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Article

By the Moonlight Shadow: Examining the Acoustic Ecology of the European Nightjar (*Caprimulgus europaeus*) in Northern Greece Using Passive Acoustic Monitoring

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Simple Summary: The European Nightjar is a bird species integrated in European folklore and famous for its distinct vocalizations. It migrates from sub-Saharan Africa to Europe to breed in early spring. The species remains little studied in many parts of its range, with knowledge of its population status and behavior remaining limited. To examine the nightjar song activity in northern Greece, we deployed six acoustic sensors at two sites to record the species' acoustic ecology across an entire breeding season (April – October 2024). The main aim was to observe nightjar seasonal calling activity and possible variations in it, related to environmental conditions (i.e. phase of the moon, wind, temperature etc.). The results showed nightjar calls started in late April, peaking in June and continued with decreasing frequency until early September. All calls occurred during dusk, night and dawn, reaching highest rates before midnight, while calling intensity generally climaxed during the peak of the breading season. Humid, windless, moonlit, short nights with no rain had significantly more nightjar calls.

Abstract: The European Nightjar (*Caprimulgus europeaus*) is a Western Palearctic bird known in Europe for its distinct breeding vocalizations during summer nights. It migrates from sub-Saharan Africa, where it overwinters, to reach its breeding grounds in Greece around early to mid-April. Although nightjar ecology has been studied in some parts of its summer range (e.g. Great Britain, Belgium), the species remains largely unstudied in southeastern Europe. Our aim was to use passive acoustic monitoring (PAM) to study the seasonal and temporal calling activity of the species at two sites in northern Greece (Mt. Chortiatis) across an entire breeding season, examining whether variances in the daily calling frequency could be explained by environmental variables (wind, temperature, air humidity, precipitation, moon phase, cloud cover, night length). We deployed three AudioMoth acoustic sensors at each site, scheduled to record at a 48 KHz sampling rate for one out of every ten minutes, from 15/4/2024 to 12/10/2024. We used the BirdNet algorithm to detect the minutes with nightjar calls (recall rate 82%). The relation of environmental variables to the daily number of minutes containing nightjar calls was assessed using generalized mixed effect models (GLMMs). They are mostly consistent with previous studies on the calling activity of the species. Calling commenced in late April and continued with decreasing frequency until early September, with variations in onset and seasonal duration across sites. Most calls occurred after dusk and before dawn (nocturnal activity), with calls taking place throughout the night during peak calling period (mid-May – mid-June). Calling frequency was higher during humid, windless, moonlit nights without precipitation and shorter duration. The results provide a baseline against which to examine possible effects of climate change on the breeding behavior of Afro-Palearctic migrant bird species, and we therefore suggest that similar studies, ideally on a continental scale, should be conducted for more species, in order to detect early climate-induced ecological changes.

Keywords: Ecoacoustics, acoustic sensors, Caprimulgiformes, vocal activity

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1. Introduction

A key identification characteristic of most birds at the species level is their vocalizations, which can be used to defend territories, attract females, and share information (e.g. alert about predators, parent-offspring communication) [1]. Studying the species' vocalization is crucial in understanding species biology and ecology [2–4], breeding behaviors, dialects and other intraspecific interactions [1-5].

While direct observations remain an important method for studying bird vocalizations [2,3,5], passive acoustic monitoring (PAM), using unattended acoustic sensors deployed for days or months at a time, is increasingly recognized as a powerful alternative. This type of monitoring minimizes the level of disturbance caused by human presence, that can potentially affect observations during field surveys. By utilizing autonomous recording units (ARUs), it allows for larger scale studies, both temporally and spatially, through lowering the costs and time required for fieldwork [6-11]. Due to such characteristics, PAM has been proven to be an effective method for studying individual species, especially for cryptic [6,7], rare [8,10] or nocturnal species, as well as long term community monitoring [9,11].

