resources was influenced by habitat configuration and composition. Given these new insights for future conservation strategies, our results also suggest that national-level land use changes, mainly due to agricultural intensification processes, have contributed to the long-term population declines in Switzerland. We therefore consider our result in the context of knowledge gaps for species that exploit complementary habitats and the potential shortcomings for conservation planning on discrete species showing complex ecological requirements.

Introduction

Knowledge about species' ecological requirements holds a pivotal role in evidence-based species conservation during the formulation of conservation strategies, the monitoring of applied restoration actions and the empirical evaluation and reporting of the outcomes (Schwartz *et al.*, 2017; de Bie, Addison & Cook, 2018). The availability of accurate knowledge on species' requirements differs greatly between taxonomical groups and is often lacking for species with a hidden lifestyle, such as crepuscular or nocturnal species (Gaston *et al.*, 2008). The absence of accurate knowledge is particularly problematic when urgent conservation actions are

required to maximize the benefits for rapidly declining species.

Studying habitat use (Johnson, 1980; Morris, 2003) is elementary to comprehend the ecological requirements of a species and spatio-temporal resource availability is a well-recognized determinant of species' distribution (Weber *et al.*, 2017). Habitat use should, herein, be considered as a multi-scale process (Fattebert *et al.*, 2018; Scherrer, Christe & Guisan, 2019). At a local scale, habitats and their associated resources might, for example, provide opportunities for a species to either breed, forage or rest (Wakefield, Phillips & Matthiopoulos, 2014). However, at a wider landscape scale their importance for a species, that is, the connection and

accessibility of complementary resources, can be determined by the composition and configuration of the local landscape (Ripperger *et al.*, 2015; Collins & Fahrig, 2017) in combination with the variation in individual space use of a species (Jones *et al.*, 2018).

Detailed animal movement data, collected from GPS logging, can be collected in large quantities and provide unbiased knowledge about species' habitat use at the finest possible spatial scale, which can subsequently be extrapolated to investigate habitat use at larger spatial scales (Kay *et al.*, 2017; Fattebert *et al.*, 2018). Such data, collected during the breeding season, are particularly valuable to understand the importance of complementary resources for breeding and foraging (Schradin *et al.*, 2010). It helps to reveal how the distribution of resources in the available landscape affects foraging behaviour, territory settlement and breeding phenology (Ropert-Coudert *et al.*, 2004; Hinsley *et al.*, 2008; Catry *et al.*, 2013) and whether conservation practices deliver the resource requirements of the species (Law & Dickman, 1998; Sutherland *et al.*, 2004; Lemieux *et al.*, 2018).

There is an urgent need to review the ecological requirements of endangered species, in order to assess the accuracy of current management practices and to introduce more effective and relevant conservation measures into future conservation planning. In this perspective, the European Nightjar (*Caprimulgus europaeus*, hereafter referred to as nightjar) can be seen as a model system for species with a hidden lifestyle that require urgent conservation actions on different spatio-temporal scales (Evens *et al.*, 2017a, 2018a). During the breeding season, it has been demonstrated that these crepuscular, insectivorous birds require complementary habitats to breed and to forage (Alexander & Cresswell, 1990; Evens *et al.*, 2017a, 2018a). The ongoing decline of this species in several European breeding populations (IUCN, 2020; Jacob *et al.*, 2010; Knaus *et al.*, 2018) may indicate that local conservation measures are most likely not applied to all required habitats and, given the high mobility of the species, not at the proper spatial scale.

In this study, we investigate the multi-scale habitat use of nightjars using fine-scaled space use data in an inner-alpine context in Switzerland. Nightjars are an endangered bird species in Switzerland (Keller *et al.*, 2010). The studied population has undergone a rapid decline in the last decades (Knaus *et al.*, 2018), despite the local application of evidence-based restoration measures to create new breeding habitats (Sierro, 2013, 2016). By following a multi-scale approach, we characterized foraging behaviour and assessed local habitat use (i.e. within home range habitat use) to define foraging habitats. Subsequently, we considered habitat selection in a wider landscape context (i.e. home range placement) to investigate whether the conservation of secondary key habitats, such as meadows and extensively cultivated grasslands, has been omitted. Finally, we extrapolated nightjars' habitat selection from the wider landscape to the national level (i.e. landscape scale) and investigated whether the disappearance of the species from many atlas grid cells (Knaus *et al.*, 2018) was related to land cover changes. We consider our result in the context of knowledge gaps for

species that exploit complementary habitats and the potential shortcomings for conservation planning on discrete species showing complex ecological requirements.

Materials and methods

We tracked the spatial use of nightjars from May to August in 2018 and 2019 at five sites in the canton of Valais (Switzerland), between Sierre (46°N, 7°E) and Visp (46°N, 8°E) in the upper Rhône valley. The sites are 4–16 km apart (Fig. 1) and hold approximately 70% of the Swiss nightjar population (Knaus *et al.*, 2018). The study sites are located on south-exposed slopes between 600 and 1800 m above sea level and are characterized by a continental climate with hot summers and a low amount of annual precipitation (550–700 mm/year) (Winiger *et al.*, 2018). These breeding habitats (Fig. 2) are characterized by semi-open landscapes, mainly dominated by oak-pine scrublands, rocky steppe and open dry forests (Sierro *et al.*, 2001). Within the same altitudinal band, the landscape is interspersed with settlements and grasslands of different degrees of intensification, such as meadows, steppe and extensively grazed pastures (Theux, 2019). On higher elevations, dense pine forests and alpine meadows are the predominant land cover types. On lower elevations, intensively managed vineyards are the predominant agricultural land cover type. Most human activities are concentrated on the lowest elevations, in the plain of the valley (Sierro & Erhardt, 2019).

