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Complementary fine-scale habitat selection of the European nightjars (Caprimulgus europaeus) in nesting and foraging sites

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Research Article

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Summary

Land-use changes are considered one of the main drivers of biodiversity loss. Agricultural intensification, pastoral abandonment, and changes in forest management have led to the homogenisation of landscapes. In particular, the encroachment of grasslands and the densification of forests that are no longer pastured threaten species that require multiple habitats to nest and forage, such as the European Nightjar *Caprimulgus europaeus*. Whereas previous studies have focused on understanding factors influencing the decrease of nightjars at regional or national scales, here, we aimed to assess fine-scaled habitat selection by nightjars within nesting and foraging sites based on high-resolution GPS tracking data. Vegetation structure and composition were quantified in the field. In the nesting habitat, nightjars prefer open forests with a low percentage of trees and where the ground is not covered by more than 40% of grass and crawling bushes (dwarf bushes such as *Juniperus* species). In contrast, when foraging, nightjars select open grasslands and biodiversity-friendly managed vineyards, both richly structured, i.e. interspersed or surrounded by other land-use types such as hedges or isolated trees. Both the nesting and foraging habitats are currently threatened, either by the abandonment of forest management, which makes stands denser and more homogeneous, or through agricultural intensification, which reduces land-use diversity. Clear habitat-specific management recommendations and political incentives are needed to simultaneously preserve and/or restore these critical habitats, which are important for nightjars that use complementary resources for nesting and foraging.

Introduction

Land-use changes and homogenisation are amongst the main drivers of biodiversity loss (Rounsevell et al. 2018). This has led to the decline of biodiversity-rich ecosystems, such as extensive grasslands (Andrey et al. 2014; Humbert et al. 2016). A lower tolerance for natural structures in fields, including hedgerows, has led to their removal to increase areas of cultivable land with the idea of facilitating management (Robinson and Sutherland 2002). In many parts of central Europe, silvicultural practices have changed towards a lower use of forested areas, resulting in increased vegetation regrowth. This has accelerated the enclosure of open forests and clearings, partially due to the abandonment of forest pastures (Buttler et al. 2012). This abandonment of pastoralism has also resulted in the homogenisation of agricultural landscapes with regeneration of woodlands in abandoned areas (Horak et al. 2014; Miklín and Čížek 2014; Pellissier et al. 2013). These changes in the mosaic of agricultural and forested landscapes affect numerous species of birds, among many taxa (MacDonald et al. 2000).

Bird species relying on traditionally managed agricultural landscapes, such as Ortolan Bunting *Emberiza hortulana* or Grey Partridge *Perdix perdix*, have declined substantially throughout Europe (Keller et al. 2020). A similar negative pattern is observed in forest species depending on silvicultural practices that maintain semi-open forests, such as the Capercaillie *Tetrao urogallus* (Braunisch et al. 2018), and species relying on multiple traditionally managed habitats to breed, forage or display are likely to be even more vulnerable to ongoing land-use changes (Demerdzhiev et al. 2022). Turtle Doves *Streptopelia turtur*, for example, need heterogeneous habitats between their breeding grounds in forests, arable fields to forage, and permanent water sources to drink (Gutierrez-Galan et al. 2019). Some species can also forage within their breeding habitats like the Ring Ouzel *Turdus torquatus* but use additional complementary foraging sites. As they breed in alpine forests and need to forage in open areas with high moisture levels, the availability of sites change rapidly throughout the season depending on snowmelt (Barras et al. 2020). These examples emphasise the importance of secondary habitats for breeding and foraging. As species–habitat relationships are often scale dependent (Bosco et al. 2019b), multiple methodological approaches are important to understand fully a species' habitat requirements. All the more so as appropriate actions and management recommendations are crucial for the conservation of such species.

The European Nightjar *Caprimulgus europaeus* is a striking example of a bird requiring multiple habitats to nest and forage. Nightjars were long assumed to feed exclusively near their nests, but radio and GPS tracking studies have shown that they can additionally forage several kilometres away from their nesting sites in complementary habitats, such as extensively cultivated meadows and recreational areas (Alexander and Cresswell 1990; Evens et al. 2018a, b; Sharps et al. 2015), which were previously considered unsuitable for the species (Sierro et al. 2001). They can cross large, fragmented habitats to reach optimal foraging grounds and are consequently threatened by combined land-use changes in agricultural landscapes and open woodland. However, this behaviour is not consistent among individuals with some individuals staying in their nesting areas to forage and others more specialised in their habitat use selecting specific areas (Mitchell et al. 2020). This variability might be related to higher prey abundance (moths) depending on the structure of habitats as some prey could be more accessible for an aerial forager such as the nightjar in open structures.