The European Nightjar (*Caprimulgus europaeus*) is a species of the Western Palearctic well known for its distinct vocalizations during summer nights. Its breeding distribution ranges from Northwest Europe through to East Asia [12], with an overall decreasing trend in its European breeding populations [13]. Its habitat is characterized by dry heathland and woodland sites, since dry ground offering high drainage is important for the birds to lay eggs on. Some such habitats include Pine tree (*Pinaceae*) forests or plantations, deciduous forests with sparse tree cover, shrubland and meadows, with the species preferring mainly the edges between them, usually used for foraging on insects [14,15]. In the Mediterranean region, the species is noted to also prefer Kermes oak (*Quercus coccifera*) shrublands and Mediterranean maquis vegetation [15,16]. In late winter to early spring, European Nightjars migrate from their wintering grounds in sub-Saharan Africa to their breeding summer grounds in Europe, reaching the Mediterranean shores of Europe in mid to late April [17]. Males tend to arrive first [18], and after establishing their territory they start extensive vocal territorial displays to attract females [18]. The territories reach up to 32 hectares [15,19], though this number does vary between different studies and foraging range can be significantly larger[20]. Breeding occurs usually from May to September. After mating, nightjars nest on the ground where the female lays a clutch of 2 to 4 eggs. Their mating system is mostly described as monogamous and cooperative [19], although there are two cases where polygyny was detected [21]. A pair may raise two broods per season [22].

Overall, the species is understudied, with most existing studies focusing on migration patterns [23-25] and hunting activity patterns [20,26]. In southern Wales, the European Nightjar starts foraging after sunset following a crepuscular pattern (i.e. peaking in the night hours after dusk and before dawn) [27]. Its foraging sites may often differ from its roosting or nesting grounds, depending on food availability and ease of hunting at each area, although the distance between them varies and seems to affect its energy consumption. Its diet consists mainly of aerial insects such as Lepidoptera and Coleoptera [28].

Regarding the song, it holds two distinct syllable types, the major (series of high frequency trills) and the minor song (series of lower frequency trills) (Fig. 1). It is constant, pitch is relatively stable with subtle changes and ends with a terminal phrase [29,30]. The duration of the major and minor song is thought to be able to provide information that could be used to identify individuals based on their vocal output [29], and that some males produce different song types as the night progresses [30].

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It has been reported that in the western flyway European Nightjar presence, and consequently its vocal activity, is strongly related with night duration, moon phase, minimum temperature, and cloud cover [26,31,32]. Studies have shown similar effects of the moon phase or its illumination on the vocal activity of other members of the *Caprimulgiformes* family as well, such as the Little Nightjar (*Setopagis parvula*) and the Common pauraque (*Nyctidromus albicollis*) [33].

Studies examining species' spatiotemporal activity can provide valuable info, since the anticipated change in climate could potentially lead into a shift of arrival dates [34], changes on onset breed [35] and increase in the danger of diseases like avian influenza which can lead to devastating results [36]. Although studies have been done in Western and Northern Europe (Western Flyway), the Eastern Flyway and more specifically the Balkan peninsula remain extremely understudied. In Greece, where the European Nightjar is common and its call typical of early summer night soundscapes in rural areas, no study has examined the species' calling activity to date.

To address this gap in the literature, we decided to use PAM methods to study the calling activity of nightjars at two localities in northern Greece for the entire breeding season (late April – early October 2024). PAM methods have reportedly been a beneficial monitoring tool for vocal nocturnal species, mostly due to its ability to record continuously or in sampling intervals for extended periods of time [9, 26]. Based on previous studies of members of the *Caprimulgiformes* family, our main hypothesis is that calling activity of the European nightjar, during the mating season, would decrease with low temperature, high wind speed, and high precipitation, and increase with long nights and high moon illumination [9,26,31-33].

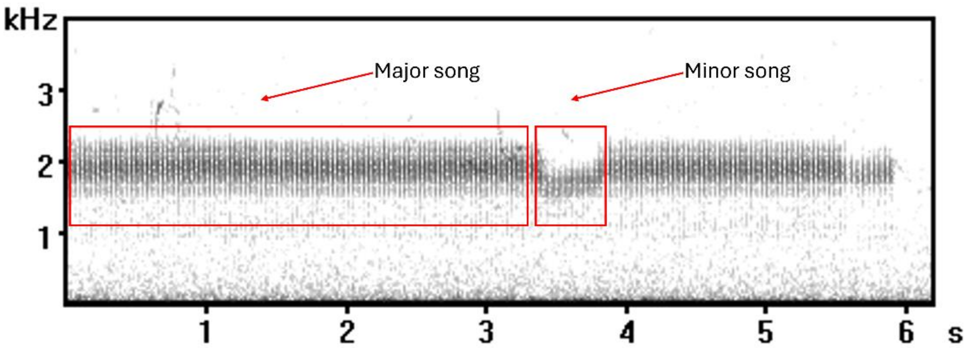

Figure 1. Part of a typical European Nightjar call containing both major and minor songs.

