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Habitat use and foraging ecology of the nightjar (*Caprimulgus europaeus*) in the Swiss Alps: towards a conservation scheme

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Abstract

The European nightjar is one of the most endangered bird species in Switzerland. As its ecology in the country is poorly understood, we collected data on resource exploitation in the upper Rhône valley (Alps). The diet of two adult birds and one nestling consisted primarily of moths (81 and 93% of biomass), which were also the most abundant prey sampled at the study site. Three radiotracked nightjars selectively exploited oak scrubland compared to vineyards and pine forests; vineyard monocultures harbour presumably insufficient moth populations, whereas dense pine stands probably do not provide the flying and foraging requirements of nightjars. The survival of nightjars in Valais probably depends both on the existence of sufficient populations of moths and on the availability of semi-open natural habitats, such as oak scrubland, which seem to offer the best suitable foraging and nesting places. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Although widespread throughout Europe, the European nightjar (*Caprimulgus europaeus*) has suffered severe population declines in several areas since the 1950s, particularly in the western and northwestern parts of the continent (Schlegel, 1967; Glutz von Blotzheim et al., 1980; Cramp et al., 1985; Sierro, 1991; Morris et al., 1994). This decrease has been attributed mainly to habitat changes induced by agricultural and forestry intensification (Hoblyn and Morris, 1997).

In Switzerland, the occurrence of the nightjar is nowadays restricted to the south of the country. About 80% of the current Swiss breeding population, which totals ca. 75 pairs, survive in the upper Rhône valley (canton of Valais; Sierro, 1991; Schmid et al., 1998). The nightjar is therefore listed as a highly endangered species in Switzerland (Zbinden et al., 1994).

In the canton of Valais, the nightjar appears today more abundant in the eastern (Upper Valais) than in the western part (Lower Valais) (see Fig. 4 in Sierro, 1991). This contrasts with a more homogeneous distribution across the whole area in the past (Desfayes, 1951). The current local distribution of the species appears inversely associated with the geographic extension of vineyards which, on south-exposed slopes — i.e. north of the river Rhône — are much more abundant in Lower than in Upper Valais (Sierro, 1991). Also, the expansion of vineyards over the past decades mainly occurred in Lower Valais (from 2717 to 5259 ha between 1939 and 1996, i.e. ca. doubling of the area; Federal Office of Statistics, Bern).

To find out what might be the most relevant conservation measures for long-term survival of the remnant population, a study of habitat selection and foraging ecology was undertaken in 1994.

2. Study site

The study took place from May to September 1994 in Central Valais (46°16′ N, 7°26′ E), on the south-exposed slope between Sion and Sierre, above Saint-Léonard.

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With < 600 mm average precipitation per year, Central Valais is the driest region of the Alps (Ozenda, 1985). At the study site, vineyards cover most of the lower foothills, from the plain at 500 m altitude up to 700–800 m. Steppe (a climactic grassland found in the driest areas of the Alps at low elevation), xeric deciduous scrubland (*Quercus pubescens*) and coniferous (*Pinus sylvestris*) forests constitute the natural vegetation. Today, they exist only as fragments among vineyards; at higher elevation, however, they still extend over wide areas. The study zone is inhabited by four to five pairs of nightjars breeding in semi-open habitats with scattered trees and shrubs, between 700 and 1000 m altitude (Sierro, 1991).

3. Methods

3.1. Radiotracking and habitat selection analysis

We captured three adult males with mist-nets set within clearings in the forest or gaps in scrubland (Squire and Alexander, 1981; Cresswell and Alexander, 1992). The birds were attracted by playing back the species' typical territorial song with recordings obtained from commercial disks and tapes. Captured birds were fitted with 1.5 to 3 g radiotags (Naef-Daenzer, 1993). The tags were glued onto the upper back after clipping a small patch of feathers between the shoulders. Skin Bond glue (Smith and Nephew United Inc., Largo, FL, USA) was used to attach the tags on skin and feather shafts. Feeding movements were studied between late May and late June (Table 1).

