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Influence of moonlight on nightjars' vocal activity: a guideline for nightjar surveys in Europe

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Abstract: Strictly nocturnal or crepuscular habits on birds are restricted to a very limited number of species such as nightjars. Physiological skills of these species combined with ecological and behavioural adaptations provide them the ability to colonise a less competitive niche. Nightjars' nocturnal ecological adaptations have been largely neglected on bird survey methods, which can bias the obtained results. Here, we studied the factors affecting vocal activity of two nightjar species, red-necked nightjar *Caprimulgus ruficollis* and European nightjar *C. europaeus* in a Mediterranean area of southern Portugal by modelling observed vocal activity of both species as a function of astronomic variables, particularly moon phase and day of the year. Red-necked nightjar vocal behaviour was positively associated with brighter moon phases and springtime, whereas European nightjar was only influenced by the season, being more active in the summer. This reveals the importance of light conditions on vocal activity of the former species. We suggest that specifically designed field surveys for these species should be preferentially conducted during brighter nights, when the lunar cycle is close to full moon. Furthermore, positive contacts with birds are maximized from late spring to early summer, at least for the red-necked nightjar.

Key words: *Caprimulgus*; nocturnal activity; bird census at night; mixed models

Introduction

Activity at night is rare among birds, and only less than 3% of the world's bird species adopted a strictly nocturnal habit in which all aspects of the life cycle are completed between dusk and dawn (Martin 1990). Physiological, ecological and behavioural adaptations have provided for these species the ability to colonize a less competitive niche.

Overall birds' activity patterns are poorly understood during true night, when moonlight is the primary source of illumination (Woods & Brigham 2008), and artificial light sources are scarce. Effects of different lunar conditions on birds behaviour are not universal and increasing activity by other animal species is often associated with full moon and bright sky, probably because visual constraints are limited during those periods (Woods & Brigham 2008 and references therein).

Caprimulgiformes (nightjars) are nocturnal and/or crepuscular birds, and probably most species are essentially visually guided insectivorous for whom ambient light levels represent a constraint on foraging opportunity and prey detection (Cleere & Nurney 1998; Cleere 1999). Monitoring nightjars is always challenging not just because of the usual difficulties in studying nocturnal birds, but also because setting up a census scheme valid for ecological studies is difficult to achieve. These issues call for the need to implement better surveying techniques, which should be designed taking into account the nightjars' species biology.

Here, we assessed the influence of moonlight and other factors on vocal activity of the two European nightjars' species, focusing on an area where both birds occur during the breeding season. The European nightjar (*Caprimulgus europaeus* L., 1758) has a widespread Palearctic breeding range and the red-necked nightjar (*C. ruficollis* Temminck, 1820) has a mainly Mediterranean-restricted range in Iberia and northern Africa (Cramp 1985; Cleere & Nurney 1998). Particularly, we evaluated the association of nightjars' vocal behaviour with a set of astronomic variables that could potentially affect the vocal activity of both species, in order to provide useful information for more effective nightjar census in Europe.

Methods

Study area

The study was conducted in southern Portugal, comprising an area with about 700 ha, most of it within the Tagus Estuary Special Protection Area in the vicinity of the Tagus Estuary Natural Reserve (38°48′ N, 8°52′ W, 10–40 m a.s.l.). Climate is Mediterranean. Landscape combines a complex mosaic of farmland, agro-forest and forest habitats that allows both nightjars species to occur in the area. Generally, red-necked nightjars are more associ-