Investigation of habitat selection is however difficult in cryptic nocturnal bird species. While nesting habitats can often be inferred via the location of singing birds, understanding fine-scaled habitat selection when foraging can prove to be very complex (Camacho 2014). Visual tracking often remains the best way to monitor fine-scale habitat use, such as foraging habitat preferences (e.g. Schaub et al. 2010). However, this method is not appropriate for nocturnal species commuting to remote foraging habitats like nightjars. The arrival of new micro-GPS-tags marked a turning point, as nocturnal birds can now be tracked over an extended time period and fine-scale habitat use can then be estimated in detailed field studies (Evens et al. 2021). In the case of nightjars, several studies have investigated their nesting habitat, for example by comparing currently occupied and abandoned sites based on song or visual observations (Winiger et al. 2018) or by using telemetry in nesting areas (Sierro et al. 2001). However, these approaches could largely underestimate the importance of remote foraging sites and potentially result in misleading conclusions. Micro-GPS-based tracking data are therefore invaluable for providing unbiased, accurate location data over long periods. Whereas Evens et al. (2021) identified coarse-scale key habitat types that probably affected nightjar decrease in Switzerland, the fine-scale requirements of the birds are still not clear. A recent study showed that nightjars select different habitat characteristics at coarse or small scale (Lathouwers et al. 2023) highlighting the importance of multi-scale analysis to fully understand this species' habitat use.

As a follow-up to Evens et al. (2021), who identified country-level habitat factors influencing nightjar decline in Switzerland, we conducted a thorough investigation of fine-scale habitat selection within nesting and complementary foraging habitats in terms of vegetation structure, vegetation diversity, and land-use type using GPS tracking data. We hypothesised that Swiss nightjars use nesting sites in semi-open forests with large amounts of bare ground and a relatively low diversity of vegetation (Winiger et al. 2018). In contrast, we expect them to use foraging sites containing a high vegetation diversity as these should host more moth species (the primary prey of nightjars) and therefore more biomass than in homogeneous landscapes (Evens et al. 2020), but also structural elements that improve aerial foraging. Using explanatory models based on nightjar tracking data obtained during the summers of 2018 and 2019 and field surveys quantifying relevant habitat features, we assessed fine-scale habitat selection of individuals from the population of Valais, a region hosting 70% of the Swiss nightjar population (Knaus et al. 2018).

Methods

Study species and area

This crepuscular insectivorous bird (mostly foraging on moths) is declining in several Western European countries (Keller et al. 2020), including Switzerland (more than 25% decline over the last 30 years, approximately 40–50 territories remaining; Swiss Red List status: "Endangered"; Knaus et al. 2021). The population here is mostly concentrated in one region that has greatly suffered from the replacement of steppe vegetation and semi-open forest in favour of vineyards. Similarly, open habitats where birds foraged were either lost to shrub and forest encroachment or turned into intensive grasslands or residential areas.

A recent GPS tracking study on nightjars' spatial use in the same study area demonstrated that individuals from this Alpine population select meadows, vineyards, and sometimes forests as complementary habitats to forage at considerable distances (1.3 km on average) from their nesting habitat, in a similar way to other Western–Eurasian nightjars (Evens et al. 2021). These foraging trips target specific habitats as semi-open forests are the dominant habitat on the slopes where the birds nest, and grasslands and vineyards represent only a small amount of the available habitat if we consider an average foraging distance of 1.3 km (2.5% for vineyards and 7.2% for extensively managed dry grassland (see Supplementary material Figure S5).

The study was conducted in the south-west of Switzerland, in the upper Rhône Valley between Sierre (Cordona 46°20'N, 7°33'E) and Visp (Oberstalden 46°16'N, 7°54'E). This region, characterised by a continental climate, is one of the driest in Switzerland, with mean yearly precipitation levels of around 639 mm recorded in Visp for the period 1981–2010 (MeteoSuisse 2021). Situated in the heart of the Swiss Alps, the region has a large altitudinal gradient. The lowlands are characterised by a Scots Pine *Pinus sylvestris* forest to the west of the study area, and agricultural land and human settlements to the east. Unlike in the central part of the canton, where vineyards are the most important vegetation type up to 800 m, our study region is characterised by semi-natural habitat on the south-exposed slopes of the valley. Nightjars in the study area breed in open forests on well-exposed slopes, mainly the south-facing parts of the Rhône Valley. Forests of Scots Pine (*Ononido-Pinion*), Downy Oak *Quercus pubescens* (*Quercion pubescen*), and steppe grassland *Stipa* spp. (*Stipo-poion*) are natural vegetation types (following the TypoCH classification from Delarze and Gonseth 2008; see also www.infoflora.ch) that can be found mostly on the south-exposed side of the valley where nightjars breed (Knaus et al. 2018). Forest or steppe vegetation is replaced by grasslands and pastures usually close to villages. These grasslands show different levels of management following a continuum from the natural steppe grasslands (*Stipo-poion*) to Central European semi-dry grasslands (*Mesobromion*), and Medio-European lowland hay meadows (*Arrhenatherion*) to artificial grasslands. Denser forests of conifers replace these habitat types at higher altitudes, interspersed with avalanche corridors on some of the steeper slopes. Nightjars in the study area nest from approximately 750 m to 1,600 m above sea level but are very mobile when foraging and have been recorded at altitudes ranging from the lowest point of the valley to 3,000 m above sea level (Evens et al. 2021).

