Identification of different song types in European nightjar *Caprimulgus europaeus*

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Abstract

Capsule:

Two distinct song types were identified for male European nightjars, with their relative frequency of use changing through the breeding season, indicating a possible link to paired status.

Aims:

To test whether two song types could be defined in audio recordings and whether use differed before and during the period when males would be expected to be established in pairs.

Methods:

Unattended acoustic recording devices were placed at a nightjar study site in Nottinghamshire, United Kingdom, and recordings of churring vocalizations were made during two periods of the breeding season. These recordings were then analysed to identify the presence/absence of the song terminal phrase and associated audible features.

Results:

The recorded audio data allowed the identification of two distinct song types, differing in their terminal phrasing and overall song duration. The number of nightjar songs with a terminal phrase increased significantly between the two sampling periods, from lower levels during the site arrival period, to higher levels during the first clutch initiation period.

Conclusion:

This study shows that the presence/absence of two different song types can be readily identified in audio recordings of nightjar song, and that the use of the song types appears to vary through the breeding season. Our findings suggest that male nightjars are more likely to produce song with a terminal phrase during the first clutch initiation period, when they would be more likely to be paired or in the presence of a female. This finding may introduce the potential to provide a minimally intrusive means of assessing the number of nightjar breeding pairs, and not just singing males, at site level or as part of a national census of the species.

Keywords:

Bioacoustics, Birdsong, Soundscape Ecology

Introduction

Bird vocalizations vary widely between and within species. They allow birds to communicate with conspecifics and other individuals, transferring information or advertising their presence. The songs and calls emitted also provide one of the main cues enabling ornithologists to survey avifauna. A change in song type during the breeding season has, in particular, been linked to male pairing status for a number of bird species (Catchpole and Slater, 2008). Paired males often appear to put less effort into their vocalizations once a mate has been attracted, with species such as great reed warbler *Acrocephalus arundinaceus* singing shorter, simpler songs (Catchpole, 1983), American redstart *Setophaga ruticilla* singing less often (Staicer *et al*., 2006), reed bunting *Emberiza schoeniclus* producing slower songs (Bessert-Nettelbeck *et al*., 2014; Nemeth, 1996), and Cerulean warbler *Setophaga cerulea* having both a slower song rate and lower minimum frequency (McKillip and Islam, 2009). In addition, a number of bird species have been found to have songs of two different types, with or without a distinctive ending - referred to as accented and unaccented respectively. The unaccented song type in these species appears to function primarily between males in the context of territorial defence, whereas the accented song type is produced more when a female is present and is associated with courtship and pair bonding (Byers, 1996; Catchpole and Slater, 2008; Kroodsma *et al.*, 1989; Morse, 1966).

The European nightjar *Caprimulgus europaeus* (hereafter nightjar) is a species of conservation concern in Britain, having suffered a decline in breeding numbers and contraction in its range (Eaton *et al*., 2015). The species has a distinctive 'churring' song, comprising an extended repetitive trill occupying a frequency band of 1-2.5 kHz, normally delivered around dusk and dawn from a perched location on a horizontal branch (Bibby *et al.*, 2000; Cadbury, 1981; Conway *et al*., 2007; Evans *et al*., 1998; Mustoe *et al*., 2005; Wilson, 1985). The song has a well-defined structure consisting of a short initial phrase, followed by alternating major and minor phrases, sometimes divided with silent intervals. The major phrases have a higher maximum frequency and are delivered at a lower repetition rate than those comprising the minor phrase (Hunter, 1980; Rebbeck *et al.,* 2001). Experienced nightjar fieldworkers have reported that the song may end in one of two ways, either with the churring ending abruptly, or with a distinctive terminal phrase. This terminal phrase sounds like a 'machine slowing down' and is sometimes accompanied by non-vocal wing-claps and 'dweep' calls (Coward, 1928; Lowe, 2011; Mullarney *et al.*, 1999; Sample, 1996; Wilson, 1985). It has been suggested that this behaviour might be used by males that are in a pair or that are in the vicinity of a female (Ferguson-Lees *et al.*, 2011; Lowe, 2011; Selous, 1899; Wilson, 1985).

Although there is a rich legacy of field observation and study of the nightjar in the United Kingdom (e.g. White, 1769), the species is difficult to observe due to its crepuscular activity patterns (Cresswell and Alexander, 1992; Wilson, 1985), and it suffers from low detectability in surveys (Johnston *et al*., 2014; Zwart *et al.,* 2014). This reduces the ability to accurately assess population sizes and trends. The latest national census, undertaken in 2004, estimated the UK population to be 4,606 singing males (95% CL +/- 913) (Conway *et al*., 2007). During such assessments, the locations of churring males are used to determine territories, based on the presence of: (1) simultaneously churring males; (2) registrations over 350m apart; or (3) clusters of registrations (Conway, 2007; Evans *et al.,* 1998). While this method does provide a useful indicator of population size, the assumption is normally made that the number of singing males/territories is equal to the number of breeding pairs. However, this is not necessarily the case, as singing males are only indicative of possible breeding (BTO, 2014) and do not, by themselves, provide evidence of breeding pairs. Moreover, male nightjars, especially unpaired individuals, can be very mobile and may vocalise repeatedly from different locations within an area of habitat (Feather, 2015; Sharps et al., 2015; Spray, 2006). Therefore, if assessments are based upon the number of churring males, there is the potential to over-estimate the number of breeding pairs at a site.