Reception ranges were up to 2 km for birds sitting or flying more than one wavelength (ca. 2 m) from the ground. Bearings were taken from two fixed antenna stations placed 360 m apart on vantage points along the slope axis, at 685 and 900 m altitude, respectively. Two phase-shifted six-element Yagis were mounted on top of a 7-m pole. Televilt RX-8910HE receivers were used (Televilt International AB, Box 53, S-71122 Lindesberg, Sweden). Null-peak bearings with this system achieve an average accuracy of about ±1.5° (Naef-Daenzer, 1993). Bearings were taken simultaneously every 5 min throughout the night, from dusk to dawn. Interval sampling was used to achieve independence of locations from behavioural parameters (White and Garrott, 1990).

Based on the average bearing error and the location of antenna stations, a map of location accuracy was calculated. The analysis of location data was restricted to the area in which location errors were < 100 m (average absolute location error of ca. 40 m). Individual home range sizes were estimated by the minimum convex polygon method (White and Garrott, 1990).

The proportion of four habitat types (vineyards, oak scrubland, pine forest, steppe) was assessed by superimposing home ranges over a vegetation map on the basis of 50×50 m grid cells, i.e. 0.25 ha. In order to investigate habitat selection, we compared, for each bird separately, the proportion of locations in each of the four habitat types with the expected proportions if birds visited these structures according to availability. We calculated the 95% confidence intervals for the proportion of locations in the respective habitat type referring to a Z-statistic. If the observed proportion was below the lower confidence limit, the respective habitat type was considered to be preferred by the bird (positive selection), and vice versa. As the number of habitat types defined was small, the proportion of locations in the categories were not independent. We therefore applied a Bonferroni correction for the estimation of the 95% confidence intervals ($\alpha^* = \alpha/2n$, where n is the number of categories). Details of this adaptation are given in Neu et al. (1974) and White and Garrott (1990).

In a further step, we analysed the density of locations in relation to the proportion of area covered by forest. It was calculated using a fixed kernel algorithm that translates the pattern of locations (points) into a density estimate. The software GRID (Naef-Daenzer, 1993) was used. The kernel density gives the number of locations within a 30-m radius from the centre of the respective cell. For 1284 random points within the home ranges of the two individuals, the coverage of forest within a 50×50 m^2 was determined according to 11 categories from 0 to 100%. The average kernel density of bird locations in each category was then analysed by analysis of variance (ANOVA).

3.2. Trophic ecology

The diet of two adults was investigated, based on 22 faecal pellets found in June underneath two perches in scrubland where the birds spent the daylight period. Pellets were softened in a solution of water and 70% ethanol. Identifiable fragments were teased apart under a binocular microscope (40×) using needles. The diet of one nestling was assessed from samples collected with a neck collar. The validity of these methods to estimate diet composition has been demonstrated several times

Table 1
Summary of telemetry experiments carried out in 1994 with three males

Individual[a]	Date of capture	Recording dates	Total number of bearings	Number of useful bearings
H783079	22 May 1994	27–31 May 1994	101	84
H783080	7 June 1994	7–17 June 1994	402	292
H783081	12 June 1994	12–25 June 1994	788	432
Total			1291	808

[a] Ring code.

(e.g. Ralph et al., 1985; Brigham, 1990; Jenni et al., 1990). Prey remains were determined by reference to the insects collected in the same area using light traps, and to various identification guides (e.g. McAney et al., 1991).

Food availability was sampled with light trapping of nocturnal insects. Three light traps were used (type Baggiolini and Stahl, 1965), one placed in each of the typical habitats available at the study plot. However, as there were four habitat categories, pine stands were sampled in June only, whereas vineyards were not sampled in that month. Three sampling sessions per month took place in June and July, four in August. Light trapping was performed simultaneously in the different habitats. It was deliberately restricted to calm and dry nights with reduced or no moonlight. Food availability analysis was based on the average between-session values obtained for a given month.

The insects collected were dried for several days by spreading them indoors on a flat surface, then placed in an oven for 1 h just prior to weighing them to the nearest 0.01 g using a precision balance. Biomass figures given refer to dry biomass.

