Habitat Selection by the European Nightjar 
*Caprimulgus europaeus* in North-Eastern Poland: 
Implications for Forest Management

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Abstract: Research Highlights: Intensive forest management practices generally have a negative effect 
on biodiversity. However, the creation of new, open habitats as a consequence of timber harvesting 
within large areas of woodland may be favorable to some bird species. Background and Objectives: 
Habitat selection of the European Nightjar *Caprimulgus europaeus* in a coniferous woodland area 
in northeastern Poland was studied in order to specify management recommendations. Materials 
and Methods. To define the influence of various environmental parameters on territory occupation, 
11 micro- and 3 macrohabitat factors were analyzed. Results: Denser vegetation in the ground layer 
deterred birds from nesting in clearings with such characteristics. Moreover, Nightjars preferentially 
inhabited sites adjacent to young stands of trees. Birds preferred plots with a higher number of 
clearings in the neighborhood, as this enabled them to enlarge their foraging area. Other microhabitat 
factors (e.g., the type, age and area of clearings), as well as macroscale factors like distances to the 
forest edge, nearest roads and human settlements, were of no importance. Conclusions: Knowledge 
of the Nightjar preferences may be useful in working out a compromise between an appropriate level 
of clear-felling and conservation of other bird species requiring preservation of old tree stands.

Keywords: habitat factors; forest management; breeding territory; clearings

1. Introduction

Woodlands play a crucial role in the protection of biodiversity resources, so management of these 
ecosystems should be based on processes and projects aimed at implementing the broadly understood 
concept of sustainable development [1–4]. From the conservation aspect, however, contemporary forest 
management practices are often perceived as having a negative impact on breeding birds, manifested 
as they are in the felling of larger and smaller wooded areas, the removal of old and dead trees and 
even the destruction of entire forest ecosystems [5–9]. Generally speaking, such activities decrease the 
local biodiversity of birds and cause many species associated with wooded habitats to abandon them 
(e.g., [10,11]). Much of the temperate forest area in Europe is dominated by conifer stands, planted 
on a wide scale in the past because they were easy to establish and manage. Rapid growth rates 
and the increasing stock of these forests led to structural homogenization, which can adversely affect 
biodiversity [12,13]. On the other hand, clearings in woodlands can offer favorable nesting conditions 
for certain bird species originally associated with open or early-regenerating stands [14,15].

One such species is the European Nightjar *Caprimulgus europaeus* (hereafter, Nightjar), a nocturnal 
insectivorous species, the distribution of which covers almost all of Europe except for the treeless areas
in the far north [16,17]. Because of the decline of Nightjar populations during the last century, it is listed on Annex 1 of the European Birds Directive (Directive on the Conservation of Wild Birds 79/409/EEC). The Nightjar originally inhabited widely different types of open areas [18–20], but with the shrinking of these habitats, it has adapted to nesting in anthropogenic areas such as military training grounds, forest nurseries and clearings [16]. As a result of its colonizing such new habitats, its population has increased in some areas [20–23]; in others, especially in the EU, its breeding populations have declined historically and are continuing to do so [21,24]. The abandonment of traditional forestry practices, which affected habitat changes and included loss of tree plantations of the suitable age, was seen as the reason for the earlier decline in its abundance [20,25], whereas nowadays, population growth may be inhibited by the reforestation or restocking of woodlands destroyed by wind or fire [23]. As a result, judicious forest management that takes advantage of the emergence of new gaps and open, unvegetated spaces in wooded areas, and protects forest feeding grounds, is deemed crucial for maintaining the Nightjar population in an appropriate state [22,26].

Despite the Nightjar being widespread in Europe, relatively little attention has been paid to its ecology. At least in part, this is probably due to its nocturnal lifestyle and the consequent difficulties in its detection. The Nightjar’s habitat preferences and the factors affecting its distribution have been analyzed qualitatively, mostly at the microscale, for the temperate zone in England and the montane forest zone in Austria (e.g., [18,20,27]). Research into the connection between quantitative and qualitative habitat components has been limited, however.