Audio recording of nightjar songs could potentially be used to improve population estimates in monitoring schemes. If the two song endings described above can be shown to be detectable in recorded songs, and linked to paired status, then this could potentially be used to refine survey data, and more accurately assess the number of pairs, instead of the number of singing males. This would lead to more accurate population assessments for the species and improved conservation action. In addition, the data for such an assessment can potentially be gathered by unattended acoustic recording devices (ARDs), which automatically capture the vocalizations of birds, offering a survey approach that is minimally intrusive and a comprehensive means of recording avian subjects (Brandes, 2008; Celis-Murillo *et al.*, 2012; Farina *et al.*, 2011; Frommolt & Tauchert, 2014; Trifa *et al.*, 2008; Zwart *et al*., 2014). The song of a male nightjar may be readily captured by such devices, allowing the detailed analysis of song components such as time and frequency characteristics, and the presence and structure of distinctive phrases. Although the terminal phrases heard by fieldworkers have been anecdotally described, they have not previously been assessed and used within a bioacoustics framework. If the terminal phrase difference between the two song types can be detected using ARDs, then this may allow pairing status to be determined and offer a valuable new census tool to determine the spatial distribution and population size of nightjar breeding pairs.

We aimed to determine whether the two song types, with and without the terminal phrase, could be recognised and quantified by reviewing audio recordings taken from the field. We then related this finding to additional information on the nightjar populations at the study site, to determine whether the use of the two song types varied through the breeding season and was therefore potentially linked to the paired status of the males present.

Methods

Study Site Selection

Nightjar is a summer migrant to the UK, where it is known to breed throughout much of the country where suitable habitat is present, but particularly in the south and east (Conway et al., 2007). The species is ground-nesting, with a clutch size of two, is sometimes double-brooded, and birds are often faithful to nest sites between years (Berry, 1979). Mate-switching between broods has been recorded by Cresswell & Alexander (1990). The species is insectivorous, foraging over a range of habitat types, and may travel some distance from the nest-sites, depending on the availability of feeding habitat nearby (Langston et al., 2007). Song territory sizes have been recorded as being in the region of 10 ha, but home ranges, including such foraging habitats, may be an order of magnitude greater than this (Bright et al., 2007; Sharps et al., 2015).

The study was conducted at Sherwood Pines Forest Park in Nottinghamshire, UK (53˚ 9’ N, 1˚ 5’ W). The site, which has a long documented history of nightjar occupancy, is managed by the Forestry Commission and consists of coniferous plantation woodland and heathland clearings over a total area of 13.4 km^2 (Lowe et al., 2014). This part of Nottinghamshire has been regarded as a stronghold for the species in the past, but the 2004 national census indicated a 10% population decline in the region (Conway et al., 2007). An annual survey of the study area, conducted for ten years between 2001 and 2010, estimated the annual breeding population at the site to be 13–20 nesting pairs (Lowe et al, 2014).

Audio Data Collection

To record nightjar vocalizations, Wildlife Acoustics Song Meter® 2+ ARDs, Firmware R.3.3.7, (Wildlife Acoustics, 2014) were located throughout the study site during the nightjar breeding season, with five devices deployed between 23 May and 22 August 2014 and ten between 24 April and 29 July 2015. More devices were employed than strictly necessary to allow for redundancy in the data collection process, and some device locations were repeated between years.

The ARDs were fitted with an SMX-II omni-directional microphone and programmed to record nightly, from 30 minutes before sunset, until 30 minutes after sunrise. They were set with a gain of +48 dB and a sampling rate of 44,100 samples per second, covering a frequency range up to 22 kHz. The recordings were saved as 30 minute duration Waveform Audio (WAV) files on to SD memory cards within the ARDs.

As the ARDs were deployed at the start of the season, prior to territories and nest sites being established, the devices were positioned under the guidance of the Birklands Ringing Group (BRG), based upon past survey data and their knowledge of the site. To avoid overlap between the ARDs in terms of the males recorded, the minimum distance between devices was 452 m, i.e. much greater than the 350 m distance recommended by Conway (2007) to separate territories, and thus minimising the chance of double counting. The use of ARDs was minimally intrusive to the population of nightjars, as it was only necessary to make a brief daytime visit to each device every two weeks in order to change the batteries and memory cards.