We captured nightjars using ultra-fine mist nets (Ecotone, 12 × 3 m) and tape lures (Evens *et al.*, 2017a). All birds were captured within their presumed breeding territories and marked with a unique alphanumeric ring from the Swiss Ornithological Institute. We identified sex [M/F] and age [≥ 1 CY, 2CY, ≥ 2 CYs] based on individual's plumage, but did not discriminate between paired or unpaired individuals because the reproductive state of tracked individuals was often unclear. We fitted a VHF/GPS logger, comprising a 0.7 g Biotrack Ltd. radio tag and a 1.8 g Pathtrack Ltd. nanoFix GPS logger, to the tail using a simple drop-off mechanism (Evens *et al.*, 2018). Tags weighed less than 3.8% of the mean weight of tagged birds (65.3 ± 5.1 g, range: [57–78.1 g], $n = 46$ weight measurements; for a list of the birds see Supporting Information). We programmed GPS loggers to start fixing positions (3 min intervals) from sunset until sunrise (i.e. 9 PM until 5 AM).

Land cover data

We used two types of land cover data: (i) high resolution (10 × 10 m) remote sensing data and (ii) a lower resolution digital land cover map (100 × 100 m). Both maps were used to study (i) within home range habitat use and (ii) home range placement and national habitat use respectively.

The high resolution (10 × 10 m) grassland productivity map contains the intensification in natural and artificial grasslands of the entire study area. This map was constructed from tailored NDVI maps, calculated from Sentinel II scenes post treated by THEIA (www.theia.cnes.fr), and containing

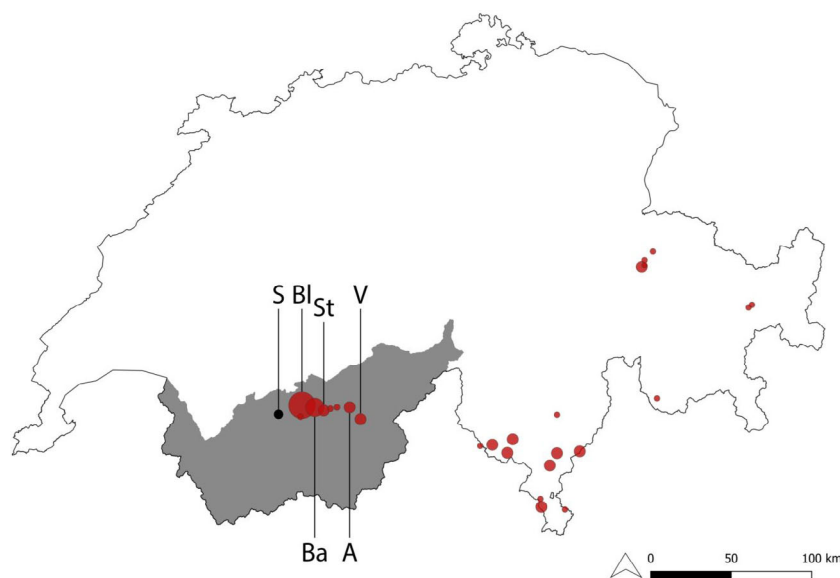


Figure 1 The five study sites (Bl = Blatte, Ba = Bannwald, St = Steppe, A = Ausserberg, V = Valais) are located in the upper Rhône valley (canton Valais, grey area inset). Red circles represent sites containing nightjar territories in Switzerland between 2013 and 2016 (largest circles = 10–6 territories, medium circles = 2–3 territories, small circles = 1 territory) (modified from Knaus *et al.*, 2018). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

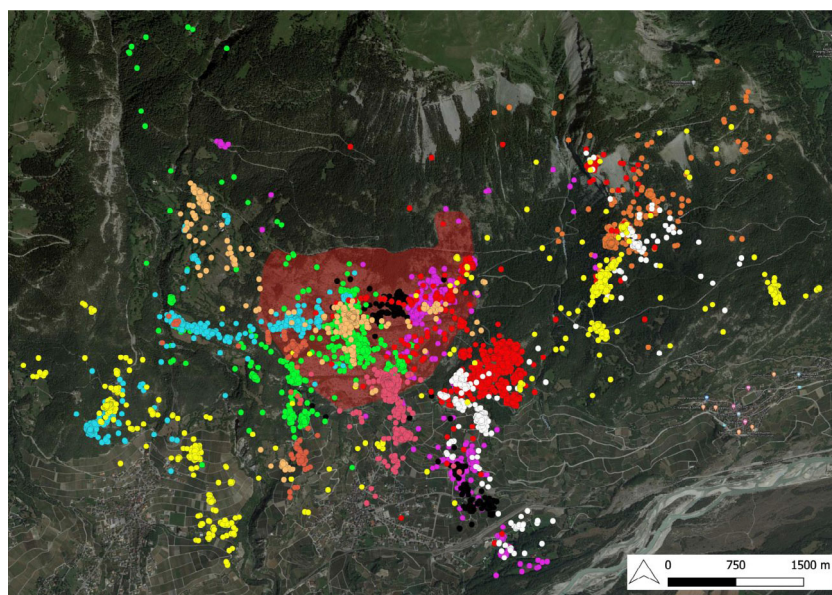


Figure 2 Tracking data collected from Nightjars in one of the five study sites (Blatte near Sion) in the upper Rhône valley (canton Valais). One colour represents all tracking data of one individual in 2019. Red area comprises the known breeding habitats (open forests and oak scrub). Individuals mainly forage in grasslands (west), vineyards (south) and Alpine meadows (north). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

only data for grasslands (for more details, see Theux, 2019). Grasslands were categorized according a grassland management intensification gradient (GIG) into four types: intensive ($GIG = 0 > x < 0.25$), semi-intensive ($GIG = -0.1 > x < 0$), semi-extensive ($GIG = -0.1 > x < 0$) and extensive grasslands ($GIG = < -0.1$; grasslands types *sensu* Delarze *et al.* (2015); Supporting Information).