The minimum prey size captured by nightjars was estimated as the average body length of moths found in the diet of one chick (see above), just prior to fledging, assuming that body size of prey at that time is representative of the average size of prey items generally taken by adults.

4. Results

4.1. Habitat selection

Altogether, we obtained 1291 locations from three different males during 33 nights of radiotracking activity (Table 1). Of these, 808 bearings (63% of the total) were accurate enough (see Section 3) to be included in the study on habitat selection. Those bearings will be referred to as "useful bearings" hereafter.

The three nightjar males spent most of their time in oak scrubland (mean = 74% of bearings; range = 52–87%). Vineyards were the second most important habitat (mean = 15% of bearings), followed by pine forests (9%) and areas covered with steppe vegetation (2%).

The habitats within the individual home ranges are presented in Table 2. Oak scrubland covered 46% of the area comprising all three home ranges, vineyards 27, pine forests 25, and steppe 3%.

For none of the radiotracked birds was the number of locations distributed amongst the four habitat categories according to their availability within the individual home ranges (χ^2-tests, all three *P*-values < 0.001; Table 3). Instead, habitat selection analysis showed that all three birds clearly preferred oak scrubland and

avoided pine forests; vineyards were avoided by two of the nightjars. We also found a highly significant preference of males for parts of the home range where forest vegetation covers 20–50% of the area (ANOVA, $F_{1,10} = 21.59$, $P < 0.001$, Fig. 1).

4.2. Trophic ecology

4.2.1. Diet

The diet of two adults consisted mostly of moths (81 and 85% of biomass, respectively) and Coleoptera (18.7 and 5%). Diptera and Hymenoptera (0.2 and 0.9% of total, respectively) were found only occasionally in droppings (Table 4).

Chick food (provisioned by parents) was studied in one nestling between 4 and 20 days of age ($n = 140$ prey items). In terms of biomass (percent, by volume), its daily diet consisted, on average (±S.D.), primarily of moths (92.7±12%, $n = 11$ nights). Neuroptera were the second most important group (6.5±11%), whereas the

Table 2
Area (hectare; ha) and percentage of the different categories of habitat available within the home ranges of the three males; home ranges were delimited from the minimum area polygons drawn from the useful bearings

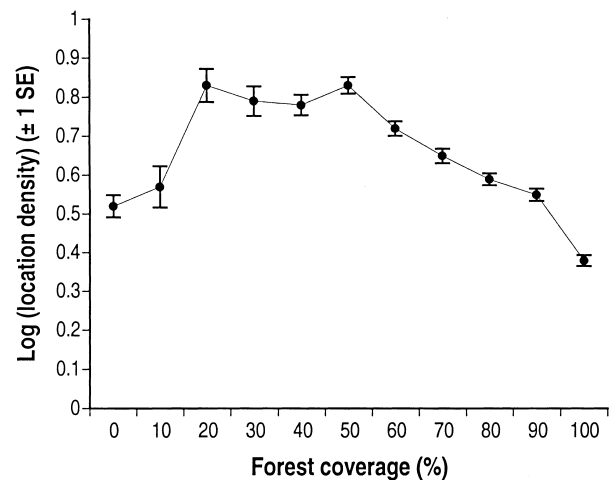| Bird	Vineyards		Steppe		Oak forest		Pine forest		Total area	
	ha	%	ha	%	ha	%	ha	%	ha	%
H783079	3.78	16.0	0.63	2.6	15.15	64.2	4.05	17.2	23.61	100
H783080	8.25	25.0	0.58	1.8	19.70	59.6	4.50	13.6	33.03	100
H783081	12.35	30.6	1.70	4.2	15.88	39.4	10.43	25.8	40.36	100
All three males	14.84	26.7	1.60	2.9	25.43	45.7	13.78	24.7	55.65	100

Fig. 1. Average (±standard errors) location density at 1284 random points within the home ranges of the radiotracked males in relation to coverage of forest vegetation. Greatest location densities were recorded in areas covered by 20–50% with forest vegetation (mainly oak stands).

other prey types (Diptera, Hymenoptera, Coleoptera) were taken occasionally (0.9±3%).