Nightjar Breeding Data Collection

During both study seasons, the BRG used a co-ordinated count technique to estimate the number of male nightjars within the study site (Conway 2007, Evans *et al*., 1998). This consisted of a number of surveyors simultaneously counting the number of 'churring' males present at dusk. This survey was repeated six times during June and July.

Nightjar nests were also located in both 2014 and 2015 using the method described by Lowe (2011), and the distance of each nightjar nest from the nearest ARD was measured after the nightjars had finished nesting and the young had fledged. This method allowed the number of breeding pairs to be determined, together with the estimated egg laying dates for each nest.

Audio Data Analysis

Two sets of audio data were sampled from the recordings made by the ARDs, each covering a period of five nights of recordings with six ARDs. An early breeding season Sample A was taken from recordings captured during the site arrival period in May, when it was assumed that males would be likely to be unpaired. This data was taken from the period after the date of the first recorded male nightjar song at the ARD location. However, five consecutive nights could not be used in all cases because some nights included an unacceptable level of background noise. When this occurred, the five nights closest to the date of the first recorded male nightjar song were selected.

A later breeding season Sample B was then taken from recordings made in June, when males were assumed to be paired. This data was selected based upon the first clutch initiation period. The date the first egg was laid at the closest nest to each ARD was designated as Night 3, with two nights before and two nights after this date being selected.

The selection of ARDs used for provision of audio data was based upon the presence of nightjar vocalizations within recordings, the spread of ARD locations within the site, available date parameters and the proximity of an active nest. The ARDs and nights utilised also excluded sites where licenced nightjar ringing or song-lure activities had taken place in close proximity to an unattended ARD. With these selection criteria, Sample A was taken from May 2015, while Sample B was taken from both June 2014 (ARDs B1-B3) and June 2015 (ARDs B4-B6).

Kaleidoscope® v2.1.0 software (Wildlife Acoustics, 2014) was used to manually analyse the audio recordings, by listening to playback and visual inspection of spectrograms. This allowed the nightjar songs to be located within the dataset - an individual male nightjar song being defined as having one or more major or minor phrases of the same signal strength and no silent intervals exceeding one minute in duration. Time and frequency variables were then measured for each song, including the duration of the song; identification of the presence/absence of a terminal phrase and its duration; and the presence of silent intervals, wing claps and terminal 'dweep'calls. Songs without a terminal phrase (and its associated characters) were termed Song Type I, and songs with a terminal phrase (and associated wing-claps and 'dweep' calls) were termed Song Type II. For each recorded song, the Sample (A/B), date, time and ARD location was noted.

Following analysis of the audio recordings, data exploration was carried out following the protocol described in Zuur *et al*. (2010). Generalised Linear Models (GLM) were used to assess the influence of variables on the production of the two song types. Each song was treated as a separate observation (n= 659), and binomial models with a logit link were fitted using function GLM in R (R Core Team, 2018). The logit link function ensures positive fitted values, and a binomial distribution was used for the binary outcome of Song Type I (coded as 0) or II (coded as 1). Categorical variables included Plot (the ARD location on the ground – a factor with n=7 levels), Sample (A or B, n=2), Year (n=2). Numerical variables were NightHour (number of hours after 19:00 hours), and its quadratic term.

Full models were checked for overdispersion and adequacy (Zuur *et al*. 2010). Model selection followed an informatic-theoretic approach (Burnham and Anderson, 2002), with models fitted for all possible combinations of explanatory variables without interactions. These were ranked by corrected Akaike Information Criteria (AICc), and the best fit model was selected. Statistical tests were conducted using MuMin, ARM and base packages in R (Barton, 2018; Gelman and Su, 2018; R Core Team 2018; RStudio Team, 2015).

Results

Nightjar Breeding Data

Using the combination of co-ordinated counts of churring males (Conway 2007, Evans *et al*., 1998) and nest searches (Lowe, 2011), the BRG estimated the study site to support 18 male nightjars during the 2014 breeding season (6 unpaired and 12 paired), and 17 male nightjars (5 unpaired and 12 paired), during the 2015 breeding season. Therefore, approximately 33% of male nightjars were unpaired during the period of the study. The distances between the Sample B ARD locations used and their nearest nest sites varied between 29m and 190m.

Audio Data

A total of 659 male nightjar songs were identified in the Sample A/B dataset. Review of the recorded 'churring' vocalisations could effectively identify the terminal phrase, when present, and differentiate the two distinct song types expected. Whilst both song types included major and minor phrases and sometimes silent intervals, the endings and durations were different (Table 1). Song Type I (Figure 1) ended abruptly and was rarely accompanied by non-vocal wing claps (only 2% of occasions). Song Type II concluded with a distinctive terminal phrase - a gradual descent in frequency with a median duration of 6 seconds (Figure 2). This was frequently accompanied by non-vocal wing claps (87% of occasions). In addition, the duration of Song Type II was, on average, shorter than that of Song Type I (medians of 57s and 132s respectively).