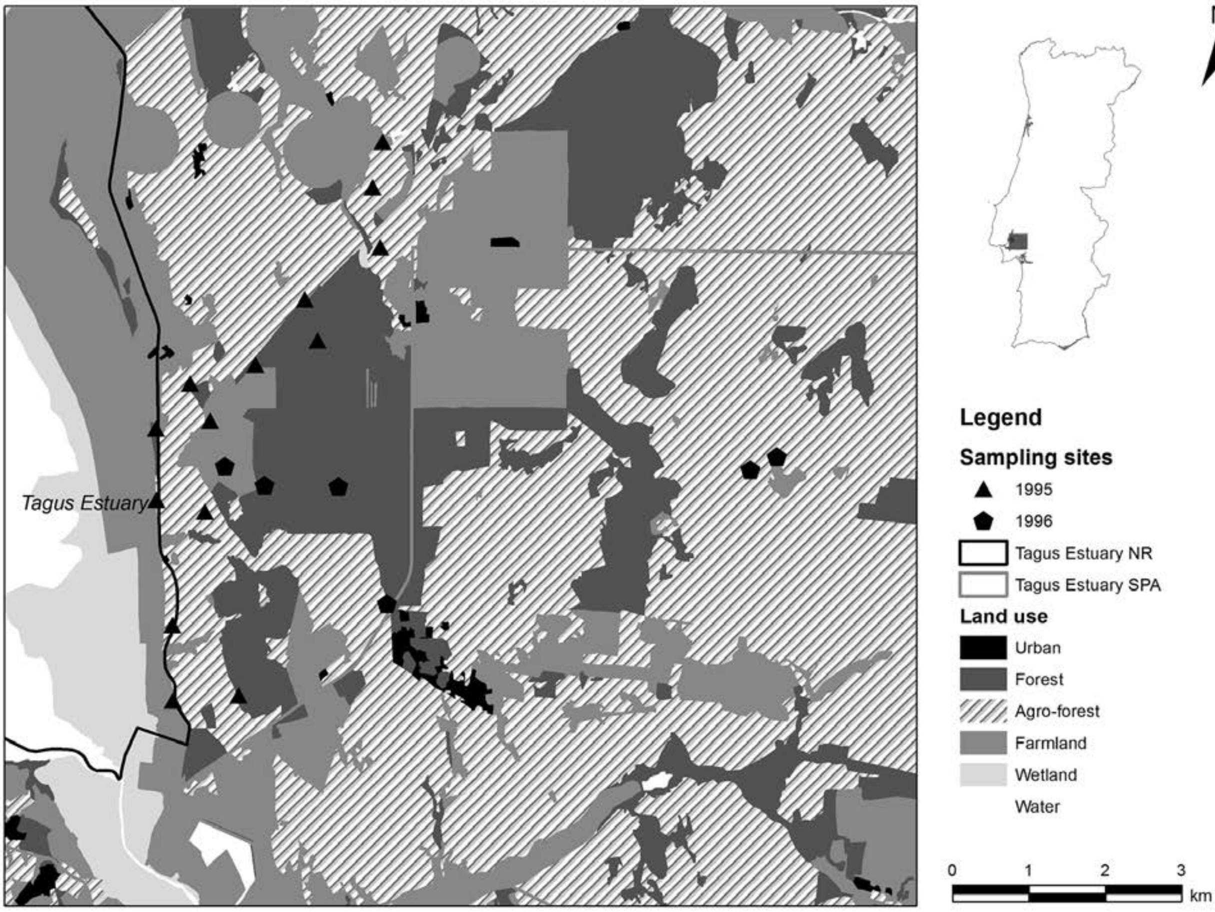

Fig. 1. Study area with the sampling point counts in 1995 and 1996, within the Tagus Estuary Natural Reserve (NR) and Tagus Estuary Special Protection Area, southern Portugal.

ated with Mediterranean habitats, including farmland and agro-forest systems, whereas European nightjars were more often associated with forest systems (Equipa Atlas 2008). Most of the agro-forest systems in the area are comprised of montado-like, i.e., savannah-like agro-forest structures dominated by cork oak trees (*Quercus suber*), sometimes mixed with umbrella pines (*Pinus pinea*) that occasionally form small scattered pinewoods. Forest areas are dominated by plantations of eucalyptus (*Eucalyptus* spp.) and maritime pine (*P. pinaster)* (Fig. 1).

Study design

The study was conducted in 20 sampling points distributed across the study area and visited in two different periods, 14 points in 1995 and six points in 1996. The small sampling size was mainly due to logistic difficulties in accessing the area during the night, because several areas in the region were private land or military areas with restricted access. Points were selected according to a stratified random procedure within farmland (six), agro-forest (eight) and forest (six) habitats in order to cover breeding habitats of both nightjars' species occurring in the area. Random locations were distributed at >500 m from each other (mean distance between points (m) = 734.9 ± 265.2) in homogeneous habitats within 200 m radius or with two habitats with equal representation. Random locations difficult to access by foot (>10 min walking from the next road or track) were excluded (Silva et al. 1996).