2. Materials and Methods

2.1. Study Sites and Fieldwork

We recorded nightjar calling activity at two sites in northern Greece, where the presence of the species was known due to previous pilot studies, and where elevation differs from one area to the other (Fig. 2). The first site (Kissos, 40.579265N, 23.090495E, 669 m) is an area announced to become a new settlement, but which remains undeveloped except for the delineation of roads (Fig. 3a). The vegetation is a natural meadow interspersed with *Q. coccifera* thickets. The second site (Ag. Vasileios 40.645358N, 23.083563E, 420m) has similar shrubland-meadow vegetation with higher percent cover of *Q. coccifera* thickets (Fig. 3b). The climate is typical of medium-elevation Mediterranean regions, with hot, dry summers and mild, wet winters [37]. In the studied areas for the year 2024 it was recorded 884 mm of annual precipitation and mean annual temperature of 17.45 °C.

At each site, we deployed three autonomous recording units (ARUs; Audiomoth v1.2 with official IPX7 case). ARUs were spaced at least 900 m apart (mean distance 1,125 m), which – based on earlier on-site observations – was sufficient to ensure that same calls were not recorded in two or more sensors. According to some studies, the radius of a nightjar's song territory reaches approximately 200 m [15]. The ARUs were scheduled to record at 48 kHz sampling rate, with medium gain, for one out of every ten minutes around the clock from April 15 to October 12, 2024. This specific scheduling was selected as a compromise between ideally continuous recording and project logistics. The SD cards (32 GB) and Lithium/Iron Disulfide AA (L91) batteries were replaced every 35 days. All

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ARUs were deployed on trees of the species *Q. coccifera*, at breast height (approx. 1.30 m), and near roads.

Since the European Nightjar is a species with territory stability [15], we assumed that the calls at each sensor represent mostly the calling activity of a single male for an entire breeding season.

2.2. Acoustic Analysis

We used the BirdNet-Analyzer v2.4 [38], accessed via Cornell University's Raven Pro 1.6.5 acoustic analysis software (Learning Detector tool), to automatically detect European nightjar mating calls. Based on the examination of all data from five days per sensor, we selected a 0.1 threshold for our analysis as it detected at least one true-positive call segment in most 1-min audio files manually confirmed to contain a nightjar call (mean sensor "sensitivity" or "recall rate" 82%; defined as true positive / (true positive + false negative) detections [39]). All putative calls were manually reviewed to remove false positives. Since multiple segments of a single call could be tagged by the detector, we did not use the count of calls per file as a metric of nightjar calling activity. Instead, we identified 1-min files as having or not at least one true positive detection. Considering that only one minute was recorded in each 10-min interval, the maximum calling rate per hour could not exceed six one-minutes intervals.

2.2. Statistical Analyses

To assess the potential effect of environmental variables on the European Nightjar's calling activity, we used the proportion of 1-minute acoustic files in each day (n = 144) that contained calls as a metric of calling activity. Since the proportions were not normally distributed (Shapiro-Wilk test < 0.05) and the number of days with zero detections was high, we developed Tweedie generalized linear mixed effect models in R (glmmTMB [40]) with night duration (the number of hours between sunset and sunrise), temperature (min, max, and mean (°C)), precipitation (mm), humidity (%), dew (°C), moon phase (%), moon illumination (moon phase * proportion of night with moon above the horizon [41], locality, windspeed (km/h), wind gust and cloud cover (%) as predictive variables, and site (acoustic sensor) as a nested random effect (fixed slope, random intercept). Weather data were obtained from the closest available weather station at the city of Thessaloniki (southeast foothills of Mt. Hortiates) (elevation 230 m), which was located 11 km southeast of the study area.

To decide on which variables to include in the final model, while also managing model complexity, we first examined support for inclusion of each variable in a baseline model having as fixed parameters only the intercept and night duration, which is well documented to be a good predictor of nightjar calling activity [31]. Model selection was based on the Akaike Information Criterion (AIC) [42]. Variables included in models with AIC lower than the baseline model were further considered. To exclude possible multicollinearities among variables, we kept from each pair of correlated variables ($r > 0.65$) the one with the lower AIC value from the previous model comparison. We used the final set of fixed variables to run all possible multivariate combinations (R package MuMIn:dredge; [43]), using AIC again for model selection. Since multiple models have $\Delta AIC<2$, a threshold often used to identify competing best models, we calculated the model average coefficients of variables from these top models using MuMIn:mod.avg. The goodness of fit of the global model was assessed using the pseudo-R^2 [43]. All analyses were conducted in R software (v4.4.1) [40,44].