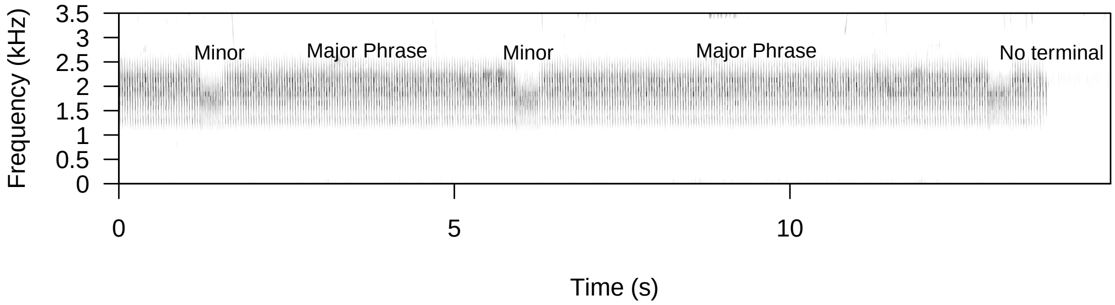

Figure 1. Spectrogram (acoustic frequency plotted against time) showing the major and minor phrases, the principal constituents of male nightjar song. This is Song Type I, without a terminal phrase, ending abruptly on either a minor phrase or a major phrase.

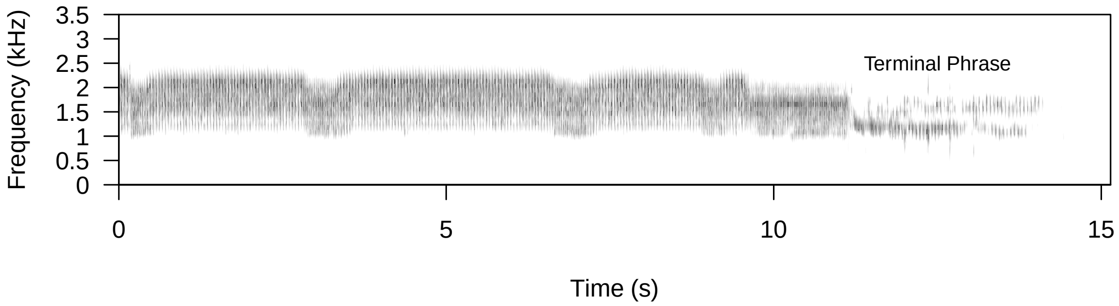

Figure 2. Spectrogram showing male nightjar Song Type II, with a terminal phrase. The terminal phrase may be preceded by either a minor phrase or a major phrase.

Table 1. Summary of measured song variables for Song Types I and II

Song Type	n	Duration of song in minutes, excluding terminal phrase (median and range)	% songs with one or more silent intervals	% songs ending with a major phrase	% songs ending with a minor phrase	% songs with associated wing claps	% songs with associated ‘dweep’ calls	Duration of terminal phrase in seconds (median and range)
Type I - without Terminal Phrase	440	2.19 (0.03-32.02)	53	66	34	2	4	NA
Type II - with Terminal Phrase	219	0.98 (0.03-16.48)	27	7	93	87	23	6 (1-54)

Both song types had similar peaks in occurrence at dusk and dawn, concentrated in the 50 minutes after sunset (to 23:00 hours) and the 80 minutes before sunrise (from 02:00 hours) (Figure 3). However, Song Type II appeared to be particularly common around dawn.