4.2.2. Prey size

The prey size in the diet of the adults could not be estimated, due to too fragmental remains in droppings. We therefore looked at the body length of the prey items brought back to the chick by its parents. There was a slight but significant increase in the average body length of prey provisioned by the adults as the breeding period progressed ($r^2 = 0.083$, $n = 140$, $P < 0.001$; from linear regression). From hatching to 10 days of age, the average (±S.D.) body length of prey items was 11.4 (±3.6) mm ($n = 60$) compared to 15.0 (±4.9) mm from age 15 to 20 days ($n = 49$). Yet, small prey items < 10 mm in length were still provisioned quite late in the breeding period. Prey items up to 20 mm were given to the young from day 4 of hatching.

4.2.3. Food availability

Given that nightjars are apparently capable of exploiting a wide range of prey sizes, all insect items found in the light traps were considered to estimate food availability. Fig. 2 shows the dry biomass of the various prey categories found in the light traps in June, July and August (note that pine woods were sampled in June only, see Section 3). Lepidoptera, which consisted almost exclusively of moths, predominated (75%), followed by Coleoptera (14%), Neuroptera (3%) and Hymenoptera (3%); together these prey categories made up for 95% of the overall biomass available. The seasonal variation did not depart much from this pattern, with Lepidoptera dominating food availability in all

months (75, 83 and 65%, for June, July and August, respectively). Lepidoptera were dominant also in each habitat, accounting for 80% of the insect biomass collected in steppe, 76% in oak scrubland, 77% in pine forest, and 64% in vineyards. The insect abundance in the various habitats was quite variable. In June, pine woods produced on average 63% of the overall biomass, compared to 22% for oak forest and 15% for steppe. In July, steppe and oak scrubland had similar biomasses (39 and 38%, respectively), whereas vineyards held 24%. In August, vineyards provided 43% of the overall biomass, compared to 36% for steppe and 21% for oak scrubland.

4.2.4. Diet versus food availability

A rough comparison of the diet of the adult birds in June (Table 4) with food availability (Fig. 2) shows that the prey making up most of the diet, namely Lepidoptera

Table 4
Estimated biomass (% by volume) of the different categories of prey found in the diet of two adult nightjars in June

Bird No.	n^a	Lepidoptera		Coleoptera		Diptera		Hymenoptera	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
A	20	81	22.5	18.7	22.5	0.3	1.1	0	0
B	2	85	21.2	5.0	7.1	0	0	10.0	14.1
A and B	22	81.4	21.9	17.5	21.8	0.2	1.1	0.9	4.3

[a] The number of faecal pellets collected at the diurnal roosts of two individuals.

Table 3
Habitat selection analysis for the three birds

Bird	Habitat type	Proportion of habitat within individual home range	Observed number of locations	Expected number of locations[a]	χ^2	Proportion of observed locations	95% Confidence intervals	Direction of selection
H783079	Vineyards	0.160	4	13.44	6.63	0.05	0–0.109	Avoided
	Steppe	0.026	1	2.18	0.64	0.01	0–0.037	–
	Oak forest	0.642	73	53.93	6.74	0.869	0.777–0.961	Preferred
	Pine forest	0.172	6	14.45	4.94	0.071	0.001–0.141	Avoided
	Total	1	84	84	18.96***	1		
H783080	Vineyards	0.25	34	73	20.84	0.116	0.069–0.163	Avoided
	Steppe	0.018	4	5.26	0.30	0.014	0–0.031	–
	Oak forest	0.596	240	174	25.0	0.822	0.766–0.878	Preferred
	Pine forest	0.136	14	39.7	16.65	0.048	0.017–0.079	Avoided
	Total	1	292	292	62.79***	1		
H783081	Vineyards	0.306	121	132.2	0.95	0.280	0.226–0.057	–
	Steppe	0.042	15	18.1	0.54	0.035	0.013–0.057	–
	Oak forest	0.394	223	170.2	16.37	0.516	0.456–0.576	Preferred
	Pine forest	0.258	73	111.5	13.27	0.169	0.124–0.214	Avoided
	Total	1	432	432	31.14***	1		