The key factors favoring the occupation of potential breeding territories by the Nightjar need to be identified so that they can be applied in forest management for future conservation planning. For this reason, we focus on the micro- and macrohabitat factors influencing the occurrence of territorial male Nightjars in their important refuge in the Knyszyn Forest (NE Poland), where over 5% of the Polish population breeds [28]. In the context of this species’ nesting preferences, we anticipated that certain microhabitat components, like the age and type of clearing, the type of undergrowth vegetation and the presence of seed trees, would play a significant role in its occurrence. Specifically, vegetation structure would enhance foraging efficiency on the one hand and create biotopes enabling the birds to remain concealed while nesting and roosting on the other [29]. We also hypothesized that more clearings and a younger tree cover in the immediate surroundings of the nesting territories would enlarge the birds’ hunting area. At the macroscale, the Nightjar’s occurrence could be negatively affected by the distance to the forest edge, nearest roads and human settlements [30].

2. Materials and Methods

2.1. Study Area

The study area was situated in the Knyszyn Forest (114 km²; NE Poland) which is characterized by a high degree of naturalness and in part is protected as a natural reserve [31]. This forest is also protected as an important breeding area for many bird species, including the Nightjar [28,32]. In the woodlands of Knyszyn Forest, the dominant stands are formed by the Scots pine *Pinus sylvestris* alone (71%) and mixed forests of Scots pine and Norway spruce *Picea abies* (11%) [31]. The average age of the tree stands is 57 years, and the dominant age ranges are 50–60 and 80–90 years. A large part of the natural forest communities in the Knyszyn Forest have been commercially replaced by planted stands, which has simplified the woodland structure, and intensive salvage cutting of spruce trees is commonplace [7]. The clearance of old forest stands is a serious threat to refuges [33].

2.2. Methods

The study was performed in 56 clearings (clear-felled areas, clear-fells) situated in the central part of the Knyszyn Forest (Figure 1). The average area of a clearing was 3.52 ha (SD = 1.412, range 0.42–11.51), and the total area of all 56 was 197.02 ha.
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All clearings were monitored three times in different sequences at intervals of about a month in the 2014 breeding season and only when the weather favored Nightjar activity (i.e., warm nights without rain or strong winds) [22]. Each survey was carried out by two experienced observers during 2–3 days. The first survey took place between 19 and 22 May and covered a total time of 12.45 h, the second was between 20 and 23 June (10.25 h) and the third between 9 and 15 July (10.50 h). The territory was considered occupied when a singing male Nightjar was detected there. Distinguishing simultaneously churring males enabled the actual number of occupied territories to be determined. To improve detection, the male’s churring song was usually played back twice a minute, with a listening interval also of one minute. When the birds were less active, between 23:00 and 01:00 h, the song was played back three times a minute, again followed by a one-minute listening interval. On the larger study plots, stimulation and listening took place at two sites about 500 m apart. The listening sessions were shorter in places where the Nightjars were active without our having to resort to playback or when the birds responded faster than the time anticipated for voice stimulation.

Apart from our nocturnal field surveys, we gathered relevant environmental data during daytime visits (i.e., edge lengths—the lengths of the edges of woodlands of different ages adjacent to the clearings—and the type of plant cover in the clearings). We divided the line of trees bordering a

Figure 1. The study area and the occurrence of Nightjars Caprimulgus europaeus.

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clearing into three age categories: young tree stands up to 40 years old, a middle age class (40–80 years old) and old stands (>80 years old). The vegetation growing in the clearing was classified on the basis of the surface area occupied by herbaceous plants. Coverage was deemed to be sparse (1) if plants were growing on 0%–33% of the clearing area, medium (2) if they were growing on 34%–67% of that area and dense (3) if 68%–100% of that area was covered by vegetation. The next categorical predictor was the presence or absence of seed trees, which are left in some clearings to provide seeds for natural regeneration [12]. Our analysis also took the area and the number of clearings in the neighborhood within a radius of 0.5 km into consideration. The age, area and type (clear-felling and patch-felling) of the monitored clearings were obtained from the State Forestry Administration. The Google Earth application [34] was used to estimate the distances from the center of an analyzed clearing to: (1) the nearest clearing, (2) the edge of dense forest area, (3) the nearest settlements and (4) the nearest roads. A total of 14 different habitat variables were examined (Table 1).