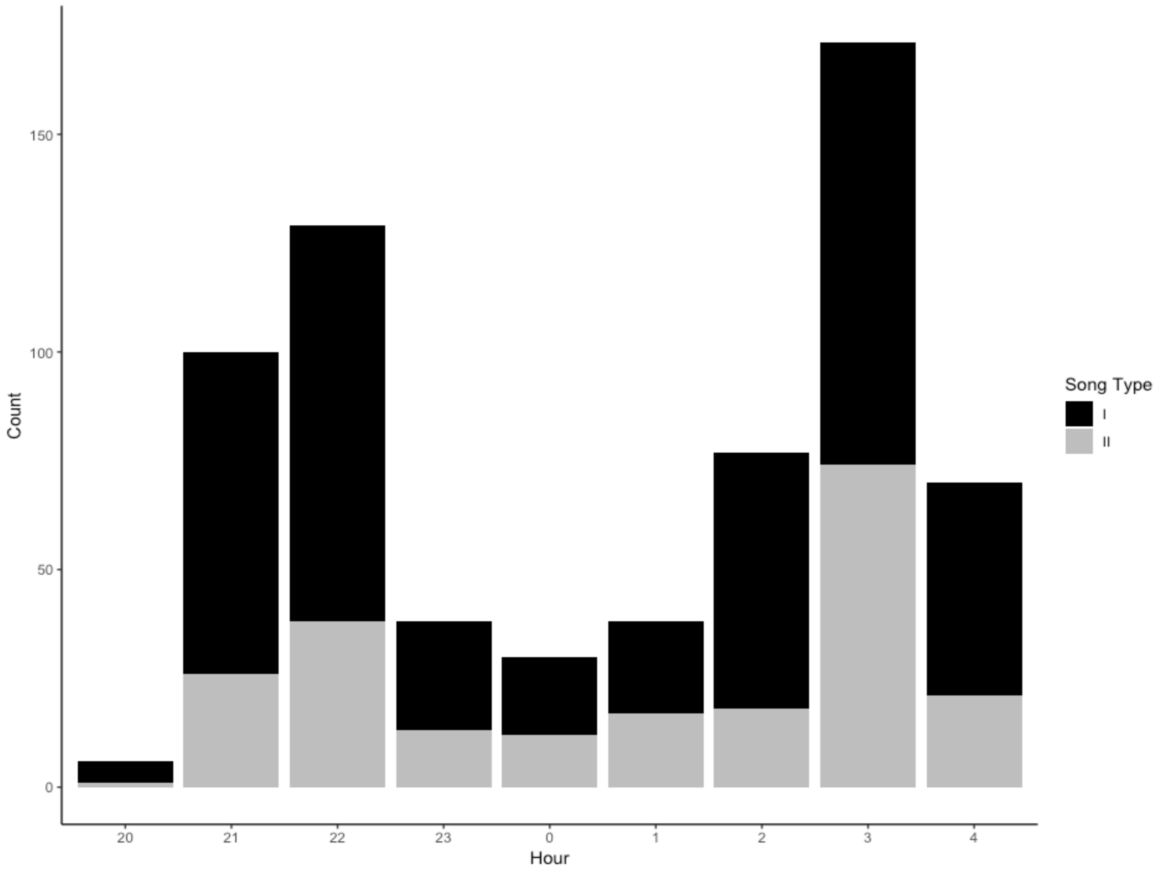

Figure 3. Timing of Type I and Type II nightjar song recordings, showing peaks in vocal activity at dusk and especially at dawn.

More nightjar songs were recorded during the later sampling period, with 32% of songs in the dataset recorded during the site arrival period (Sample A), and 68% during the first clutch initiation period (Sample B). Of the 659 songs, 67% were Song Type I and 33% Song Type II (Table 2). The proportion of Song Type II was higher in Sample B, with each ARD deployment having 27-47% (38% overall) Song Type II, while the proportions in Sample A were 13-39% (24% overall) (Table 3).

Table 2. Numbers of nightjar Song Type I (without Terminal Phrase) and Song Type II (with Terminal Phrase) produced during the Site Arrival Period and during the First Clutch Initiation Period.

Song Output	Sample A Site Arrival Period	Sample B First Clutch Initiation Period	Total
Song Type I	163 (76%)	277 (62%)	440 (67%)
Song Type II	51 (24%)	168 (38%)	219 (33%)
Total Nightjar Songs	214 (32%)	445 (68%)	659

Table 3. Audio sampling periods and number of nightjar songs recorded at each ARD location used.

ARD	Location (OS GR)	Start Date (Night 1)	End Date (Night 5)	Datum*	Number of Songs	Song Type II (%)
A.1	SK60616169	12 May 2015	16 May 2015	7 May 2015	44	39
A.2	SK60176224	13 May 2015	20 May 2015	10 May 2015	24	25
A.3	SK61916040	14 May 2015	18 May 2015	10 May 2015	41	24
A.4	SK61166183	12 May 2015	16 May 2015	11 May 2015	55	13
A.5	SK61216106	15 May 2015	22 May 2015	12 May 2015	17	18
A.6	SK61876085	19 May 2015	23 May 2015	16 May 2015	33	24
B.1	SK60596103	1 Jun 2014	5 Jun 2014	3 Jun 2014	55	47
B.2	SK62036066	5 Jun 2014	9 Jun 2014	7 Jun 2014	74	38
B.3	SK61146180	6 Jun 2014	10 Jun 2014	8 Jun 2014	152	39
B.4	SK60536097	7 Jun 2015	11 Jun 2015	9 Jun 2015	64	42
B.5	SK60176224	8 Jun 2015	14 Jun 2015	12 Jun 2015	36	31
B.6	SK61166183	20 Jun 2015	24 Jun 2015	22 Jun 2015	64	27

* Datum Events: A.1 to A.6 - Date of the first recorded male nightjar song, B.1 to B.6 - Date first egg laid at first nest.
Notes: ARD A.2 positioned at the same location as ARD B.5, ARD A.4 at the same location as ARD B.6.
OS GR = Ordnance Survey Grid Reference.