Bird sampling

Nightjar surveys involved repeated visits to each point (mean visits per point = 6.9, min–max = 4–9) with a total of 138 visits over a period of four months (from 4 April to 28 July) in both years (104 visits in 1995 and 34 in 1996). Bird surveys were made after sunset (between 21h30 and 2h00) by two experienced observers (LR and TS), and were carried out in general with good weather condition (without rain and moderate to strong wind). Birds were vocally detected during 12 minutes at each point-count. We considered territorial vocalization of both male and females of red-necked nightjar, but only male territorial vocalizations of European nightjar were considered (see Cleere 1999). Typical territorial vocalizations are produced by repeating identical notes in long and rapid series, which is common to many Caprimulgidae species (Cleere 1999). To solicit vocalizations, both species playback territorial vocalisations were used. Playback vocalizations are widely used methodology for sampling both nocturnal birds (e.g., Skoruppa et al. 2009), and Caprimulgiformes in particular (Vilella & Zwank 1993; Woods & Brigham 2008), by helping the detection, particularly in forest habitats. Therefore, paybacks may offer a powerful tool for studying Caprimulgiformes (Holyoak 2001), besides some concerns raised by some authors (e.g., Conway et al. 2007). In this study, we used the following playback protocol: 3 min of silence; 6 min of both species territorial vocalizations (set of two times repeated sequence

Table 1. Variables considered for modelling the nightjars' vocal activity in two consecutive years (1995–1996).

Variables	Description
Day duration	Cosine of the number of days past the winter solstice divided by 365 and scaled to 0–2π
Before/After summer solstice	Binary variable
Moon fraction[1]	Cosine of the illuminated fraction of the moon, scaled to 0–π
Before/After full moon[1]	Binary variable
Minutes after sunset	Time elapsed past sunset
Cloud cover	Percentage of cloud cover
Light level	Compound index calculated from visible moon phase and percentage cloud cover (Table 2)
Minimum temperature	Daily minimum temperature recorded at the date of the census, in ℃
Presence of *C. ruficollis*	Presence of *C. ruficollis.* Binary variable
Presence of *C. europaeus*	Presence of *C. europaeus.* Binary variable
Insolation[2]	Number of hours of sunlight in the sampling day per year, hour

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with 30 s of European nightjar territorial vocalizations, 30 s of silence, 30 s of red-necked nightjar territorial vocalizations and 30 s of silence); and finally 3 min of silence.

Data analyses

To model the vocal activity of each species of nightjar, we started with a set of astronomic and local site variables (Table 1), including the presence of the other species to account for possible species-site exclusion, and the time of sampling relative to sunset, as it is known to be important in nightjar detection.

Astronomic variables included the lunar stage within its cycle, described by the sine and cosine (Nelson et al. 1979; Bingham et al. 1982). The cosine was proportional to the illuminated fraction of the moon and was used as is, while the sine was classified into a binary variable, which indicated whether the moon was in waxing or waning phase. The purpose was to eliminate the correlation with the cosine, while maintaining the non-redundant information provided. We also included two variables describing the earth stage within the year cycle, applying the same procedure as for the lunar stage. In this case, the cosine was proportional to the duration of the day and the sine was classified so that censuses before and after the summer solstice were told apart.

Local site variables included a visual field estimation of cloud cover, insolation, minimum temperature and a compound index estimating the light levels at the moment of sampling. Details of calculations are provided in Table 1.

For each species, we started by adjusting univariate generalized linear mixed models with a Poisson error distribution and a log-link function to test changes in abundance of vocalizing birds (dependent variable) at random point counts in relation to each variable alone (Pinheiro & Bates 2000). This approach enabled us to account for the lack of independence in the data due to repeated counts at each site (e.g., Pinheiro & Bates 2000; Zuur et al. 2009; Reino et al. 2009).

From the full set of variables and for each species, we started by excluding those that were not significantly related to each species' vocal activity in the univariate models (at a 5% level of significance). Secondly, because light level was, by construction, dependent on moon fraction and cloud cover, to avoid collinearity in the next stage we only retained light level in the reduced set of variables because it had a higher explanatory power than its components. Lastly, a pairwise Pearson correlation matrix was computed to ensure that no variables with a correlation (in absolute value) higher than 0.40 were included in the next stage.

Table 2. Empirical index of illumination based on visible moon phase and cloud cover (%).

