Combining bioacoustics and occupancy modelling for improved monitoring of rare breeding bird populations

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DECLARATION OF AUTHORSHIP

CA conceived the ideas, designed methodology; collected and analysed the data. CA led the writing of the manuscript, with MG contributing to occupancy modelling methods and development of the text. Both authors contributed critically to the drafts and gave final approval for publication.

HIGHLIGHTS

- Bioacoustic recording is used to generate occupancy and detectability estimates
- Rare heathland breeding birds varied in their occupancy between 0.68 and 0.13
- Detectability varied from 0.74 to 0.20, and was affected by habitat
- Bioacoustics can be used to provide improved data over traditional survey methods

ABSTRACT

Effective monitoring of rare and declining species is critical to enable their conservation, but can often be difficult due to detectability or survey constraints. However, developments in acoustic recorders are enabling an important new approach for improved monitoring that is especially applicable for long-term studies, and for use in difficult environments or with cryptic species.

Bioacoustic data may be effectively analysed within an occupancy modelling framework, as presence/absence can be determined, and repeated survey events can be accommodated. Hence, both occupancy and detectability estimates can be produced from large, coherent datasets. However, the most effective methods for the practical detection and identification of call data are still far from established. We assessed a novel combination of automated clustering and manual verification to detect and identify heathland bird vocalizations, covering a period of six days at 44 sampling locations

Occupancy (Ψ) and detectability (p) were modelled for each species, and the best fit models provided values of: nightjar Ψ=0.684, p=0.740, Dartford warbler Ψ=0.449 p=0.196 and woodlark Ψ=0.13 p=0.996. Including environmental covariates within the occupancy models indicated that tree, wetland and heather cover were important variables, particularly influencing detectability.

The protocol used here allowed robust and consistent survey data to be gathered, with limited fieldwork resourcing, allowing population estimates to be generated for the target bird species. The combination of

bioacoustics and occupancy modelling can provide a valuable new monitoring approach, allowing population trends to be identified, and the effects of environmental change and site management to be assessed.

KEYWORDS

Acoustic ecology, autonomous recorder, bird survey, heathland, occupancy model.

1. INTRODUCTION

1.1 Bioacoustics for Biodiversity Monitoring

Biodiversity monitoring is central to nature conservation, allowing species status to be evaluated or assessments to be made of biological responses to environmental changes (Pereira & Cooper, 2006). Long-term monitoring of designated nature conservation sites is particularly needed to identify population trends and inform management planning efforts, especially in the context of factors such as climate change and habitat loss/severance (Noss, 1990; Furnas & Callas, 2015). However, existing monitoring practices and protocols are often sub-optimal, especially in terms of unbiased spatial coverage, sampling effort optimization, the statistical use of the data, and the lack of repeated sampling (Schmeller et al., 2012).

We assessed the potential to improve the existing monitoring methods currently used on sites that are internationally important for their breeding bird populations. The most common methods for monitoring of bird numbers and distributions are transect or point count surveys by human observers. These have recognised disadvantages, such as observer bias, the availability of skilled/experienced surveyors (Brandes, 2008; Celis-Murillo et al., 2009; Rempel et al., 2005; Sedláček et al., 2015), and the infrequent and short-term nature of survey visits (Shonfield & Bayne, 2017; Zwart et al., 2014). In response to these issues, passive acoustic monitoring is increasingly being used as an alternative monitoring technique. This method uses automated recording units, which can be deployed in the field for days or weeks at a time to capture animal sounds. The advantages of this approach include the production of a standardised, long-duration, permanent dataset and record of species identification, which can be repeatedly analysed and subject to validation by independent reviewers (Abrahams & Denny, 2018; Celis-Murillo et al., 2009; Rempel et al., 2005). Automated recorders can be synchronized to occur simultaneously across large spatial extents, reducing temporal variability in studies (Brandes, 2008; Furnas & Callas, 2015; MacKenzie & Nichols, 2004), and offering large data volumes at low cost and with little resourcing requirement (Acevedo & Villanueva-Rivera, 2006; Hill et al., 2018; Holmes et al., 2014; Zwart et al., 2014). Due to potential benefits such as these, the use of automated recorders has increased significantly over the last ten years (Shonfield & Bayne, 2017), and some researchers have advocated the use of automated recorders instead of expert personnel for conducting surveys (Darras et al., 2018; Rempel et al., 2005; Brandes, 2008; Zwart et al., 2014).

There are potential barriers to the widespread uptake of passive acoustic monitoring for bird surveys. These include the need for specific expertise and the increased time required for post-processing compared to some traditional surveys (Banner et al., 2018; Knight et al., 2017), together with the costs of equipment (Beason et al., 2018; Farina et al., 2014; Hill et al., 2018). However, open source or low-cost recording devices are being produced and post-processing methods are constantly improving – although automated species identification, including machine-learning approaches, is still in development (Acevedo et al., 2009; Salamon et al., 2016). For fieldwork, a practical disadvantage is the fact that acoustic monitoring does not allow the collection of visual clues which can sometimes be vital for the identification of cryptic/quiet species, or for assessing abundance (Klingbeil & Willig, 2015; Sedláček et al., 2015). In some cases, the use of audio recording units has resulted in detection of fewer species and detection at shorter distances than human observers (Holmes et al., 2014; Yip et al., 2017), but the potential for longer term data capture with recording units means that this constraint can normally be addressed by longer deployment times (Darras et al., 2018; Sedláček et al., 2015; Shonfield & Bayne, 2017; Zwart et al., 2014). However, microphone performance and maintenance needs to be considered as part of the planning of fieldwork campaigns (Turgeon et al., 2017; Yip et al., 2017).