The data exploration found no constraints in terms of outliers, collinearity or zero-inflation. Model validation was also suitable, with no evidence of over-dispersion from review of a binned residual plot. The best-fit model used Sample and the quadratic term for NightHour as covariates, with Sample B (the first clutch initiation period) and later night hours resulting in higher probabilities for Song Type II (Table 4, Appendix 1). This indicates that males appeared to use Song Type II more readily during the first clutch initiation period (Figure 4), compared to site arrival, and that it was used more at dawn than dusk (Figure 5).

Table 4. Results of best-fit Generalised Linear Model, indicating significant positive relationships with NightHour and Sample variables.

	B(SE)	95% CI for odds ratio		
		Lower	Odds Ratio	Upper
Constant	-1.54 *** (0.22)			
Night Hour (quadratic)	0.008 ** (0.003)	1.002	1.008	1.015
Sample B	0.75 *** (0.19)	1.45	2.11	3.10

Note: R^2 = .023 (Hosmer-Lemeshow), .029 (Cox-Snell), .04 (Nagelkerke).
Model $X^2(2)$ = 19.39, p = <0.01. Signif. codes: 0 '***' 0.001 '**'
Night Hour = number of hours after 19:00.
Sample = A (site arrival) or B (first clutch initiation)

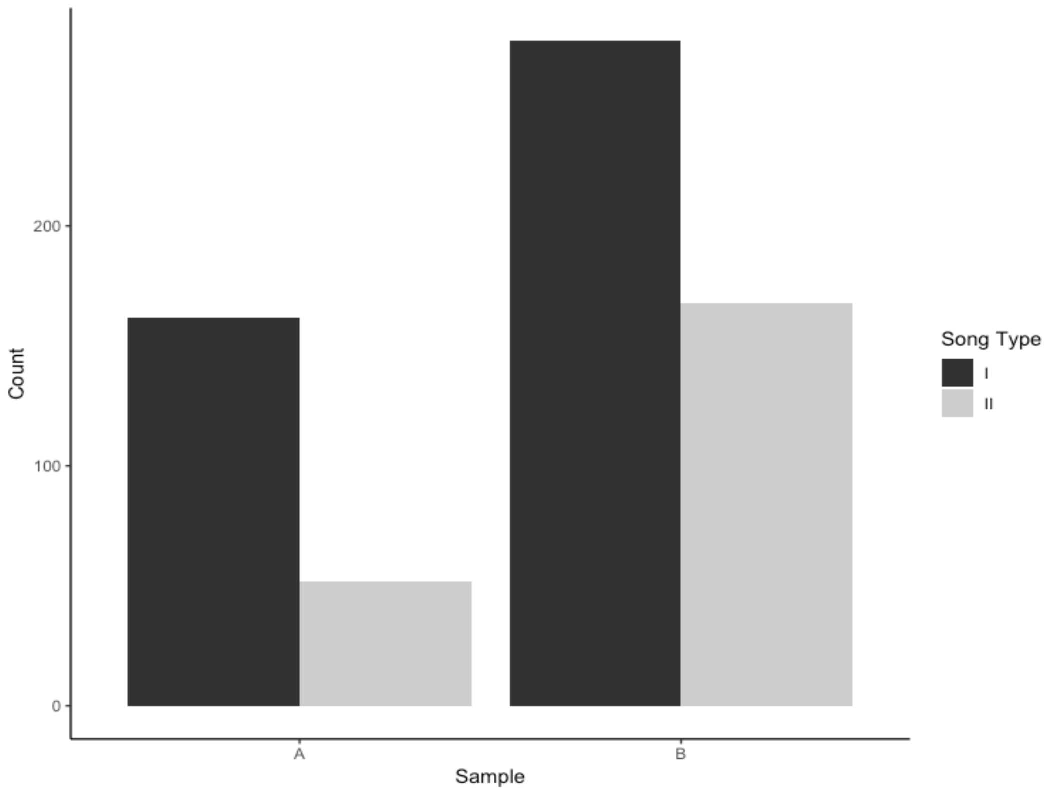

Figure 4. Numbers of Song Type I and Song Type II recorded in Sample A (site arrival) and Sample B (first clutch initiation), showing higher proportion of Type II songs in Sample B.