The digital habitat layers containing information on land cover on a 100×100 m grid, available for 3 time periods (1979–1985, 1992–1997, 2004–2009; Swiss Federal Statistical Office, 2019). We reclassified 72 available habitat types into 12 relevant habitat types (Sierro *et al.*, 2001; Evens *et al.*, 2017a, Evens *et al.*, 2018a,b; Supporting Information). To investigate changes in land cover on a national scale, we

used habitat layers for the periods 1979–1985, 1992–1997 and 2004–2009. To investigate home range placement, we used the most recent land cover map (period 2004–2009; hereafter referred to as structural habitat map). From the structural habitat map, we then created a functional landscape map by grouping 12 habitat types into three functional categories: (i) breeding or roosting habitat, (ii) foraging habitat and (iii) other habitat types (Evens *et al.*, 2018).

Available habitat maps

To delineate the area of available habitat and to derive the measures of landscape heterogeneity for each foraging flight, we cut out four circular maps (two from the structural and two from the functional habitat map) (*sensu* Evens *et al.*, 2018a). We made the circular maps and determined their specific scale to avoid inclusion of large areas of unrepresentative habitat related to foraging activity (Evens *et al.*, 2018a).

We defined extra-territorial flights and foraging flights *sensu* Evens *et al.* (2018a). Extra-territorial flights include the start in breeding habitat, an outbound flight, an inbound flight to the breeding habitat and arrival in the breeding habitat. An extra-territorial flight can be further defined as a foraging flight when an individual also perches between the outbound and inbound section. In this case, foraging activity is defined as an individual remaining stationary (i.e. flycatching when perching) in presumed foraging habitat. This approach did not account for foraging by hawking (i.e. foraging when flying) (Alexander & Cresswell, 1990) or foraging behaviour within breeding areas, which is not detectable using current GPS-tracking technologies. We used information on foraging activity to calculate Euclidean foraging distance, foraging duration and the timing of foraging events (Evens *et al.*, 2018a).

The centre of each circular available habitat map was always placed at the start position of the corresponding foraging flight. For each habitat map, thus both the structural and functional habitat map, a circular surface was cut with a radius equal to the Euclidean foraging distance (hereafter referred to as 'foraging buffer') and another with a radius equal to the mean foraging distance (1311 m; calculated as the mean foraging distance of all foraging flights for all individuals; hereafter referred to as 'mean foraging buffer'). For each foraging flight, we then quantified four landscape characteristics: two measures of habitat composition (the percentage of available foraging habitat [functional habitat, mean foraging buffer] and habitat diversity [Shannon diversity index; structural habitat, foraging buffer]) and two measures of habitat configuration (Moran's I [functional habitat; foraging buffer] and mean patch size of foraging habitat [functional habitat; foraging buffer]) (*sensu* Evens *et al.*, 2018a).

Within home range habitat use

To investigate the effect of individual variables (age and sex) and landscape characteristics on foraging distance, we fitted linear mixed models to our data with individual nested within year (2018 or 2019) and study site as a random factor. After a backward selection procedure, individual

variables (age and sex) were removed from the models as fixed effects because they did not significantly affect foraging distance. The selection procedure was initiated from two separate models to account for multicollinearity issues. More specific, we found a correlation between the following environmental variables: the size of foraging sites and Moran's I, habitat diversity and Moran's I, the amount of available foraging habitat and the size of foraging sites, and amount of available foraging habitat and habitat diversity. Finally, three models were fitted containing foraging distance (log-transformed) as outcome variable. The first model contained mean size of foraging habitats [calculated using the foraging buffer; km²] and structural habitat diversity [calculated using the foraging buffer; Shannon Index] as fixed effects. The second model contained mean size of foraging habitats [calculated using the foraging buffer; km²] and functional habitat diversity [calculated using the foraging buffer; Shannon Index] as fixed effects. The third model contained amount of foraging habitat [calculated using the mean foraging buffer; % cover] and Moran's I [calculated using the foraging buffer; classified as random, dispersed or clustered] as fixed effects.

We also collected information on within home range habitat use by extracting data from the structural habitat map for each GPS position. We investigated the use of specific grassland types by extracting data from the fine-scaled grassland map for each GPS position falling in a grassland pixel. We fitted general linear mixed models to assess possible differences in i) grassland use between breeding and foraging sites and ii) grassland availability between occupied and historically managed sites (Table 2, Fig. 3).

Home range placement

Using GPS positions, we calculated the home range of each individual in each year with a kernel density estimator (KDE) (fixed kernel), using Ranges 7 v0.77 (Anatrack Ltd.) (Aebischer, Robertson & Kenward, 1993). We calculated 50% (core area) and 95% (home range) kernels (Evens *et al.*, 2017a). We used a fixed multiplier, between 0.3 and 2, that limited the number of multimodal home ranges or the inclusion of large unused areas (Fieberg, 2007; Supporting Information). To compare our results with earlier studies (Sierro *et al.*, 2001) and to get a more general assessment of the space covered by individuals, we also calculated the 95% minimum convex polygon for each individual (Aebischer *et al.*, 1993).