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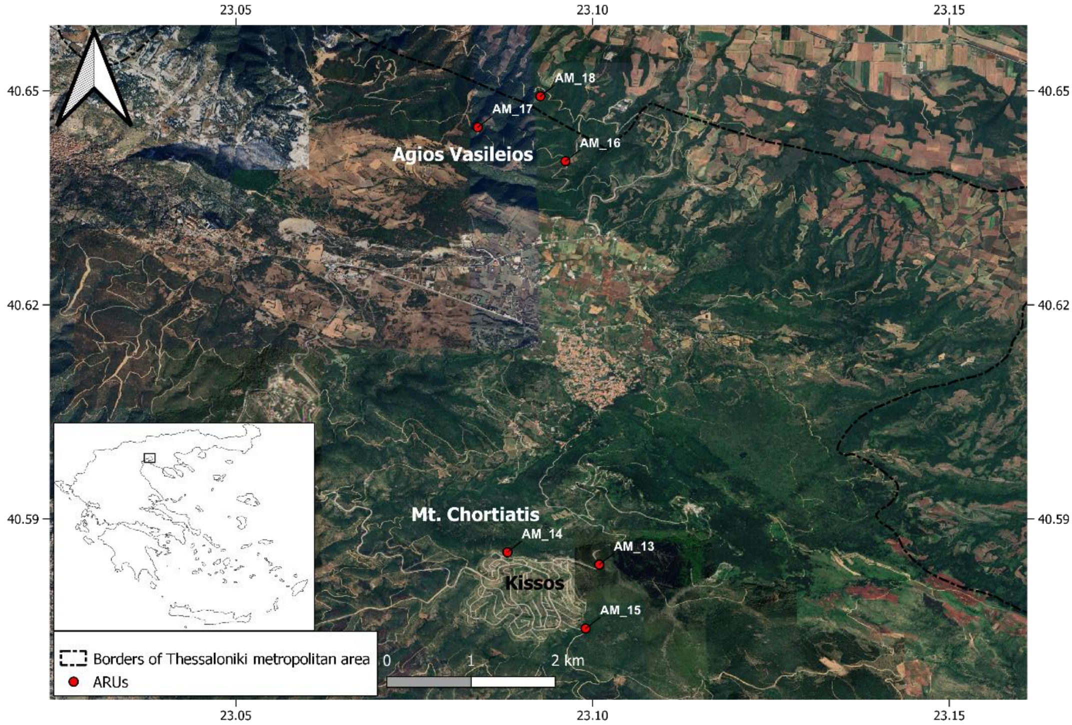

Figure 2. Map of the study area.

3. Results

All six sensors operated for 180 days (April 15 – Oct 12). In total, 39,373 sound clips were reviewed, resulting in nightjars being detected in 2,914 of the 1-min acoustic files recorded (1.9%; n = 155,520) across all sensors (range 137 – 857 files) (Table 1). The days with nightjar calling activity (i.e. ≥ 1 file with calls) ranged from 58 to 112 per sensor (mean 88 ± 22.8 SD) (Table 1). Overall calling activity across the two sites was similar (Kissos: 1,360 files; Agios Vasileios: 1,554 files), with each having a sensor with low (100 - 200), medium (500-550) and high (> 700) count of files with nightjar calls.

The recall rate of the BirdNet algorithm (0.1 threshold) of 1-min files containing nightjar calls ranged from 71 – 91.3% per sensor (mean 82%), based on the manual review of 4,320 files (five days from each sensor) containing 326 files with calls (Table 2).

Table 1. Nightjar detection frequency per sensor during the study period (15/4 – 12/10/2024). All sensors recorded all days (n = 180). Number of 1-min files per day is 144 (one every ten minutes).

Site	Sensor	Algorithm detections	1-min files with nightjar calls	Days with calls	Mean number 1-min files with calls per day (excl. inactive days)
	AM13	6,527	523	95	5.50
Kissos	AM14	3,939	700	104	6.73
	AM15	2,888	137	58	2.36
	AM16	6,064	505	98	5.15
Ag. Vasileios	AM17	15,173	857	112	7.65
	AM18	4,782	192	61	3.14

Table 2. Detections with Raven pro learning detector vs hand browsed and the recall rate of the algorithm, calculated at five (different) days for each sensor.