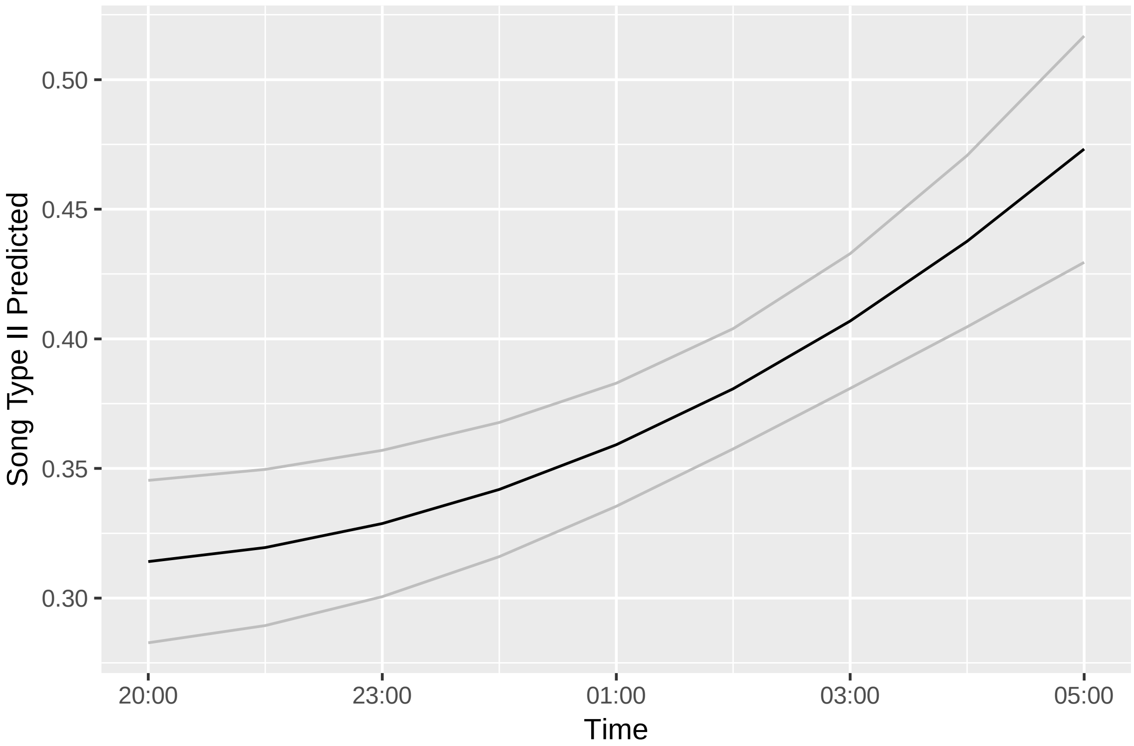

Figure 5. The predicted song rate from the best-fit GLM model indicates that the proportion of Song Type II increases through the night.

Discussion

Use of Different Song Types

Our bioacoustic approach, analysing recordings taken from ARDs, allowed two nightjar song types to be differentiated, based upon the presence or absence of a distinctive terminal phrase, and differences in the song duration (Song Type II including the terminal phrase and being of shorter duration). To our knowledge, this is the first time this has been confirmed for nightjar using spectrogram analysis. Although the use of these two song types by nightjar remains unclear, previous work on a range of other species shows that song character changes and vocal effort declines in paired males (Bessert-Nettelbeck *et al*., 2014; Byers, 1996; Catchpole and Slater, 2008; Catchpole, 1983; Kroodsma *et al.*, 1989; McKillip and Islam, 2009; Morse, 1966; Nemeth, 1996; Staicer *et al*., 2006).

The two song types were confirmed to differ in their prevalence between the two recording periods - Type II, with the terminal phrase, being significantly more common during the first clutch initiation period in June, compared to the site arrival period in May. Although we have identified this temporal difference in song type use, the relationship with paired status is still not entirely clear. Despite the terminal phrase being long-reported as a part of the song repertoire for nightjar males, its function is not understood. Anecdotal reports have linked it to the presence of nearby females, which may be mates – but whether it is a communication towards the female or an advertisement to other males is unknown. Song Type II was more common in Sample B - the June first clutch initiation period. These recordings were taken from territories where a breeding pair and nest was present within 200m, and were captured during a period when male birds would be expected to be actively displaying. It is known that paired males tend to stay close to their breeding territory when churring, whilst unpaired males roam over a larger area in search of a female (Feather, 2015; Spray, 2006; Wilson, 1985). However, in this study, we have not definitively linked the Type II song to known paired males. Our results therefore only give limited support to the hypothesis previously raised by field workers that the Type II song is related to paired status and the presence of a female.

One confounding factor to this hypothesis is that Song Type II was recorded during the site arrival period, when males would not be expected to be paired. This use may be due to Song Type II not being exclusive to paired males, but being used more generally in the presence of females. In this case, the occurrence of Song Type II in the early season could arise if some females arrived early from migration to the breeding grounds (Mullarney *et al.*, 1999) - despite females average arrival time often being several days after the males (Berry and Bibby, 1981 found an average of 10.9 days whilst Lowe *et al*., 2014 noted a range of 1-10 days). Although it was not known when the females arrived at the site, it is possible that unpaired males may initially react to the presence of a female at the breeding grounds but then increase their output of Song Type II once paired with a female.

One issue with the analysis of the audio data is dependency of the song type at a recorder location, as songs are highly likely to be the same individuals sampled on multiple occasions. Without the identification of individual males, this pseudoreplication is hard to deal with. Further studies to identify the use of the terminal phrase by individual known birds, with defined paired status, would clearly be beneficial. This could potentially be done by combining vocal individuality data (Rebbeck, 2001) with that obtained from radio-tracking or GPS-based studies (Spray, 2006).