To quantify habitat availability for each individual, and to avoid the inclusion of large areas of unrepresentative habitats (Evens *et al.*, 2017a, 2018a), we created a habitat availability map (hereafter referred to as 'focal buffers') by cutting out a circular surface from the structural map (center = focal position/mean observation in breeding habitat, radius = furthest observation per individual; *sensu* Evens *et al.*, 2018). The furthest observation per individual is not necessarily the same as an individual's longest foraging distance. To assess the availability of specific grassland types in proximity of nightjars' territories and historically managed sites (Sierro, 2016), we also created a 'mean buffer'. The centroid of the mean buffer was placed on individuals' focal position and

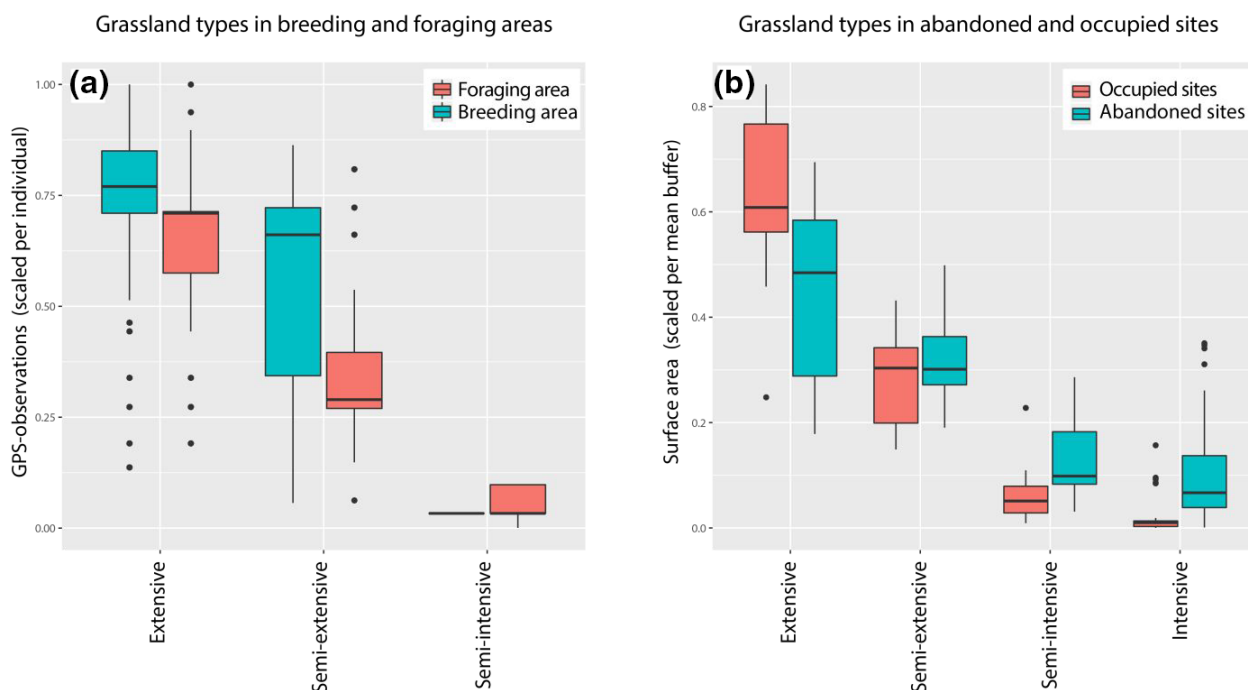


Figure 3 Observations for different grassland types, ranging from extensive to intensive grasslands. Boxplots show the range (median [thick black line], 25% and 75% quantiles [thin box], 90% range [whiskers] and outliers [black dots]) of proportion of observations of each grassland type, scaled per individual (a; GPS observations) and mean buffer (b; mean buffer = 1905 m). Panel a shows the types of grasslands used while birds were residing in breeding areas and when they were perched in foraging areas. Panel b shows the proportion of grassland types that are available in mean buffers drawn around nightjars' focal site (occupied sites) and centroids of historically managed sites. [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com/doi/10.1111/zsl.12444).]

on the centroid of historical managed sites. The radius of these buffers was equal to the mean of the distance to the furthest observation of all individuals (1905 m).

To determine regional habitat selection, we compared home range placement (50% and 95% kernels; i.e. habitat use) with the tailored habitat availability maps (focal buffer; i.e. habitat availability). Hence, we carried out a classical compositional analysis (Aebischer *et al.*, 1993) using the R-package 'adehabitatHS' (Calenge, 2011). Paired t-tests determined the differences between habitats (habitats ranked, independent of availability, based on positive differences). Zero values were replaced with $10E-7$ and 1000 iterations were chosen for data randomization (Evens *et al.*, 2017a).

National dynamics

In order to assess whether land cover changes in recent decades could have contributed to the decline of the nightjar population in Switzerland, we combined information from the three reclassified land cover maps (1979–1985, 1992–1997 and 2004–2009; Swiss Federal Statistical Office [2019]) with three occupancy maps of the Swiss bird atlas. The occupancy maps contain information on the presence of breeding nightjars in Switzerland for 467 10×10 km squares and three atlas periods: 1972–1976 (Schifferli *et al.*, 1980), 1993–1996 (Schmid *et al.*, 1998) and 2013–2016 (Knaus *et al.*, 2018). For each atlas period, we calculated the

proportion of the different habitat types in each 10×10 km square for the most relevant land cover map: atlas period 1972–1976 with land cover map 1979–1985, atlas period 1993–1996 with land cover map 1992–1997, and atlas period 2013–2016 with land cover map 2004–2009.