Sensor	Date	Learning Detector	visual browsing	Recall Rate %
AM13	1 - 5/7/2024	17	19	89.5
AM14	12 - 16/6/2024	46	62	74.2
AM15	3 - 7/6/2024	21	23	91.3
AM16	20 - 24/5/2024	76	107	71.0
AM17	7 - 11/5/2024	69	77	89.6
AM18	29/6- 3/7/2024	29	38	76.3

Nightjar calls were first detected, sporadically, in Agios Vasileios (sensors AM16, AM17) in late April, with calling activity subsequently peaking in most sensors between mid-May and mid-June (Fig. 4). Calls continued throughout July, with the calling frequency dropping rapidly after mid-August, and stopping altogether by early September.

Most calling occurs after dusk and before dawn, reaching their pick near midnight (nocturnal activity), with calls taking place throughout the night during peak calling period. Practically no calls were recorded during daytime (Fig. 4). There was very little variation in the diel calling activity pattern of all sensors at seasonal level (Fig. A2).

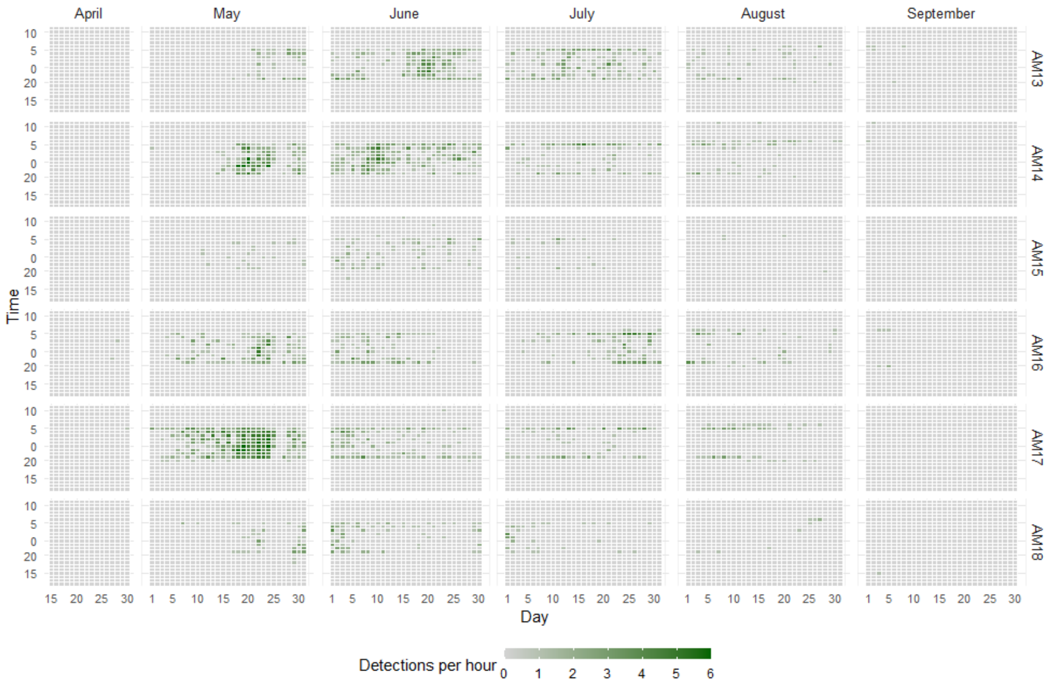

Figure 3. Distribution and count of 1-min audio files containing European Nightjar (*Caprimulgus Europaeus*) mating calls per hour, day, month, and acoustic sensor. Since the sensors only recorded 1 min out of each 10-min period, the maximum count of files with calls per hour is six. October is omitted from the graph since no calls were recorded then.

The percentage of night-time 1-min files containing nightjar calls during different quarters of the moon phase (1st, 2nd, 3rd and Full Moon) varied significantly across sensors (Fig. 4). Moon phase (as percent illuminated; 0-1 range) was included in the final model of nightjar calling activity, having a significant positive effect (Table 3). In general, the model showed that nightjar calling activity was higher during humid, moonlit, shorter nights without precipitation. Temperature (minimum), when included in the multivariate model, did not have a significant effect on nightjar calling activity.