Visible Moon Phase	Cloud Cover			
	(0–25)	(26–50)	(51–75)	(76–100)
New Moon	1	1	1	1
Waxing Gibbous	3	2	1	1
Full Moon	4	3	2	1

With the reduced variable set, we undertook an Information Theoretical Approach (ITA; Burnham & Anderson 2002) by adjusting models corresponding to all possible alternative hypotheses with the available variables concerning the nightjars' vocal activity patterns. For each set of alternative candidate hypotheses (different for each species), we computed the Akaike Information Criterion (AIC) of each model and their respective Akaike weights (w_i). Akaike weights are estimates of the probabilities that each model is the best of those considered (Burnham & Anderson 2002). Weights were then used to compute the average model coefficients for all variables. We opted to base our study on the average model rather than the most likely model because there was no candidate model clearly better than the others.

All models were fitted in the R 3.1.0 software (R Core Team 2014) using the 'lmer' function of the lme4 package (Bates et al. 2014). Model averaging and associated computations were undertaken with the MuMIn package (Bartoń 2014).

Results

Red-necked nightjar was the most abundant species, with 121 responding males and females (0–3 birds per visit, Fig. 2) in 90% of the sites. European nightjars occurred in 50% of the sites, with 39 males responding (0–2 birds per visit, Fig. 2).

The average model for the red-necked nightjars (Table 3) suggested a strong influence of the light level on vocalizations, being these more frequent in more illuminated nights, and also a weak negative effect of Insolation. These effects were consistent with the best fitting model ($AIC_{wi} = 0.11$, results not shown). The

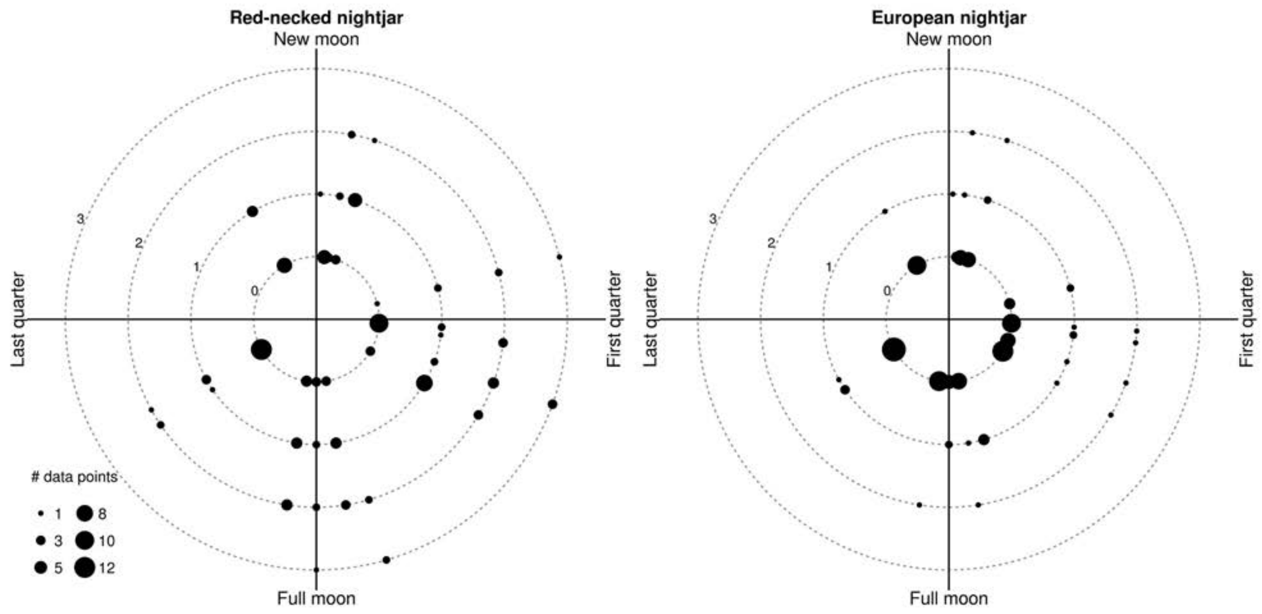

Fig. 2. *Caprimulgus ruficollis* and *C. europaeus* abundance as function of the moon phase. The size of the circles is proportional to the number of stacked data points; abundance scale (counts) corresponds to the concentric circles.