Spatio-temporal logistic Bernoulli models were fitted to estimate the effect of available habitat per 10×10 km square on nightjar presence. We used period-specific conditional autoregressive (CAR, Besag, York & Mollié, 1991) random effects, with a shared precision parameter, to capture compositional heterogeneity. The covariate effects of time and habitat coverage, which comprises 12 proportional habitat availability variables, were modelled univariately to avoid multicollinearity issues. The habitat availability variables were transformed through a folded exponential transformation (Piepho, 2003). An additional normally distributed unstructured normal random effect that was shared among the three periods accommodated additional overdispersion. This yielded 14 models, which were fitted using Markov chain Monte Carlo (MCMC) via the R (version 3.4.4) package R2OpenBUGS 3.2 (for full model specifications, see Supporting Information).

Animals subjects

The authors declare that all experiments have been performed according to the ethical guidelines of the Swiss veterinarian service under license number VS032018.

Results

We deployed 85 GPS loggers on 46 individuals and recovered 80 GPS loggers from 42 individuals. In total, 73 GPS loggers contained useful tracking data from 25 individuals in 2018 and from 30 individuals in 2019. Fifteen individuals were tracked more than once within a season and 13 individuals were tracked in both years. In order to account for possible differences in the habitat use between years, caused by habitat management, environmental or unknown factors, we will refer to a maximal sample size of 55 year-individuals in this manuscript, except in case of the linear mixed models where individual was nested within year (2018 or 2019). Altogether the GPS loggers contained 42816 observations on the spatial use and foraging behaviour of nightjars (808 ± 470 observations per individual per year, $n = 55$, [20–2049 observations]; mean $\pm$ standard deviation and [range]). We excluded eight individuals from home range analysis because of presumed nomadic behaviour and long-distance movements of unpaired males in search for a territory and two other individuals were removed from foraging-distance analysis because no foraging behaviour was detected (i.e. unpaired males remaining in a small territory) (Evens *et al.*, 2018b).

Within home range habitat use

We collected 34310 observations while birds were present in the known breeding habitats (for an overview see Table 1), mainly comprising open forests (mean proportion per individual: $32 \pm 35\%$ of observations, [0–100%]; mean $\pm$ standard deviation and [range]), dense forests ($25 \pm 29\%$ of observations, [0–86%]) and scrub ($14 \pm 20\%$ of observations, [0–72%]). Due to the presence of two irrigation channels in the breeding area of one study area, open water was also classified as an important breeding habitat ($15 \pm 15\%$ of observations, [0–81%]).

We identified 452 flights leaving the breeding habitats (for an overview see Table 1), containing 312 foraging flights. The mean foraging distance is 1.3 ± 0.7 km ([0.2–4.3 km], $n = 312$ flights of 45 individuals). We did not find any differences in foraging distance between sexes and ages (Table 2). Most foraging flights start 30 min after sundown and 90 min before sunrise (Supporting Information). Nightjars were absent from their breeding habitats for 59 ± 75 min per flight ([3–450 min], $n = 452$) and forage during 43 ± 73 min ([3–435 min], $n = 312$).

We collected 7024 observations when the birds were foraging (for a complete overview see Supporting Information), predominantly in dense forests (mean proportion per individual: $25 \pm 26\%$, [0–100%]), vineyards ($14 \pm 23\%$, [0–88%]), extensively cultivate agricultural lands ($12 \pm 16\%$, [0–68%]), open forests ($11 \pm 17\%$, [0–70%]) and alpine meadows ($11 \pm 15\%$, [0–48%]) (Table 1).

Foraging distance was modelled via three models (for details, see Table 2). In the first model, we show that foraging distance increases when structural habitat diversity increases (estimate = 2.38, $SD = 0.11$, $df_N = 1$, $df_D = 303$, $F = 457.91$, $P < 0.0001$). In the second model, we show that foraging distance decreases when functional habitat diversity increases (estimate = -7.78 , $SD = 1.59$, $df_N = 1$, $df_D = 294$, $F = 22.97$, $P < 0.0001$). From the third model, we found that foraging distance increases when the functional habitats were clustered (estimate = -0.69 , $SD = 0.21$, z -value = -3.25 , $P = 0.003$) or dispersed (estimate = -0.34 , $SD = 0.13$, z -value = -2.7 , $P = 0.018$).

Concerning the use of grasslands, we found a significant difference between the types of grasslands used in breeding and foraging areas (estimate = -0.222 , $SD = 0.025$, z -value = 55, $Pr(>|z|) = <0.0001$; Supporting Information). The difference between the two seems to arise due to a higher proportion of extensive and semi-extensive grasslands in the breeding areas and presence of semi-intensive grasslands in foraging areas (Table 2, Fig. 3). When comparing the

Table 1 Proportion of habitat types used in breeding and foraging habitat. The table shows mean ($\pm$ standard deviation) and maximum percentages of each habitat type used by individual nightjars

Category	Functional category	Breeding area			Foraging area		
		Mean	SD	Max	Mean	SD	Max
Town	Other	1	2	16	0	1	7
Gardens	Other	0	2	14	4	14	70
Recreation	Other	1	2	9	4	8	41
Intensively used agriculture	Other	3	10	62	8	17	72
Extensively used agriculture	Foraging	1	2	9	12	16	68
Vineyards	Foraging	0	1	5	14	23	88
Alpine meadows	Foraging	1	1	7	11	15	48
Dense forests	Breeding	25	29	86	25	26	100
Open forests	Breeding	32	35	100	11	17	70
Small landscape elements	Foraging	8	17	83	3	5	20
Water	Other	15	15	81	5	13	66
Scrub	Breeding	14	20	72	4	12	57

The estimates are based on the amount of GPS observations made in breeding areas and while birds are presumed to be foraging (perched) for each habitat type (Supporting Information).