GPS tagging

In 2018 and 2019, during the months of May, June, and July, 85 GPS loggers were deployed on 46 individuals with recovery of 80 GPS from 42 individuals. Useful tracking GPS data could be extracted from 73 loggers (i.e. invalid data could be due to an early loss during the same night as deployment), from 25 individuals in 2018 and 30 individuals in 2019. A total of 15 individuals were tracked at least twice during a single season and 13 individuals were tracked during both seasons (detailed information can be found in Evens et al. 2021; Appendix S1). Among these birds, 9 were females and 33 were males with 10% of birds in their first calendar year, 60% in their second calendar year, and 30% older (these percentages are in line with previous studies from Evens et al. 2018b). The birds were lured using tape recordings of their song and caught using ultra-fine mist nets (Ecotone, 12 × 3 m; Evens et al. 2018a, 2021). The GPS loggers, which consisted of a 0.7 g Biotrack Ltd radio tag and a 1.8 g Pathtrack Ltd nanoFix GPS logger, were attached to the birds' tails using water-soluble string that dissolved as soon as it rained (Evens et al. 2018a). The radio tag then enabled the recovery of the GPS logger. With a total of 2.5 g, the loggers weighed less than 5% of the bird's body weight (average weight of tagged birds: 65.3 +/- 5.1 g, n = 46). The GPS loggers collected data from sunset to sunrise at three-minute intervals with an average of 808 GPS points per bird for a total of 42,816 GPS points. Six individuals were excluded from the home-range analysis because the presumed nomadic behaviour and long-distance flights of unpaired males made the link to the habitat very difficult. Additionally, two individuals did not show behaviour that could be related to distant foraging.

Sampling design

Based on the GPS data collected in 2018 and 2019, the home range of nightjars was calculated for each bird and year separately using a 50% (core nesting habitat) kernel density estimator (KDE) (Aebischer et al. 1993; Evens et al. 2021; Figure S2). The kernels were calculated for each individual each year using Range 7 v0.77 (Anatrack Ltd, Wareham, UK). The kernels were built with night-time GPS data and with a fixed multiplier between 0.3 and 2 limiting the inclusion of large unused areas (more details in Evens et al. 2021). We used 50% kernels as a basis to select the sampling points for the nesting habitats. For foraging habitats, we used already classified GPS locations from Evens et al. (2021) based on 452 identified flights leaving the nesting areas. Nightjars also forage within nesting habitats but for simplicity, we will hereafter refer to these as nesting habitats only. In this previous study foraging and nesting locations were defined using time stamps of GPS data to identify flights leaving the nesting habitats towards foraging habitats. We defined foraging sites for each individual and collected habitat variables based on the number of foraging clusters detected per individual (minimum one cluster, maximum five clusters). We defined a cluster by the presence of a minimum of 10 GPS points, representing 30 minutes of foraging. In an earlier paper (Evens et al. 2021), the use by breeding birds of secondary habitats for foraging was documented but not investigated at a fine scale. To complement this previous study, here we describe how we sampled within the two different habitats, i.e. that used for nesting (open forests) and disjunct foraging areas, distinguishing between meadows and vineyards.

Nesting habitat

Within the 50% kernel of territorial birds (yearly kernels were combined if the nightjar was tagged in both study years), three sampling points were randomly generated in ArcMap (ESRI, version 10.7) to represent available nesting habitat. The number of sampling points per individual within the kernel could however drop to one or two if a distance of 50 m to the proximity of other sampling points (from the same individual or from other individuals) could not be ensured. This was the case in some territories with a high density of birds. The avoidance distance of 50 m in these mosaics of semi-open habitats ensured a real change in microhabitat structures but within the same type of habitat. For most birds, we did not actively search for nest locations due to the risk of an increased predation rate when approaching ground-breeding birds (Bühler et al. 2017; Langston et al. 2007). For each sampling point, a corresponding number of control points where nightjars were absent were generated randomly within a buffer of 500 m around the 50% kernel, avoiding the kernels of neighbouring breeding nightjars and keeping the points in similar habitat types (open forests). In total, 120 nesting points (used by n = 36 individuals) and 120 control points were visited, a total of 240 points for nesting habitats (Figure 1).

Foraging habitat

To investigate fine-scale habitat selection within foraging habitats, we classified GPS data to determine the location of foraging points outside the nesting habitat. Foraging sites could be readily identified as clusters of locations near extensively cultivated fields or vineyards outside known nesting areas. This classification was conducted by Evens et al. (2021) based on the GPS locations and their respective timing to identify flights outside the nesting areas (50% kernels). Two birds did not leave their nesting habitat during the time they were tagged, probably mostly foraging within the nesting habitat. As the nesting habitat of these birds was already taken into account in the previous analysis, we therefore did not consider them in this part of the study.

The sampling points were placed at the centroid of the foraging cluster (the densest part of the foraging points cluster) (Figure S3). For each foraging point, a control point was randomly generated in ArcGIS (ArcGIS Desktop v. 10.7, ESRI) within 500 m of the sampled site (or any other sampled site) but in a similar habitat type. We sampled 41 presence points and 41 random controls on grasslands used by 20 individuals, and 11 presence and 11 random controls on vineyards used by six individuals (for a map of the whole sampling area see Figure 1).