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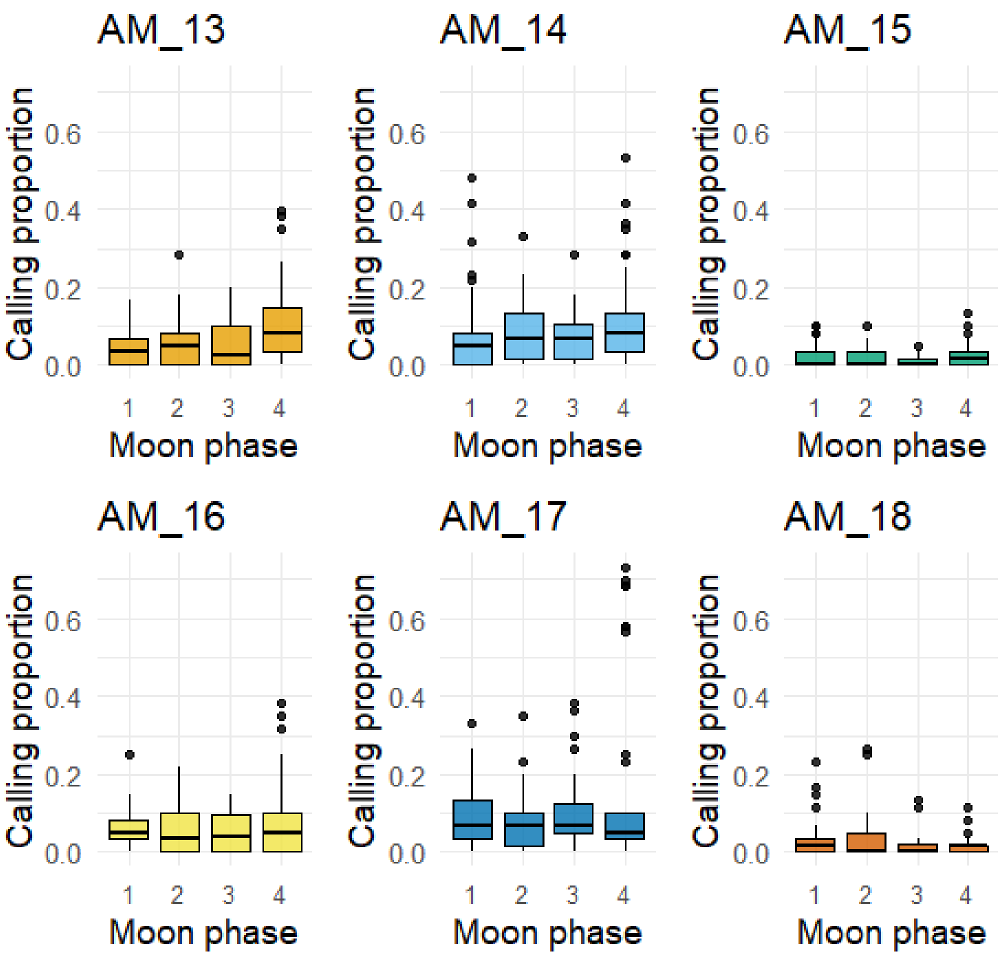

Figure 4. Box plots of proportion of night 1-min files containing at least one nightjar mating call, (May – August). Moon phase: *(1) First quarter of the moon, (2) Second quarter of the moon, (3) Third quarter of the moon, (4) Full moon*.

Table 3. Estimates and significance of the fixed effect variables predicting European Nightjar mating calling activity, as measured in number of 1-min files with calls per day per sensor. [*AIC*: - 1665.5, pseudo-R^2 (conditional) = 0.817 (marginal) = 0.711; generalized linear mixed effect model with sensor as a random effect (intercept only)].

Variable	Estimate	Std. Error	Adjusted SE	Z-value	Lower 95 % CI	Lower 95 % CI	Pr(>|z|)
(Intercept)	10.293	0.782	0.783	13.141	8.760	11.825	< 0.001 ***
Humidity	3.133	0.511	0.512	6.122	2.131	4.134	< 0.001 ***
Moon Phase	0.265	0.107	0.107	2.474	0.055	0.474	0.013 *
Precipitation	- 1.761	0.400	0.400	4.401	- 2.545	- 0.977	< 0.001 ***
Wind gust	- 0.342	0.312	0.313	1.095	- 0.953	0.270	0.274
Night duration	- 40.935	1.837	1.839	22.254	- 44.535	- 37.334	< 0.001 ***
Temperature (Min)	- 0.021	0.114	0.114	0.185	- 0.244	0.202	0.853

4. Discussion

Our findings describe the calling activity of the European Nightjar (*Caprimulgus europaeus*) throughout an entire breeding period (April – October) at two sites in northern Greece. The original

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hypothesis, namely that calling activity would be lower during days with high wind and precipitation and higher during days with increased proportion of the moon illuminated, is supported by the results.