[a] If a bird visited the habitats according to their availability within its own home range. ***$P < 0.001$.
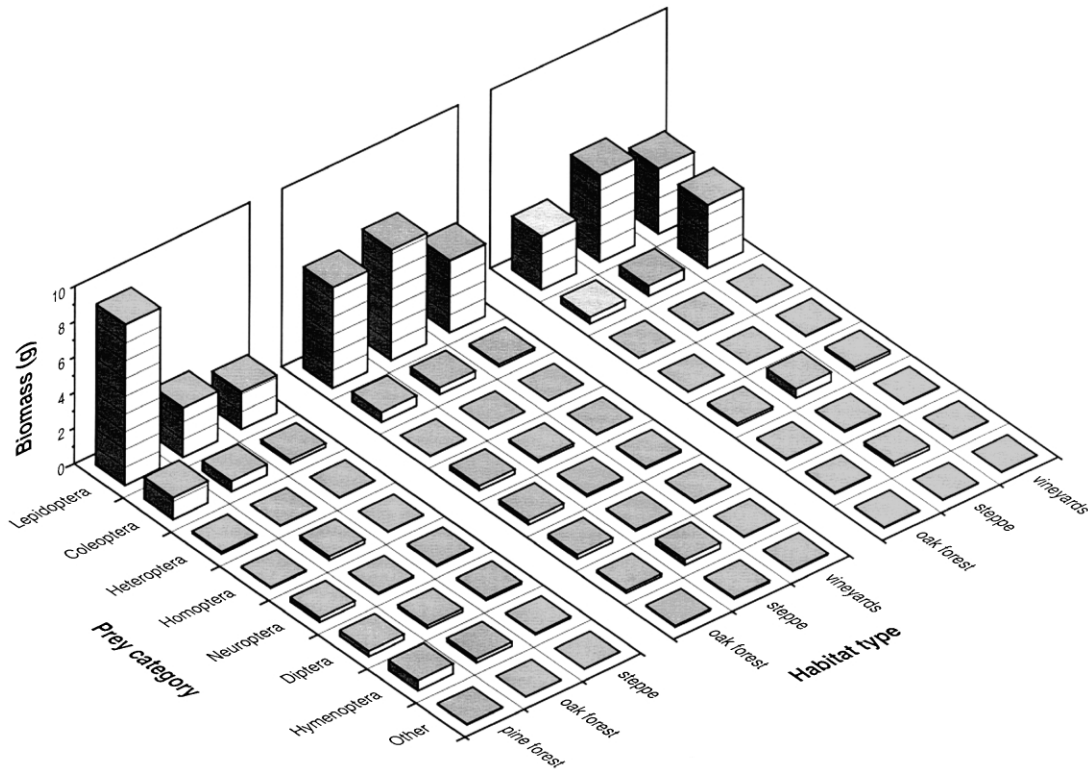
Fig. 2. Mean dry insect biomass found in the light traps during the months of June (left graph), July (middle) and August (right) in four different types of habitat; notice that pine forest was sampled only in June when vineyards were not sampled. The category "other" comprises Ephemeroptera, Dermaptera, Blattoptera, Raphidioptera and Trichoptera.

and Coleoptera, were also the most abundant insects found in the environment at that time. In nestling food, there was some discrepancy between diet composition and food availability, with Neuroptera constituting the second most abundant prey in diet, whereas Coleoptera were found in a comparatively smaller proportion than expected from their availability.

5. Discussion

5.1. Trophic ecology

In the study area, the diet of *Caprimulgus europaeus* consisted mainly of moths. Similar findings were obtained by Schlegel (1967). Moths were also the most abundant prey found in all habitats investigated in this study. Light traps are particularly efficient for capturing nocturnal insects with strongly positive phototactism such as moths (Bowden, 1982; Muirhead-Thomson, 1991). They are thus unlikely to underestimate the moth supply relative to other insect groups. The relatively high proportion of Neuroptera and the virtual absence of Coleoptera in chick diet may result from the fact that adults prefer to feed nestlings with "soft-skinned" food, at least in their early stages of development (cf. Schlegel, 1967).