Habitat variables

We collected vegetation structures in the field between 3 June and 26 August 2020. In foraging areas, data were mostly collected in June to fit the dates when the points were visited by the birds. For nesting areas, data were collected in July and August to avoid disturbance to nesting birds. Despite the vegetation data being collected one or two years later than the tracking data (2018–2019), we believe that this data collection is legitimate, as variation in vegetation structure and diversity among sites is likely to be highly repeatable between years, especially in

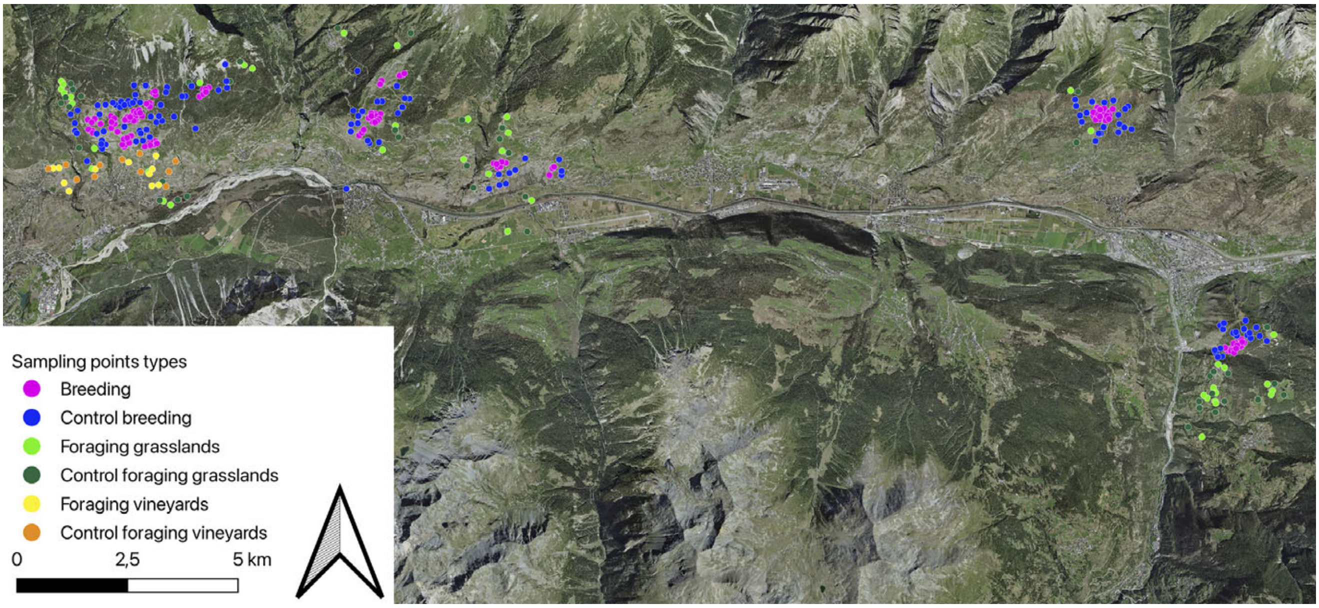

Figure 1. Sample points where data were collected. In breeding habitats, 240 points were sampled (blue and purple), in foraging habitats (grasslands), 82 points were sampled (light and dark green), and finally in vineyards, 22 points were sampled (yellow and orange). Base layer: Swissimage©Swisstopo.

climactic forests where nightjars breed. Moreover, no major change in land use could be detected in foraging grounds during data collection.

Vegetation structure variables were estimated at two different scales within square-shaped sample plots, following the methodology of Winiger et al. (2018) (see also Figure S4). This study targeted abandoned versus occupied nesting habitats and keeping the same methodology enabled direct comparisons with the results. Accordingly, we used the same scales, respectively 10 m × 10 m and 40 m × 40 m. While the small scale allows us to understand fine habitat structures, 40 m × 40 m plots are the largest plots where estimations of habitat structures are possible in such complex habitats. The goal of this method was to understand within the nesting and foraging habitats (defined previously in Evens et al. 2020 as breeding and foraging) the drivers responsible for the attraction of these fine-scale specific sites for the species. This methodology separates the *z* dimension into four categories to calculate vegetation coverage for all these different layers: ground, regeneration cover (<1.3 m), shrub (1.3–5 m), and tree layer (>5 m). Finer scale characteristics, such as vegetation height or amount of rocky ground, were estimated on a 10 m × 10 m plot; larger structures such as vegetation types were estimated on both 10 m × 10 m and 40 m × 40 m plots. Each plot was divided into four equal squares (5 m × 5 m and 20 m × 20 m, respectively) to allow for more accurate estimations in the field (Figure S4). Details on which features were estimated in the field are described in Table S1.

GIS-derived variables

We used ArcGIS to extract the exact coverage of roads, vineyards, extensive and intensive grasslands, extensive and intensive pastures, and other landscape elements such as water (running or standing) and buildings with more precision at the larger scale (40 m × 40 m). The categorisation of grasslands and pastures was estimated directly in the field using the TypoCH categories (Delarze and Gonseth 2008; Table S1).

For the total coverage of woody vegetation (from tree, shrub, and regeneration layers, called total regeneration) in the different strata, we summed all the values measured for the different species in the field per stratum. We also created separate variables for coniferous and deciduous regeneration, shrub, and tree variables.

Diversity indexes

For all plots, we calculated their woody species diversity at both the 10 m × 10 m and 40 m × 40 m scales based on the coverage of the different species. For this purpose, we used the Shannon Index parameter of the "diversity" function of the vegan package in R. We calculated this for each stratum separately, all strata combined, and tree and shrub combined. We used the same function to calculate the diversity of different land-use types in foraging plots (Shannon Index, named structure diversity afterwards); we included coverage of intensive and extensive grassland, intensive and extensive pasture, roads, hedges/wooded borders, forest, water, and other land-use types (such as gardens or orchards).