Table 2 Summary of the results from the statistical analyses. For each analysis we show the outcome variables, random and fixed effects

Analysis	Model	Outcome	Random Effects Variable	Fixed Effects Estimation (SD)	Posthoc Tests Variable	Estimation (SD)	F	d.f.	Df.res	Pr(>F)	Difference	Estimate (SD)	z-value	P-value
1	GLMM	ln (Foraging distance)	Bird ID: year	0.051 (0.225)	Intercept	2.28 (0.3)	57.9	1	17	<0.0001				
			Study site	0.197 (0.444)	Habitat diversity (structural)	2.38 (0.11)	457.91	1	303	<0.0001				
			Year	0.112 (0.043)	Size of foraging habitat patches	0.003 (0.02)	0.02	1	285	0.895				
2	GLMM	ln (Foraging distance)	Bird ID: year	0.176 (0.419)	Intercept	12.04 (1.05)	126.46	1	270	<0.0001				
			Study site	0.087 (0.295)	Habitat diversity (functional)	-7.78 (1.59)	22.97	1	294	<0.0001				
			Year	0.14 (0.375)	Size of foraging habitat patches	-0.02 (0.03)	0.37	1	280	0.546				
3	GLMM	ln (Foraging distance)	Bird ID: year	0.144 (0.38)	Intercept	8.25 (0.42)	351.39	1	92	<0.0001				
			Study site	0.04 (0.199)	Amount of foraging habitat	-0.2 (0.1)	2.53	1	172	0.114				
			Year	0.008 (0.382)	Moran's I		8.74	2	285	0.0002	dispersed vs. clustered	-0.34 (0.25)	-1.4	0.326
4	GLMM	Scaled (Grassland)	Bird ID	0.002 (0.047)	Breeding vs foraging	0.222 (0.004)	55	1	17014	<0.0001	random vs. clustered	-0.69 (0.21)	-3.25	0.003
5	GLMM	Scaled (Amount per mean buffer)	Study site		Occupied vs. Abandoned	-0.0013 (0.025)	<0.01	1	326	0.958	random vs. Dispersed	-0.34 (0.13)	-2.7	0.018

Posthoc tests = Tukey-adjusted *P*-values.

availability of grassland types between occupied and historically managed sites, we found no clear difference between both groups (estimate = -0.001 , $SD = 0.025$, t -value = -0.053 , $Pr(>|z|) = 0.958$; Table 2), both breeding grounds sharing similar extensive grasslands habitat types.

Home range placement

Home range size was 33 ± 29 ha (95% kernels, [5–192 ha], $n = 47$) with core areas of 7 ± 5 ha (50% kernels, [2–31 ha], $n = 47$) and MCP of 142 ± 191 ha (95% MCP, [3–1062 ha], $n = 47$). Following the outcomes of the compositional analysis, habitat use of nightjars was not random in both 50% kernels (focal buffer: $\lambda = 0.104$, $P = 0.001$) and 95% kernels (focal buffer: $\lambda = 0.099$, $P = 0.001$). Habitats were ranked from most to least (12–0) selected, indicating that habitat use was slightly different between 50% and 95% kernels (Fig. 2, Supporting Information). Within breeding habitats (core areas) open and dense forests, and scrub vegetation were significantly more used compared with other available habitats (e.g. different types of agricultural land; Supporting Information). When nightjars flew further from the breeding habitat (home ranges) alpine meadows, vineyards and agricultural lands (comprising semi-intensive and semi-extensive grasslands) became more important than in the core areas.

National dynamics

Our results suggest a negative tendency (borderline 'non-significant' when applying a 5% significance level) in the Swiss nightjar population during the last 40 years related to land cover changes ($\alpha_2 = -0.765$, 95% credible interval (CI) = $[-1.858; 0.034]$; Supporting Information). More specifically, our data indicate that increases in the amount of intensively used agricultural areas ($\beta_1 = -8.217$, 95% CI = $[-12.750; -4.557]$) have occurred where the nightjar population disappeared, whereas increases in the amounts of extensively used agricultural lands ($\beta_1 = 17.245$, 95% CI = $[9.933; 29.50]$), small landscape elements ($\beta_1 = 33.223$, 95% CI = $[16.549; 54.831]$) and dense forest ($\beta_1 = 9.013$, 95% CI = $[2.635; 20.900]$) occurred where nightjars remained. Furthermore, we have found weak indications that the amount of meadows increased in sites that were abandoned by nightjars ($\beta_1 = -3.970$, 95% CI = $[-13.510; -0.561]$).

Discussion

This study highlights the importance of using fine-scaled movement data to obtain insight into complex multi-scale habitat requirements of a crepuscular species. Nightjars used multiple habitat types indicating the importance of complementary resources to breed and to forage. Requirements to breeding habitats of the studied population are in line with previous findings (Sierro *et al.*, 2001; Winiger *et al.*, 2018), while (i) the preference for specific grassland types, alpine meadows and vineyards to forage and (ii) the requirement of a larger space, on average six times higher per individual

compared with previous estimates (Sierro *et al.*, 2001), shed new light on future conservation strategies. Furthermore, our results suggest that the land use changes, especially in potential foraging habitat, have contributed to the long-term population declines in Switzerland.

Multiple habitat use

Breeding habitat, in our study, mainly comprises open, low-nutrient habitats such as oak-pine scrubland and pine forests. Here nightjars laid eggs on bare ground close to open vegetation, such as shrub or low-growing oak trees (personal observations). These findings are in line with earlier studies in Switzerland (Sierro *et al.*, 2001; Winiger *et al.*, 2018) and elsewhere in Europe where nightjars have been observed to breed in various types of semi-open, low-nutrient habitats (Wichmann, 2004; Conway *et al.*, 2007; Evens *et al.*, 2017a). It has been suggested that nightjars would also stay within their breeding habitats to forage owing to sufficient food supplies (Sierro *et al.*, 2001; Sharps *et al.*, 2015a) or suitable micro-habitat structures to forage (Sierro *et al.*, 2001; Wichmann, 2004). The lacking evidence of multiple habitat requirements, for the Swiss population, resulted in conservation measures mostly focusing on the management and restoration of lost breeding habitats (Sierro, 2013, 2016). However, almost all tracked nightjars (visual inspection of tracking data) in our study have been recorded foraging in extensively cultivated agricultural grasslands, alpine meadows or in vineyards.