Table 1. Habitat variables taken into consideration for analyzing the choice of breeding territories by Nightjars *Caprimulgus europaeus*.

| Code   | Description                                           |
|--------|-------------------------------------------------------|
| AREA   | Area of monitored clearings (ha)                     |
| AGE    | Age of monitored clearings (year)                    |
| TYPE   | Type of clearings: clear-felling and patch-felling   |
| VEGETAT| Categories of undergrowth vegetation: sparse, medium and dense |
| SEEDTREE| Occurrence of the seed tree: present and absent       |
| CLEARNUMB | Number of clearings in radius of 0.5 km          |
| OLD    | Edge lengths of old forest (m)                       |
| MEDIUM | Edge lengths of medium age trees (m)                 |
| YOUNG  | Edge lengths of the young stands of the trees (m)    |
| TREEAGE| Average age of surrounding trees (year)               |
| DISCLEAR | Distance to nearest clearing (km)                  |
| DISROAD | Distance to nearest roads (km)                       |
| DISSETTL | Distance to nearest settlements (km)                |
| DISEDGE | Distance to forest edge (km)                         |

The influence of habitat variables on Nightjar occurrence was analyzed using general linear models (GLM) with a binary distribution and logit link function. Occupied territories (1) and unoccupied clearings (0) were treated as binomial dependent variables. Three habitat variables (type of clearing, type of undergrowth vegetation, occurrence of seed trees) were categorical predictors, while 11 other variables were continuous independent factors. The models were constructed using the glmer function in the lme4 package for R [35]. Model selection was performed using the information-theoretic approach proposed by Burnham and Anderson [36]. All possible combinations of the global model were analyzed using the dredge function in the MuMln package for R [37]. Only the models with the difference between the model and the best model in the data set by Akaike’s information criterion (ΔAICc) ≤ 2 are presented because they are treated as being equally supported [36]. Multiple competing models were assessed with regard to their fit to the data using AIC as the leading criterion, and the models with the lowest AIC value were selected as the best-fitting models. All data were analyzed in the R environment [38].

3. Results

Male nightjars were found at 17 sites (30.4% of all the monitored clearings). Fifty-five models containing 14 habitat predictors were created on the basis of Akaike’s information criterion (AIC), while seven models reached a value of ΔAICc ≤ 2 (Table 2). These models contained from three to five variables, but three predictors were the same in all seven models.
Table 2. Results of seven models describing the influence of habitat factors on Nightjar occurrence. Degrees of freedom (df), model log-likelihood (LL), corrected AIC criterion (AIC<sub>c</sub>), difference between the model and the best model in the data set (ΔAIC<sub>c</sub>) and weight for the model (AIC<sub>c</sub>wt) are shown.

| Model (Fixed Effects)                      | df | LL    | AIC<sub>c</sub> | ΔAIC<sub>c</sub> | AIC<sub>c</sub>wt |
|--------------------------------------------|----|-------|-----------------|-----------------|-------------------|
| CLEARNUMB + VEGETAT + YOUNG + OLD          | 6  | −14.245 | 42.2           | 0.00           | 0.019              |
| CLEARNUMB + VEGETAT + YOUNG + MEDIUM       | 6  | −14.521 | 42.8           | 0.55           | 0.014              |
| CLEARNUMB + VEGETAT + YOUNG + MEDIUM + OLD | 7  | −13.348 | 43.0           | 0.83           | 0.012              |
| CLEARNUMB + VEGETAT + YOUNG + OLD + TREEAGE| 7  | −13.376 | 43.1           | 0.88           | 0.012              |
| CLEARNUMB + VEGETAT + YOUNG + TREEAGE      | 6  | −14.726 | 43.2           | 0.96           | 0.011              |
| CLEARNUMB + VEGETAT + YOUNG                | 5  | −16.281 | 43.8           | 1.56           | 0.008              |
| CLEARNUMB + VEGETAT + YOUNG + OLD + DISEDGE| 7  | −13.824 | 44.0           | 1.78           | 0.008              |

The first model presented in Table 2 was selected as the best one describing the probability of a clearing being occupied, and it included four factors: the edge length of old forest, the edge length of young stands, the number of clearings in the neighborhood and the type of undergrowth vegetation (Table 3).

Table 3. Estimates of model coefficients for the best general linear models (GLM) of Nightjar occurrence.

| Parameters | Estimate | Standard Error | Z Value | p Value |
|------------|----------|----------------|---------|---------|
| Intercept  | 1.194    | 2.061          | 0.579   | 0.562   |
| OLD        | −0.004   | 0.003          | −1.589  | 0.112   |
| YOUNG      | 0.007    | 0.003          | 2.285   | 0.023   |
| CLEARNUMB  | 1.237    | 0.494          | 2.505   | 0.012   |
| VEGETAT: Medium | −4.127  | 2.085         | −1.979  | 0.048   |
| VEGETAT: Dense | −6.170  | 2.388         | −2.583  | 0.010   |

The GLM showed that the edge length of old forest did not influence the occurrence of Nightjars, but that the edge length of young stands of trees did have a positive effect (Figure 2).