Variable selection

To investigate habitat selection for nesting sites, we used a within-home-range approach by comparing used with unused points, which differs from other study designs (occupied vs abandoned points; Evens et al. 2018a; Winiger et al. 2018). To select the best scale (10 m vs 40 m) for each predictor measured at 10 m and 40 m to model nightjars' habitat selection, we first removed zero-inflated and then strongly correlated variables (correlation coefficient >|0.7|) keeping the variables based on ecological reasoning (i.e. keeping the variables that we thought to be ecologically more relevant in the context of this study). The number of variables was further reduced using a Principal Component Analysis (PCA) (package factoextra; Kassambara and Mundt 2020), keeping only the variables with the highest

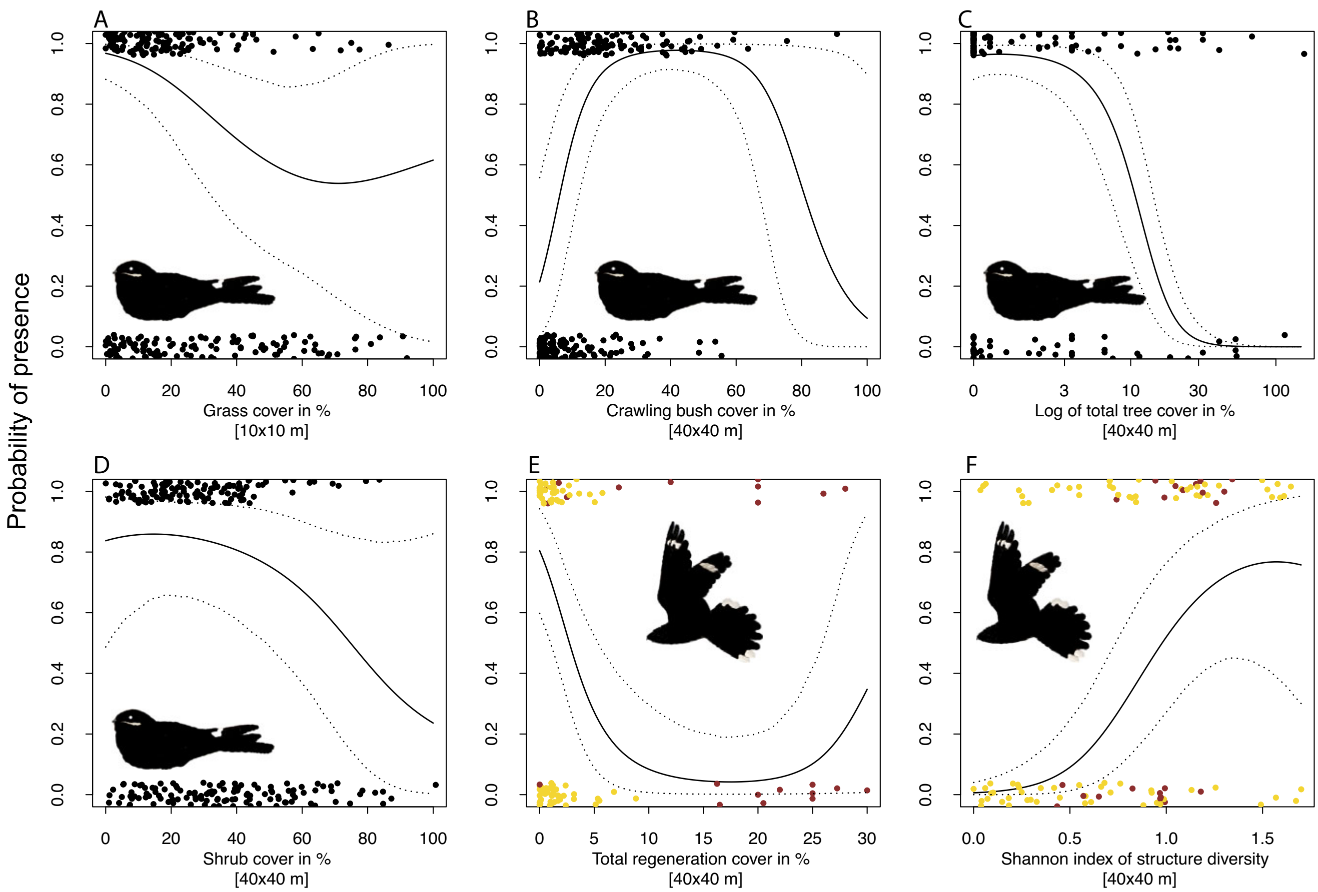

Figure 2. Habitat preference based on presence/absence of nightjars according to the main nesting and foraging variables; main variables for breeding (A, B, C and D) and foraging (E and F). The plain line represents the average estimate of a relative habitat preference, the dotted lines the credible intervals (95%). The points in black correspond to forests sites and related controls, grasslands are represented in yellow, and vineyards in red. For more visibility, some variance has been added to the points on the *y* axis. Predictors not shown in a plot are set to their mean.

contribution to the whole PCA. When several variables showed a close contribution, we selected the most ecologically relevant one keeping a ratio of 10:1 for the number of presence/absence points and the variables. Based on our assumptions on the effect of the variable on nightjar presence, we then used either linear (l) or both linear and quadratic terms (l and q) with nightjar presence/absence as a response variable in the models. We repeated this method for the two different models (nesting and foraging). Models investigating fine-scale habitat selection in nesting points and foraging points contained study site and individual identity as random factors.