Vocal Activity Levels

We recorded nightjar vocal activity throughout the night, but found that it was concentrated around dusk and dawn, confirming previous findings by Cadbury (1981) and Zwart *et al.* (2014).

Alongside differences in the proportion of song types, varying levels of vocal activity were found between the two Sample A/B periods. Matched amounts of acoustic recording time were undertaken for each period and twice as many nightjar songs were recorded during the first clutch initiation period in June compared to site arrival in May. This could potentially be due to: (i) fewer males initially being present, as the full cohort arrives over a period of time, and/or (ii) males only singing sporadically on arrival, as they recover from migration. More frequent singing around egg-laying time would then be expected, as all males are now present, paired males are maintaining territories, and males that remain unpaired are displaying actively to challenge for females, perhaps aiming to mate for second broods (Cresswell and Alexander, 1990; Lack, 1930; Wilson, 1985). In our dataset, a small number of spectrograms contained simultaneous ‘churring’ i.e. at least two males singing at the same time and place.

Implications for Survey, Surveillance and Monitoring

The breeding status of birds is sub-divided by the British Trust for Ornithology (BTO) into four classifications: non-breeding, possible, probable and confirmed breeding; according to the evidence available (BTO, 2014). For nightjar, current survey methods assume that any churring male holds an active territory and is part of a breeding pair. However, this is unlikely to be true. The findings of this study point the way to a possible refinement of this assessment, based upon the prevalence of Song Type II at a sampling location. Now that this song type has been positively identified using acoustic analysis, it may be possible to link its use more definitively to paired status, and then use this information to help define the breeding status of recorded males. For example, it could be possible to establish a threshold value for Song Type II, above which probable breeding status may be ascribed. Based upon this study, a threshold value in the region of 30% or more Song Type II would define a sample indicating a probable paired male (with limited mis-classification in either direction).

The potential to more accurately define paired status in nightjar is an important goal for advancing survey and evaluation methods for this species, enabling the assessment of favourable conservation status. The findings of this study are a useful step forward in bioacoustic monitoring for this purpose, highlighting the potential of song type analysis to provide individual behavioural information. Further developments should allow improved counts of the numbers of breeding pairs of nightjars, adding to the already proven use of bioacoustics to determine presence/absence (Zwart *et al*., 2014).

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Declaration of Authorship

SD conceived the ideas, designed the methodology and analysed the audio data. SD and AL conducted the fieldwork. CA and SD wrote the manuscript, with CA conducting the statistical analysis. All authors contributed critically to the drafts and gave final approval for publication.

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Appendix 1 Supplementary Information: GLM Model Parameters and AIC Scores

NightHour	NightHour^2	Sample	Year	Location	AICc	AICdelta	AICwt
-	0.01	+	-	-	826.03	0.00	0.14
0.09	-	+	-	-	826.30	0.27	0.12
-	0.01	+	+	-	826.51	0.48	0.11
0.09	-	+	+	-	826.94	0.91	0.09
-0.05	0.01	+	-	-	828.02	1.99	0.05
-	0.01	-	-	+	828.31	2.28	0.04
-	0.01	+	-	+	828.31	2.28	0.04
-	0.01	-	+	+	828.31	2.28	0.04
-	0.01	+	+	+	828.31	2.28	0.04
-0.12	0.02	+	+	-	828.34	2.30	0.04
0.10	-	-	-	+	828.44	2.41	0.04
0.10	-	+	-	+	828.44	2.41	0.04
0.10	-	-	+	+	828.44	2.41	0.04
0.10	-	+	+	+	828.44	2.41	0.04
0.00	0.01	-	-	+	830.40	4.37	0.02
0.00	0.01	+	-	+	830.40	4.37	0.02
0.00	0.01	-	+	+	830.40	4.37	0.02
0.00	0.01	+	+	+	830.40	4.37	0.02
0.07	-	-	+	-	830.43	4.40	0.02
-	0.01	-	+	-	830.48	4.45	0.01
-	-	+	-	-	831.27	5.24	0.01
-	-	+	+	-	831.31	5.28	0.01
0.06	0.00	-	+	-	832.45	6.42	0.01
-	-	-	+	-	833.18	7.15	0.00
-	-	-	-	+	835.05	9.02	0.00
-	-	+	-	+	835.05	9.02	0.00
-	-	-	+	+	835.05	9.02	0.00
-	-	+	+	+	835.05	9.02	0.00
0.07	-	-	-	-	838.86	12.83	0.00
0.35	-0.03	-	-	-	839.23	13.20	0.00
-	0.01	-	-	-	839.72	13.69	0.00
-	-	-	-	-	841.39	15.36	0.00