5.2. Habitat selection and distribution in Valais

At the study site, nightjars clearly preferred oak scrubland and used steppe in proportion to availability, whereas vineyards and pine forests were visited less frequently than expected. Similar patterns of habitat selection have been described in the UK (Alexander and Cresswell, 1990). Unfortunately, our radiotracking method was not adequate to clearly identify the reason for visiting a particular type of habitat at night. Some locations may refer to foraging activity, others to reproductive behaviour, or simply to commuting flights. Yet, assuming that the majority of contacts concerned foraging, the pattern of space use observed is surprising because vineyards and pine forests, which are avoided, hold apparently fairly large numbers of moths. Factors linked either to further possible methodological biases, or to mere foraging constraints, may explain this apparent discrepancy between space use and food availability. First, although placed within homogeneous habitats, light traps may have attracted insects originating from other habitat types. Many of the insects trapped among vineyards may, for instance, come from biologically more productive habitats (e.g. woodlands, oak scrubland and steppe). This seems probable because vineyards in Central Valais harbour no ground vegetation, since they are regularly sprayed with herbicides.

Second, some forests may remain unexploited by nightjars for structural reasons impeding foraging flights. Pine woodlands in the study area are very dense forests consisting of small- and medium-sized trees. European nightjars apparently spot potential prey against the sky light from perches close to the ground level or in low-flight, and catch them in the air (Schlegel, 1967; Alexander, 1985; Alexander and Cresswell, 1990; A. Sierro, unpublished). This technique cannot be applied in the local pine forests as there is not sufficient space for flying and as the background is darkened by the dense canopy. By contrast, oak scrubland at the study site are xeric formations growing on a thin substrate, with sparse shrubs and trees, and are easily accessible to a flying bird. The same applies to areas covered by steppe. We, therefore, believe that the under-exploitation of vineyards, which would certainly offer suitable structural conditions for foraging, is due to lack of prey within that habitat — contrary to what is suggested by our light trap data — whereas pine woods are avoided for structural reasons. Correspondingly, oak scrubland may be selected for both trophic and structural reasons.

The local distribution of nightjars in Valais supports this view. *C. europaeus* is much more frequent in areas where vineyards are rare or absent, as in Upper Valais. This suggests that the homogeneous areas primarily devoted to intensive grape cultivation in Lower Valais are no longer suitable breeding zones for nightjars, possibly due to insufficient food resources. The area of vineyards in Valais has nearly doubled from 1939 to 1996, largely by the destruction of the natural vegetation covering the south-exposed slopes, especially in Lower Valais. There are also fewer suitable semi-open habitats in Lower Valais because of its wetter climate than in Upper Valais.

5.3. Possible implications for conservation

As fairly specialized moth predators, European nightjars presumably need habitats holding this prey in sufficient abundance for successful breeding. In addition, they require open, semi-wooded habitats which provide easy access to cover on the ground for nesting. Although the density of nightjars in Upper Valais is still fairly high, some population decline took place over the past decades in Lower Valais (Sierro, 1991; Schmid et al., 1998; R. Arlettaz, unpublished), probably because one or both of the requirements mentioned above are no longer met.

As conservation measures, we suggest, first, a total protection of the current area of oak scrubland. This habitat has suffered numerous alterations by human activities over past decades, mostly by transformation to vineyards, especially in Lower Valais.

Secondly, habitat diversification should be initiated within vineyard monocultures; for instance, bushes and hedges should be re-integrated in the vineyard landscape and ground vegetation should be promoted within the vineyards. The current systematic use of herbicides clearly prevents the development of a diverse fauna at the ground level, and this is particularly crucial as it concerns prey of the nightjar such as noctuid moths.

Third, an action plan that aims to create clearings within dense oak or pine forests as breeding habitats in areas where the species was still present some decades ago should be launched in close collaboration with local foresters.

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