Finally, we included seven variables (linear + quadratic) for the nesting model ($n_{presence}$ = 120), and three variables for the foraging model ($n_{presence}$ = 41). The seven variables for the final model (12 if we count the linear and quadratic terms) for the nesting sites were: grass coverage l+q [coverage in %, 10 m × 10 m], rocky ground l+q [coverage in %, 10 m × 10 m], diversity of woody vegetation l [Shannon Index, 10 m × 10 m], diversity of shrubs l [Shannon Index, 10 m × 10 m], crawling bush coverage l+q [coverage in %, 40 m × 40 m], shrub coverage l+q [coverage of shrubs between 1.3 m and 5 m in %, 40 m × 40 m], and tree coverage l+q [coverage of trees > 5m in %, 40 m × 40 m]. Similarly, three variables were selected for the final model on foraging habitat (grasslands and vineyards): total regeneration l+q [coverage in %, 40 m × 40 m], structure diversity l+q [Shannon Index, 40 m × 40 m], and Shannon Index of woody vegetation l+q [Shannon Index, 40 m × 40 m]. Even though crawling bush and shrub cover seem similar, crawling bushes are often below 1.3 m and are not considered in the shrub coverage variable.

Modelling

We used conditional logistic regression mixed models, using the "stan_clogit" function of the rstanarm package (Goodrich et al. 2022) to investigate the relative probability that the bird uses a site given the different variables. We built separate models for nesting points and foraging points using the set of predictors selected for each habitat type as described above. All models were fitted using R (version 4.0.4; R Core Team 2024). We used 4,000 draws from the joint posterior distribution, which were used to obtain 95% credible intervals for parameter estimates and regression lines in effect plots showing habitat preferences.

We then estimated the inter-individual variance using the RInSp packages (Zaccarelli et al. 2013) based on Roughgarden analysis (Roughgarden 1972) and complemented by PCA.

Results

Nesting habitat

Among the six variables, grass coverage, rocky ground, crawling bush coverage, and tree coverage were the most important in explaining nightjar presence (with credible intervals excluding 0; Figure 2 and Table 1). The chance of finding nightjars was higher at

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low grass cover (Figure 2A). The crawling bush coverage was at an optimum between 20% and 60% (Figure 2B, mean = 15%), whereas the chances of finding nightjars decreased as shrub coverage increased over 32% (Figure 4D). Similarly, an increase in tree cover of >6% decreased the chances of finding nightjars (Figure 2C). A high cover of rocky ground (>40%) increased the chances of finding a nightjar compared with the mean (average rocky ground cover 18%). However, a very low cover could also benefit nightjars' presence. Finally, the vegetation index of diversity and shrub coverage showed no clear effects.

Foraging habitat selection in grasslands and vineyards

Among these three variables, total regeneration and structure diversity showed clear effects on nightjar presence (Figure 2D and E and Table 1). There was a lower chance of finding a nightjar foraging when the regeneration layer cover increased, i.e. when the meadows were closed by woody vegetation, but an increased chance of finding a nightjar foraging when the diversity of the structures increased. On average, even a low presence of regeneration layer in the foraging ground decreased the chances of finding a nightjar, meaning that the birds forage mostly in open grassland areas, but the effect is reversed in richly structured vineyards where a high regeneration cover increases the chances of finding nightjars (Figure 2, red dots). The chance of finding a nightjar in a foraging area increased in structurally rich habitats, grasslands or vineyards (i.e. hedgerows, isolated trees) showing the interest of these birds in heterogeneous areas.

Table 1. Summary of the estimates and credible interval (CI) (95%) in the models for nightjar breeding and foraging habitats. Terms with CIs not including 0 are shown in bold. The numbers in superscript indicate the variable at the quadratic level. See Table S1 for details on the variables

Nesting	Estimate	95% CI
Crawling bush	1.6	[–0.83; 2.40]
Crawling bush^2	**–1.2**	**[–1.81; –0.55]**
Tree	**–4.3**	**[–5.99; –2.79]**
Tree^2	**–1.5**	**[–2.42; –0.72]**
Shrub diversity	–0.3	[–0.96; 0.25]
Total shrub	**–0.6**	**[–1.24; –0.12]**
Total shrub^2	–0.3	[–0.81; 0.30]
Grass coverage	**–1.1**	**[–1.79; –0.46]**
Grass coverage^2	0.4	[–0.19; 0.98]
Rocky ground	0.4	[–0.31; 1.08]
Rocky ground^2	**0.9**	**[0.34; 1.43]**
Shannon Index	–0.1	[–0.76; 0.63]
Foraging	Estimate	95% CI
Total regeneration	**–1.4**	**[–2.52; -0.47]**
Total regeneration^2	**0.8**	**[0.17; 1.50]**
Structure diversity	**2.4**	**[1.20; 3.85]**
Structure diversity^2	–0.6	[–1.41; 0.10]
Total Shannon Index	–0.2	[–1.18; 0.78]
Total Shannon Index^2	0.4	[–0.19; 1.12]

In both nesting and foraging habitats, individuals showed a rather generalist use of the different habitat variables (nesting: Araujo's E: 0.28; foraging: 0.30, but not with significant *P* values; WIC/TNW nesting: 0.98; foraging: 0.82). Only one individual foraged solely in vineyards whereas the other used both habitat types (Figure S6).