Figure 2. Mean values (points) and 95% confidence limits (whiskers) of edge lengths of tree stands in three age categories bordering unoccupied clearings (open circles) and Nightjar territories (black circles).
The number of clearings within a radius of 0.5 km around the study plots increased the probability of a clearing being occupied. The plots occupied by Nightjars were surrounded by a greater number of clearings (mean = 1.8, SD = 1.29) than unoccupied ones (mean = 0.9, SD = 0.90). Breeding territories were also sparsely vegetated in comparison to unoccupied clearings (Figure 3).

Figure 3. Number of unoccupied clearings (grey columns) and Nightjar territories (black columns) in three categories of undergrowth vegetation.

On the other hand, medium and dense vegetation was more often found on plots without active males. The distribution of Nightjars was not influenced by the other six micro- and four macrohabitat factors.

4. Discussion

Our results revealed the importance of three habitat factors explaining the occurrence of Nightjars in their important refuge in the Knyszyn Forest. Although these findings come from a large coniferous complex in northeastern Poland, they are applicable in forest management for future conservation planning in other woodland areas in Europe. We found that Nightjars were more likely to colonize clearings with sparse vegetation and tended to avoid those with denser undergrowth. This is most probably related to the availability of nesting sites, as Nightjars often prefer dry, low-growth areas with sandy soil [22]. On the other hand, a certain amount of low vegetation in Nightjar territories is important, as it conceals birds nesting or roosting during the day. This is supported by two important findings from England: (1) the rate of flushing of Nightjars from their nests was related to the extent of nest cover and the height of vegetation around the nest, and (2) egg predation was one of the key causes of Nightjar nest failure [30].

The abundance of feeding grounds also appears to be related to the age of the tree stands surrounding the clearings. We found that a larger area of the young tree stands in close proximity to the clearings had a positive effect on Nightjar territory occupancy. This, however, contradicts some other results from Austria, where these birds preferred old tree stands in the immediate neighborhood of their nests, as this enabled them to perch on dead branches [27]. Our results partially correspond with those of Alexander and Cresswell [39], who found that, to increase hunting efficiency, Nightjars preferred younger tree stands instead of older tree stands. In Switzerland, too, birds usually foraged in and around oak thickets instead of in taller and older pine forests [40]. Nightjars preferred areas where hunting would be easier and more effective (young tree stands), even when they lay up to 2 km from
the breeding territory. At the same time, they ignored overgrown and hardly accessible forest areas, despite the greater abundance of potential victims [41].

It appears that the size and type of clearings occupied by birds may be important because these factors are associated with food richness and the occupation of larger areas elsewhere [16,20,25,27,42]. In our study, however, these habitat parameters did not affect Nightjar occurrence. We found that the number of clearings in the nearest neighborhood was of greater importance. This increased the hunting area, an aspect that may be as crucial as favorable conditions in the nesting territory. To hunt more efficiently, Nightjars can move to other clearings, thereby enlarging their foraging area [39].

Despite their expected impact, the macrohabitat factors analyzed here did not affect the occurrence of Nightjars within the study area. Because of the significant impact of anthropogenic factors on the abundance of these birds [30], we expected the distance to the nearest villages and roads to have an influence on the occurrence of this species. The presence of human settlements near areas inhabited by Nightjars means they will be more heavily used by people, dogs and cats, and such disturbances will affect the territorial occupancy of these birds [30]. In contrast, the study plots in the Knyszyn Forest were situated mostly quite far from places more frequently used by people, which explains the lack of such a relationship. Studies of the related Nubian Nightjar Caprimulgus nubicus showed that these birds efficiently caught their prey against the sky over roads, which they also used as a resting place, where they could digest their food [43]. Moreover, the warming up of tarred roads during the daytime increases the density of moths, which are preyed upon by Nightjars, so such places are attractive to them [43]. However, in the study area, the busier roads also lay well away from Nightjar territories; so they, too, were insignificant in regards to the occurrence of these birds.

5. Conclusions

In conclusion, forest management practices in large commercial coniferous woodlands promote the creation of breeding biotopes for Nightjars. Under optimum conditions, the territories occupied by Nightjars are sparsely vegetated, with numerous other clearings and stands of young trees in close proximity. Knowledge of these preferences may be very useful in forestry management planning as a compromise between an appropriate level of clear-felling and conservation of other bird species requiring preservation of old tree stands.

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