Night duration was found to be the single most informative parameter affecting (negatively) nightjar calling activity, which is not surprising since night duration is shorter during late spring and summer, when breeding takes place. With the available data, we are unable to infer whether shorter nights trigger breeding behavior in the species or not. The reported effect of night duration and moon phase on the calling activity of Caprimulgiformes species has been reported before [26,31-33,45]. The effect of moon phase however is not universal, as it has no effect in the calling activity of the red-necked nightjar (*Caprimulgus ruficollis*) [46].

While a previous study by Reino et al. [31] reported lower European nightjar calling activity during cooler, cloudy nights, our results did not find such a relationship. The cloud cover was not informative enough to be included in the final set of explanatory variables (averaged model) and minimum temperature had a weak and non-significant effect.

Our finding that precipitation negatively affected nightjar calling activity is not surprising, as this relationship has been reported for birds before [47]. However, our study is the first – to our knowledge – to document this effect for the European nightjar. Unlike precipitation though, air humidity was significantly positively related to nightjar calling activity. Given that sound travels further in humid air [48], the relationship observed may reflect increased detection range by the acoustic sensors of nightjar calls and/or an actual behavioral change by the species to capitalize on this physical effect. Other species are known to benefit from this phenomenon, like those of the *Apterygidae* family [49].

Regarding the timing of the European Nightjar's spring migrationour findings are in agreement with previous studies which reported mid to late April arrival of the species in the Mediterranean regions of southern Europe [17-19].

One potential limitation of the study is its non-continuous recording schedule, dictated by technical limitations of the acoustic sensor used – namely the maximum recording duration possible with the provided battery pack. Ideally, a continuous recording would provide higher temporal resolution on nightjar calling activity variations. The fact that the species calls often and for extended periods of time during the night makes us believe that the resolution lost is not such that would affect our conclusions. However, future studies could – at least at some recording stations – compare the impact of our recording schedule against that of a continuous one. In general, given the increased analytical effort required for continuous recordings, the recommendation of PAM protocols for birds is often to record around the clock with a given interval (similar to what we have done) [50]. Although there are studies supporting PAM as a good practice for monitoring Nightjars, there's criticism by others. According to the findings of Zwart et al. [51], ARUs were found to be better at detecting nightjar calls than traditional human surveys. But in study of Eisenring et al. [52]hey were found to perform insufficiently. Another limitation of our study is the distance between the study sites and the meteorological station. As mentioned in the "materials and methods" chapter, data were obtained from the closest available weather station with continuous recordings. Although these measurements might not capture microclimatic differences between the exact locations, we believe that they adequately represent the regional weather patterns in which this study focuses, as is done in other similar studies [9].

5. Conclusions

The findings of the study are mostly consistent with previous studies on the calling activity of the European Nightjar during summer breeding season. While small in spatial scale, the study is the first of its kind for the species in the Balkan peninsula, included data from an entire breeding season, and showcases the value of passive acoustic monitoring (PAM) as a tool for effectively studying the behavior of cryptic/nocturnal species such as the European Nightjar. The results also serve as a baseline against which to examine possible effects of climate change on the breeding behavior of Afro-Palearctic migrant bird species (e.g. onset, duration, response to changes in environmental variables) in the future. We propose that similar studies, across a larger – ideally continental - scale,

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are conducted across a range of species to provide early warning of climate-induced ecological changes. To achieve this, we propose that national level PAM grids are developed across Europe, following the example of the Australian Acoustic Observatory [53], with recording and analysis protocols being coordinated at EU level. Given the high spatiotemporal resolution provided by PAM, the decreasing costs of deploying and operating PAM grids, and the increasingly automated analysis of the datasets (e.g. using algorithms such as BirdNet), we believe that developing an EU-wide acoustic observatory is primarily an issue of coordination, collaboration and political priority settings, and less of funding limitations.

Author Contributions: Conceptualization, D.T., C.A. and E.N.; methodology, D.T. and C.A.; software, D.T. and A.R.; validation, D.T., A.R., E.N., A.K., T.P. and C.A.; formal analysis, D.T. and A.R.; investigation, D.T., C.A. and T.P.; resources, C.A.; data curation, D.T. and A.R.; writing—original draft preparation, D.T. and C.A.; writing—review and editing, D.T., A.R., E.N., A.K., T.P. and C.A.; visualization, D.T.; supervision, C.A. and TP ; project administration, D.T. and C.A.; funding acquisition, C.A.; All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Appendix A

(**a**) (**b**)

Figure A1. Representative landscape photographs of the two studied areas: (**a**) Kissos; (**b**) Agios Vasileios.