Discussion

Fine-scale habitat selection, based on high-resolution GPS data, differs between nesting and foraging areas. Nesting sites are found in semi-open, primarily coniferous forests that are abundant in crawling bushes and small rocks with low vegetation cover. These areas correspond to locations where topographical, climatic or human-induced conditions are too severe to support complete (100% cover) coverage of forests or herbaceous growth. In contrast, foraging nightjars select open meadows or pastures with a high proportion of structures such as bushes, hedges, and individual trees. In addition, biodiversity-friendly managed vineyards appear to meet the nightjar's foraging needs showing new potential for the conservation of this species in Switzerland.

Nesting habitat preferences of nightjars

Nesting sites of nightjars in Switzerland consist of areas where natural or anthropogenic conditions lead to harsh conditions for vegetation. Areas with limited forest cover (commonly dominated by Scots Pine) are selected, with a small number of old trees and low to intermediate bushy vegetation cover. Among these bushes, nightjars select crawling bushes that stay close to the ground and offer good shelters for roosting birds (Figure 2A–D). Grassy vegetation is also avoided in nesting grounds as the birds aim for areas with an important piece of unproductive ground like rocks. Usually, nesting sites show a low "succession potential", i.e. a low regeneration speed of shrubs. Here, we additionally demonstrated that high proportions of crawling bushes (i.e. dwarf juniper bushes such as *Juniperus communis* and *J. sabina*) at ground level are important. Both juniper species grow on poor substrate and need a lot of light, which is made possible by the low coverage of trees and shrubs. The importance of high amounts of crawling bushes in nesting areas is in line with other studies in Europe where heather *Calluna vulgaris*, a dwarf bush similar in structure to the two dwarf juniper species in our study, was repeatedly shown to be an important feature (Verstraeten et al. 2011; Wichmann 2004). This type of vegetation structure has been shown to reduce nesting failure (Langston et al. 2007) and is important as cover during the day, particularly for juvenile birds (Berry 1979). Since most of our study sites have undergone natural catastrophes such as wildfires or avalanches during the last decades, they are now in a recolonisation phase for the vegetation that seems to be attractive to this species. For exactly how long these sites will remain suitable for nightjars is unclear but habitat quality is expected to decrease due to on-going succession (Rey et al. 2019). These results, based on high-resolution GPS data and comparing presence with neighbouring absence points, are largely in line with previous studies on nightjars that used a different methodology (Sharps et al. 2015; Winiger et al. 2018). This convergence among studies is promising. On the one hand regarding the results on the habitat requirements of the nightjar, but also the different methodological approaches. For the description of nesting habitat, it seems acceptable to base analyses on occurrence

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data based on visual or auditory observations. Especially so for Critically Endangered species where handling should be minimised. However, the major caveat of this observational approach concerns species that use multiple habitats and for which detectability in foraging grounds is low. This will lead to an overestimation of the nesting grounds thereby neglecting the importance of foraging habitats.

Nightjar use of complementary foraging habitats

Nightjars are known to commute up to several kilometres to complementary foraging habitats, mostly grasslands but also vineyards (Evens et al. 2021; Sharps et al. 2015). The delimitation of these distant feeding grounds could only be determined with the help of tracking data. The secretive and nocturnal activity patterns are best captured with high-resolution GPS data and would be clearly underestimated by observation data. Within foraging habitats, nightjars selected at fine-scale sites where the structural diversity was high with small structures such as hedges or isolated trees (Figure 2F). These habitat features probably have two important roles. Firstly, monotonous grasslands or vineyards with a lack of structures likely impede possibilities of performing flycatching behaviour, where the nightjars sit on a perch and wait for prey, forcing them to feed on the wing (Cresswell and Alexander 1990). Secondly, the presence of several different structures provides a higher diversity of host plants for moths, the nightjar's main prey. In such a context, nightjars probably profit from the edge effect. The multiplication of landscape elements increases biodiversity at their interface – or ecotones (sensu Lindell et al. 2007), in our case between vineyards, grasslands, and woodlands.

In addition to nesting areas, both types of remote foraging areas are also under pressure. Due to the decline in traditional agriculture, existing extensive grasslands, pastures, and meadows are threatened by shrub encroachment. This trend has increased significantly over the last decades and resulted in a negative impact on foraging habitats (Evens et al. 2021). Although the rapid increase of vineyards in the study area over the last decades (Reynard et al. 2007) led to a loss of natural habitat and thus also to a decline in the nightjar population, vineyards may have great potential as a secondary foraging habitat. This was addressed by Sierro et al. (2001) 30 years ago who recognised the potential of vineyards as foraging habitat in terms of structure but noted their deficiencies in terms of poor insect biomass at that time, as well as the lack of hedgerows and ground vegetation. Over the last decade, management has become more biodiversity friendly as a result of policy changes. On the one hand, there has been an increase in ground cover with a drastic reduction in herbicide use, but also a change in structural diversity with the planting of hedgerows and isolated trees adding to the variety of land-use types.