The use of extensively cultivated grasslands for foraging seems to be common among nightjars (Alexander & Cresswell, 1990; Evens *et al.*, 2018a). In our study, both extensive and semi-extensive grasslands, and not the natural xerophilic vegetation, are the predominant grassland types used by nightjars in foraging sites (Fig. 3A). The former grasslands are managed with a low to intermediate level of fertilizers; and it may be that these grasslands host a higher biomass of invertebrate fauna than natural grasslands, despite the presence of rare fauna and flora in the latter (Andrey *et al.* 2016).

Due to the high availability of vineyards, the compositional analysis probably did not identify nightjars' preference for this habitat type. From GPS-based foraging data, however, we observe that some individuals almost exclusively forage in vineyards. From field observations we expect that nightjars most likely select specific vineyards with a biodiversity-friendly management and a diverse ground vegetation that is known to promote invertebrate abundance (Bosco, Arlettaz, Jacot 2019a, Bosco *et al.*, 2019b). That nightjars selected intensively managed vineyards would not be expected but can be explained by ongoing changes in management techniques. While still roughly 80% of vineyards in Valais are intensively managed and use herbicides to kill the ground vegetation, a growing minority is applying a more biodiversity-friendly management. Such parcels show a permanent ground vegetation that has a positive effect on insectivorous birds and their prey (Bosco *et al.*, 2019a). In addition, semi-natural structures such as bushes and

hedges on or around vineyard plots are known to be important structures for perching and foraging (Guyot *et al.*, 2017).

It is important to stress that it remains challenging to assess the actual importance small landscape elements or remnants of specific habitat types when such fragments are misclassified at larger spatial scales and important environmental information is lost (English *et al.*, 2017). For this reason, we assume that the actual importance of extensively cultivated agricultural grasslands and biologically managed vineyards is not identified by the compositional analysis in our study, due to their fragmentation within the surrounding intensively cultivated landscape.

Landscape complementation

In order to reach foraging habitats, nightjars flew considerable distances (mean foraging distance: 1.3 ± 0.7 km), even into the urbanized valley. The recorded foraging distances are in line with other telemetry (2.6 ± 1.1 km in Evens *et al.* [2017a], 3.1 ± 1.2 km in Alexander and Cresswell, 1990) and GPS-tracking studies (range 0.6–3.3 km in Evens *et al.*, 2018a, 2018b) performed elsewhere in Europe, but foraging distances in our study are higher compared to an earlier telemetry-based study (0.7 ± 0.5 km in Sharps *et al.* [2015]). Nightjars are able to connect complementary habitats, even when these are separated by several kilometres (Alexander & Cresswell, 1990; Camacho *et al.*, 2014; Evens *et al.*, 2018a). Herein, landscape heterogeneity influences the connectivity between complementary resources. In case of habitat composition, shorter foraging distances are observed when structural habitat diversity is lower and functional habitat diversity is higher. In our particular case, these findings seem to suggest that high structural habitat diversity was mainly explained by high diversity of unsuitable and breeding/roosting habitat types, whereas low functional habitat diversity most likely is determined by the overabundance of one of these functional habitats. This could imply that nightjars are more reluctant to traverse a high amounts of (unsuitable) habitat in order to reach foraging sites. In line with these findings, we observe that foraging distance is also shorter in randomly distributed landscapes where breeding and foraging habitats probably can be found on a much smaller spatial scale.

Although our study has been performed in a different environment compared to Western-European studies on the same species (Alexander & Cresswell, 1990; Evens *et al.*, 2018a), our results confirm that nightjars require complementary habitats to breed and to forage (Alexander & Cresswell, 1990; Evens *et al.*, 2018a), something which has also been demonstrated for other species of Nightjars (e.g. *Caprimulgus ruficollis* in Camacho *et al.*, 2014). These findings further support the belief that complementary habitat requirements are common among nightjars. Because habitat composition and configuration influence nightjars' foraging distance in our study, it is clear that landscape heterogeneity affects landscape complementation (*sensu* Dunning, Danielson & Pulliam, 1992) for nightjars. The similar observations in the afore-mentioned studies suggest that ongoing

landscape homogenization and fragmentation of foraging habitats, and in particular those further from breeding habitats, may increase travel distance between non-suitable resources and thus affect nightjar populations. Landscape complementation has a strong influence on the viability of a wide range of animal communities (e.g. Chadés *et al.*, 2015; Ripperger *et al.*, 2015; Collins & Fahrig, 2017), contributing to species occurrence over time (Ikin *et al.*, 2018), yet, factors beyond landscape heterogeneity might also be driving rapid declines of the aerial insectivore guild (English *et al.*, 2017; Grubisic *et al.*, 2018; Wagner, 2020). At a wider landscape scale (e.g. home range placement), animals might select areas where complementary resources are close to minimize movement costs (i.e. high landscape complementation). Yet at a local scale (e.g. within home range habitat use), resource depletion may lead to habitat patches that are ultimately avoided by these animals (Valls-Fox *et al.*, 2018). In our study area, we have no proof of resource depletion in foraging sites since many individuals have been observed to repeatedly forage in the same spot together during the entire study period (personal observations). Urbanization drives global environmental change causing, among many things, severe declines of aerial insects (Kronfeld-Schor *et al.*, 2013; Owens & Lewis, 2018; Piano *et al.*, 2020). Unfortunately it is still unclear how nightjars respond to changes in food availability in breeding (Sierro *et al.*, 2001; Sharps *et al.*, 2015b) or foraging habitats (Evens *et al.*, 2018a) and whether alterations in micro-habitat structures (Sierro *et al.*, 2001; Wichmann, 2004; Camacho, 2014) or perhaps even anthropogenically mediated food availability (personal observations; Jackson, 2003; Sierro & Erhardt, 2019) might play a role in the habitat and spatial use of nightjars.