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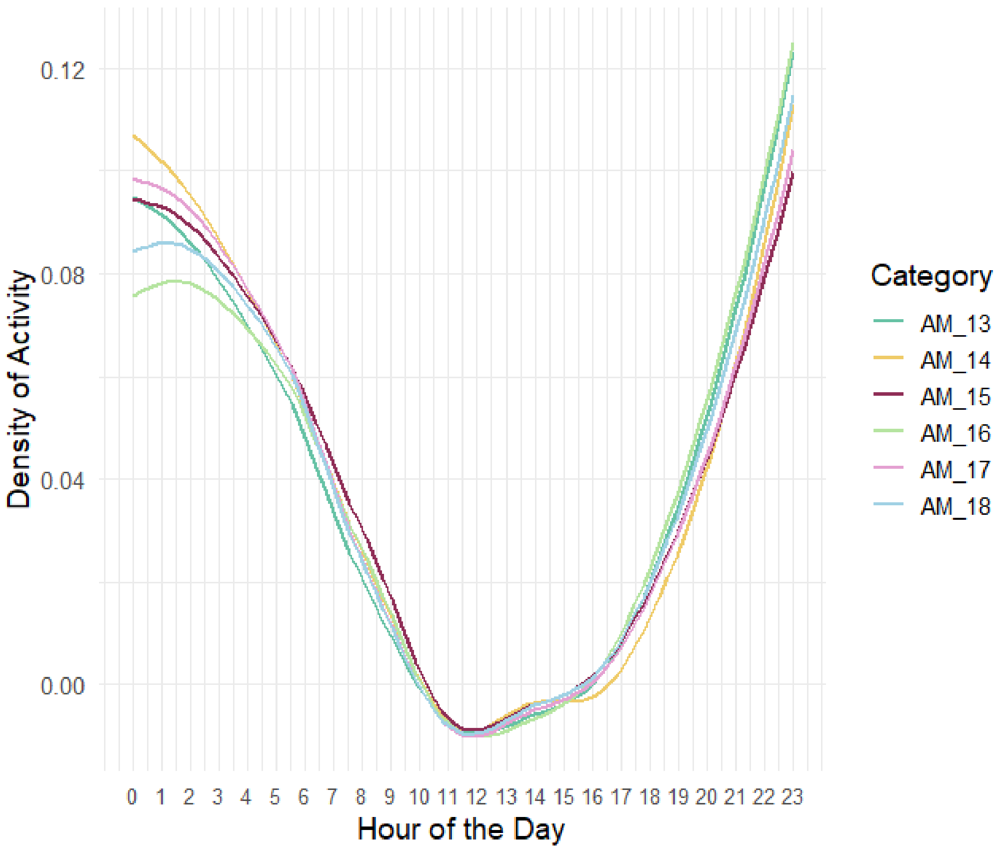

Figure A2. Hourly distribution of 1-min files containing European Nightjar calls per sensor, for the duration of the study period.

Table A1. Akaike Information Criterion based model selection of univariable models and baseline model (daily proportion of activity ~ Night duration + (1|Sensor)) used to identify informative variables which were subsequently considered in multivariable models.

Model	AIC score	ΔAIC score
Humidity	- 1635.716	0
Temperature Min	- 1622.213	13.503
Temperature Mean	- 1620.230	15.486
Wind gust	- 1616.328	19.388
Moon Phase	- 1614.372	21.345
Temperature Max	- 1614.227	21.489
Precipitation	- 1609.066	26.650
Illuminocity index	- 1608.762	26.954
Cloud cover	- 1608.300	27.416
Baseline model	- 1607.721	27.995
Windspeed	- 1606.082	29.634
Locality	- 1605.890	29.826
Dew	- 1605.741	29.975

Table A2. Monthly detections per locality and sensor. .

Sensor	April	May	June	July	August	September	October
Kissos:							
AM13	0	56	232	181	49	5	0

AM14	0	215	314	105	64	2	0
AM15	0	23	88	22	4	0	0
Ag. Vasileios:	2	179	110	149	59	6	0
AM16	1	552	152	90	62	0	0
AM17 AM18	0	56	89	37	9	1	0

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