Limitations of the study

Given that most of the tagging efforts were concentrated in the earlier phase of the reproductive season mostly based on males, it is possible to underestimate the full potential of habitat use of the species, especially as interindividual variation can be quite large (Mitchell et al. 2020). In our study region some individuals have been shown to travel to alpine meadows (Evens et al. 2021), probably trying to match peaks in prey abundance (e.g. Larch Budmoth *Zeiraphera griseana*; Baltensweiler et al. 1988). Habitat-specific selection patterns, especially for foraging activities during the breeding or even the annual cycle, are expected to vary according to peaks in prey abundance. Birds in general are expected to attempt to match their breeding season to food availability (English et al. 2018), with any mismatch expected to negatively affect breeding success. The nightjar, with its moth diet, should be no exception and the use of complementary foraging habitats could offer the necessary flexibility to follow habitat-specific peaks in prey abundance. To fully understand variation in movement patterns, further investigations on habitat-specific moth abundance throughout the season would be necessary as we quantified the foraging habits of nightjars solely based on habitat type and structure without considering the availability of their main prey (Evens et al. 2020).

Implications for conservation

This study allowed us to shed light on important vegetation structure and land-use characteristics that have previously not been considered when making decisions for conservation strategies in favour of nightjars in Switzerland. Whereas the artificial light at night was pointed out as a potential cause of range constriction in Valais (Sierro and Erhardt 2019; however, see Evens et al. 2023), actions need to be taken in nesting and complementary foraging habitats. Indeed, previous measures targeted the creation of clearings in forests without considering foraging habitats, but it is now clear that the species suffers from two on-going processes. On one hand, land abandonment and consecutive encroachment have a negative impact on nightjar nesting and foraging grounds closing open forests and unmown meadows. On the other hand, intensification of the remaining agricultural surfaces leads to uniform and insect-unfriendly pastures, meadows, and vineyards (Bosco et al. 2019a; Humbert et al. 2021; Wagner et al. 2021). The long-term process of clearing openings in Switzerland for nightjar conservation was probably unsuccessful due to the lack of suitable grasslands in the surroundings, but also due to the rapid recolonisation of herbaceous vegetation limiting the availability of bare grounds to nest.

In such a context, we need to maintain semi-open habitats formerly created by natural events or forestry measures such as wildfires or avalanches. Apart from extreme events, in the study site, semi-open forests are only present in limited areas where suitably harsh conditions occur (south-facing exposure and minimal soil). Most of the actual nightjar sites are related to old natural events like fire or avalanches or human-induced open forests. It is important to maintain sustainable forestry in these areas including extensive grazing by cattle to keep the forest open. However, the use by nightjars of multiple habitats during the breeding period was probably the most important reason for the failure of past conservation measures in Switzerland. Selected sites for conservation have often concerned places where complementary foraging habitats were no longer available. Given the nightjar's need for a combination of poor diversity in nesting sites and high diversity in foraging sites, the ongoing homogenisation of the Swiss landscape is likely to have led to its current decline (Evens et al. 2021). Actual conservation strategies should focus on (1) maintaining and creating semi-open forests (maximum 20% of old trees) with crawling bush-like structures (20–60% maximum) with a low grass cover (<25%) and, ideally, with intermediate rocky ground cover which will limit grass and bush regrowth, and finally low to intermediate shrub coverage (maximum 50%), but (2) the managed areas should also consider the surroundings of the breeding locations and aim to promote small landscape elements in grasslands or vineyards with different types of land use in the direct surroundings of the nesting habitats (1.3–2 km max; Evens et al. 2021) to also guarantee appropriate foraging grounds. These elements will be used by nightjars for foraging and will serve as stepping stones for all the biodiversity suffering from landscape homogenisation (i.e. Woodlark *Lullula arborea*). Close to nesting areas, promoting zones of extensively managed grassland, but especially vineyards, with ground vegetation and structured hedges would be beneficial, as the latter is the most common type of land use under 800 m above sea level in the central Valais. This would increase foraging opportunities in the lowlands. Avian diversity in general, including priority species for Switzerland such as Woodlark and Cirl Bunting *Emberiza cirlus*, would also benefit from such measures (Assandri et al. 2016).

Conclusions

This study highlighted the microhabitat preferences of nightjars in nesting and foraging habitats in Switzerland, pointing out the importance of very different complementary habitats to forage. This phenomenon is well studied in nightjars (i.e. European Nightjar; Evens et al. 2021; Egyptian Nightjar; Wasserlauf et al. 2023) and is extremely important for their conservation, as it is for many other bird species. In this study, we pointed out the importance of dwarf bushes in semi-open forests with limited grass and tree cover for nesting sites, as well as the necessity of heterogeneous and species-rich agricultural landscapes in the areas surrounding the nesting sites. If we are to hope for the recolonisation of abandoned sites, restoration of extensive grasslands in the lowlands and pastures combined with the promotion of structure-rich vineyards with sufficient ground vegetation are probably key factors that will have to be linked to sustainable forest management in former breeding sites.

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