Table 3. Average model coefficients obtained from mixed effects count regression models for the reduced set of variables, and respective 95% confidence intervals. Underlined values denote estimates whose confidence interval does not include the zero (bold type) or only marginally includes zero.

Variables	*Caprimulgus ruficollis*	*Caprimulgus europaeus*
Intercept	**–1.23 (–2.44, –0.03)**	**–3.02 (–4.34, –1.70)**
Light level	**0.56 (0.38, 0.75)**	0.16 (–0.25, 0.58)
Day duration	–0.35 (–1.69, 1.00)	
Before/After summer solstice*	0.24 (–0.32, 0.80)	
Before/After full moon*	0.10 (–0.38, 0.58)	0.72 (–0.14, 1.59)
Presence of *C. ruficollis*		0.83 (–0.14, 1.80)
Presence of *C. europaeus*	0.30 (–0.11, 0.71)	
Insolation	–0.06 (–0.12, 0.01)	

Explanations: *positive coefficients mean a positive association with before solstice/full moon.

effect of light was far stronger than that of its two component variables on which it depended, i.e., Moon fraction and Cloud cover (results not shown). Also, including Light level in the variable set used for model selection largely invalidated the effects of all other variables which were important when Light level was not included (results not shown).

Contrariwise, the European nightjar showed very weak correlations with all variables, including Light level (plot not shown). Despite that, results suggest that the presence of the congeneric species seemed to increase vocalization frequency, and that the species tended to be more active before the full moon.

The time elapsed after sunset and minimum temperature did not have any effect on the activity of both nightjars, hence were not included in the model selection stage.

Discussion

This study suggested the importance of brighter nights in Caprimulgiformes, mainly in the vocal activity of red-necked nightjar. Mills (1986) suggested that *Caprimulgus* species are 'lunarphilic', meaning that they are mainly restricted to foraging during crepuscular periods of the night with moonlight. The association with brighter nights are the direct result of the lunar cycle influence in the vocal activity and this influence has been widely reported in other studies not only in the calling behaviour, but also in foraging activity and laying date of different species of Caprimulgiformes (e.g., Perrins & Crick 1996; Cleere & Nurney 1998; Woods & Brigham 2008). Results for European nightjars were inconclusive in respect to the influence of light level. However, this outcome should be regarded with caution, mainly because this species is scarcer in the study area, being more difficult to detect because it inhabits areas with higher density of trees, often dominated by eucalyptus and pinewood forests.

Interpretation of these results, however, requires due consideration of a number of factors, including the study design and the use of playbacks. The non-significant relation found between time after sunset and nightjar's activity may be surprising due to the known increased vocal activity of European nightjars around the hours of dusk and dawn (e.g., Zwart et al. 2014). These results may be explained because most of the counts were conducted during the first night hours with considerable few point counts after midnight, which probably hindered the detection of the effect of this variable. Besides more recent technological developments pointing to the importance of automated acoustic monitoring of bird populations (e.g., Brandes 2008; Bardeli et al. 2010; Zwart et al. 2014) at different scales, we advocate the importance of empirical and experimental studies like this study, though these studies may be improved by the combination of both approaches.

Implications for nightjars monitoring

Censuses of nightjar species have the constraint of being conducted primarily during crepuscular periods or at night when light conditions are generally poor. To minimize the possible effect of this constraint on the quality of data collected we suggest conducting nightjar field surveys on brighter nights, when the lunar cycle is around or close to full moon and the sky is clear, which may maximize positive contacts. This was particular evident for red-necked nightjars, but is likely to apply also to European nightjars, although our data poorly performed for this species. Also, monitoring efforts should also consider that species as the red-necked nightjar seem to be very sensitive to cool weather (see Camacho 2013), which may originate a reduction in both nightjars' activity (e.g., partial torpor) and detection by observers.

To conclude, this study suggested that nightjar activity and ecology may be partially synchronized to the lunar cycle, which has also been supported by other studies of *Caprimulgus* nightjars (Mills 1986; Perrins & Crick 1996; Jetz et al. 2003; Ashdown & McKechnie 2008; Woods & Brigham 2008). By accounting for this synchronization, nightjar surveys can be optimised in order to maximize the probability of detecting the presence of these otherwise difficult to survey species.

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