Conservation

Our national approach suggests that, during the last four decades, the Swiss nightjar population has suffered from declines due to land cover changes in foraging habitats. Recently, other factors, such as light pollution, have been proposed to negatively influence the relationship between the nightjar breeding populations in Valais and the growing human population (Sierro & Erhardt, 2019). It is, however, still unclear which factors during the breeding (e.g. light pollution, food availability, land cover change, disturbance or predation) and the non-breeding period (e.g. land cover change or climate change) actually contributed to the decline of nightjars in Switzerland.

Missing the appropriate knowledge on nightjars' requirement for complementary habitats to breed and to forage, might have substantially contributed to the low efficiency of conservation measures taken during the last decades in our study population. This idea is further supported by our observations that suitable foraging habitats are still available close to the remaining breeding sites in Valais, but have disappeared from breeding sites where most historical conservation measures have taken place. Most of the managed breeding areas are small isolated clearings on southern slopes in areas where semi-extensive meadows have disappeared

and have been replaced by vineyard and forest; or in the lowland on less dry and exposed areas close to intensive agricultural fields. As a result, the surroundings of the restored sites actually comprise monotone agricultural fields or intensive grasslands used for silage without small landscape elements. We expect that their suitability as foraging habitats is comparable with intensively managed grasslands (e.g. artificially sown meadows). Furthermore, we expect that, without small landscape elements to perch, the access to these grasslands is low since foraging site selection also reflects the ease of prey capture (Sierro *et al.*, 2001) and predator avoidance (Camacho, 2014; Evens *et al.*, 2017b).

Albeit the concept of landscape complementation is all but novel in conservation biology (Dunning *et al.*, 1992), it cannot be considered as long as knowledge about species' ecological requirements is lacking. For long, the conservation action plan for the nightjar in Switzerland has focused on the optimization of forest structure used as breeding grounds (Sierro, 2016) while important habitats for this endangered species were disappearing. As a result, the process resulting in the abandonment of an important part of the Swiss nightjar territories is still slowly ongoing. Near occupied breeding areas, extensive and semi-natural grasslands are more and more scattered and isolated. These habitats are heavily affected by on-going land use changes and thus considered among the most threatened habitats in mountainous landscapes (Canals & Sebastià, 2000).

Areas with high complementarity between different resources support high population densities (e.g. Brotons *et al.*, 2005; Haynes, Diekötter & Crist, 2007), also in case of nightjars (Camacho *et al.*, 2014). To promote landscape complementarity, conservationists should improve species' accessibility to complementary habitats (Pope, Fahrig & Gray, 2000) by considering both habitat configuration and composition (Haase *et al.*, 2017). The similar findings between recent nightjar studies across Western Europe suggest that refining current conservation programs for nightjars in Europe could be done by (i) creating or restoring breeding grounds in proximity of suitable foraging habitats and (ii) focusing on creating/restoring foraging habitats in proximity to breeding habitats. Although higher amounts of habitat can support a higher diversity of macro-moth species (Merckx *et al.* 2019), the significance of small habitat patches for conservation purposes should not be neglected (Fahrig *et al.*, 2019; Fahrig, 2020) to increase landscape complementation (Fahrig, 2017). This has also been demonstrated in our study by many nightjars foraging at the same time in remnant foraging patches near more intensively managed grasslands or vineyards (personal observations, Supporting Information). Particularly, the preservation and restoration of semi-extensive grassland habitats should be promoted in order to retain a high abundance, diversity and biomass of invertebrates. In the special case of vineyards, we also learnt from field observations that nightjars selected biologically managed vineyards. Since land-sharing policies provide higher ecological value than land-sparing policies (Fahrig, 2017), we suggest to support initiatives that want to create biologically managed vineyards. Moreover, in combination with unproductive areas between vineyards and

small, extensively cultivated grasslands comprising small landscape elements such trees, bushes and hedges (Supporting Information), this may have a positive effect on habitat selection processes in nightjars as has been shown for a number of avian species (Guyot *et al.*, 2017).

Acknowledgements

The authors wish to thank M. Evens for his help during fieldwork and R. Spaar, A. Loenders, K. Vanmarcke, and Fien and Fleur Evens for their support and relevant comments on this paper. Permissions were granted by the Laboratoire cantonal et affaires vétérinaires Valais (VS032018). Open access funding enabled and organized by Projekt DEAL.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Ringing and deployment details.

Appendix S2. Definition of grassland types following Theux (2019).

Appendix S3. Reclassified habitat types

Appendix S4. Spatio-temporal CAR convolution Bernoulli model specification

Appendix S5. Within-home range habitat use based on GPS-observations within breeding habitats and while presumed foraging (perched).

Appendix S6. Workflow to obtain estimates of within home range habitat use, home range placement and national dynamics.

Appendix S7. Foraging distance per study area.

Appendix S8. Departure of foraging trips in relation to sundown and sunrise

Appendix S9. Detailed results from the compositional analysis.

Appendix S10. Effect sizes and credible intervals of land cover change on the Swiss nightjar population.

Appendix S11. Example of a foraging nightjar in a Vineyard.