1.2 Occupancy Models

Alongside the technological advances in bioacoustics, there has been a dramatic recent increase in the development and application of occupancy models that explicitly incorporate species detectability (Furnas & McGrann, 2018; MacKenzie & Nichols, 2004; MacKenzie et al., 2002; MacKenzie et al., 2006). The presence/absence of a species in a sample can be used to calculate occupancy (Ψ) - the proportion of an area, or number of sites, occupied by a species. The frequency with which a species is repeatedly recorded at each sampling site can also be used to assess detectability (p), to allow for the estimation of, and correction for, imperfect detection (Banner et al., 2018; MacKenzie et al., 2002; MacKenzie et al., 2006). The ability to factor these two parameters into assessments allows improved estimates of populations and greater understanding of ecological patterns such as species/habitat relationships (MacKenzie et al., 2006).

Despite the clear potential and utility of combining bioacoustic techniques and occupancy models, only a few studies have united these methodological developments to model the population status of a range of vocal species (Yates & Muzika 2006; Furnas & Callas 2015; Kalan et al. 2015; Campos-Cerqueira & Aide 2016; Stiffler et al. 2018; Wood et al., 2019). This study, therefore, provides an important additional case-study in new geographical, habitat and spatiotemporal contexts. Furthermore, it also addresses one of the most critical questions in this area of study - how to most effectively extract useful information from acoustic recorders to feed into the occupancy models and allow population estimates to be generated.

Although fine-grained data can be gained from acoustic recorders, a significant benefit of the occupancy modelling approach in field studies is that it relies only on presence/absence data, rather than metrics of abundance such as counts of individuals (MacKenzie et al., 2006). This is normally much easier to determine, requiring less interpretation in the field/lab, and counteracting the potential for inter-observer or inter-survey error (MacKenzie et al., 2006). Although some information is perhaps lost by this approach, data accuracy may be gained as, for rare species, it can be very difficult to correctly estimate abundance during surveys, whereas estimation of occupancy may still be possible with a high level of confidence (Campos-Cerqueira & Aide, 2016; Mackenzie & Royle, 2005). Finally, occupancy and abundance will be linked in most populations, and at small spatial scales and with territorial species, occupancy may be regarded as equivalent to population size and can be used for investigating population dynamics or spatial variation (MacKenzie et al., 2006; Royle & Nichols, 2003; Furnas & Callas, 2015; Campos-Cerqueira & Aide, 2016; Wood et al., 2019).

1.3 Heathland Bird Monitoring

Our study was conducted on European nightjar *Caprimulgus europaeus*, woodlark *Lullula arborea* and Dartford warbler *Sylvia undata*. These three birds are specialists of lowland heathland habitats, and are rare and declining species considered to be of international conservation importance (Clark & Eyre, 2012). Despite significant legal and policy protection, however, their breeding site habitats are threatened by air pollution, urban development, inappropriate management and recreational disturbance (Fagúndez, 2013; Mallord et al., 2007).

Monitoring a variety of bird species, with differing behaviours, over extensive heathland sites, presents significant challenges for conservation managers. In particular, a number of different surveyors are inevitably involved in the surveys used for monitoring the target species. Inter-observer differences are therefore likely to produce variations in data, particularly with nocturnal nightjar surveys, where it is hard to differentiate individuals and accurately map territories (Liley & Fearnley, 2014). Automated recorders, used by themselves or in conjunction with existing methods, have great potential to reduce bias and variability in survey results and account for the effects of detectability between sites and surveys, to produce more reliable and consistent population estimates.

Our goal in this study is to establish effective methods for combining bioacoustic techniques and occupancy models in the monitoring of rare breeding bird populations. We capture an acoustic dataset and demonstrate how to efficiently process recordings to detect and identify species vocalizations within this, using a novel clustering technique. We then analyse the acoustic data to estimate occupancy and detectability for the three target species, using single-species, single-season occupancy models, and combine this with environmental covariates, to determine the effects of habitat on model outputs. This provides useful occupancy and detectability estimates for the target species, highlighting the potential for bioacoustic methods to be used as an alternative or complement to current monitoring practices, with benefits in terms of consistent, verifiable and permanent field data.

2. MATERIALS AND METHODS

2.1 Study Area

We conducted the study on parts of the Thames Basin Heaths SPA and the Wealden Heaths SPA. These are two large, internationally important, nature conservation sites in southern England, made up of 18 heathland sites of varying size and character. These sites comprise a mix of dry and wet heath vegetation, with mire, bog, waterbodies, permanent grassland, scrub and blocks of woodland (Figure 1). Together, they cover a total of 12,199 ha, of which 5,702 ha is classified as lowland heath (Clark & Eyre, 2012). Within this overall context, we gathered data at three heathland sites to which access could be readily gained: Chobham Common, Horsell Common and Thursley Common, which together cover an area of 992 ha.

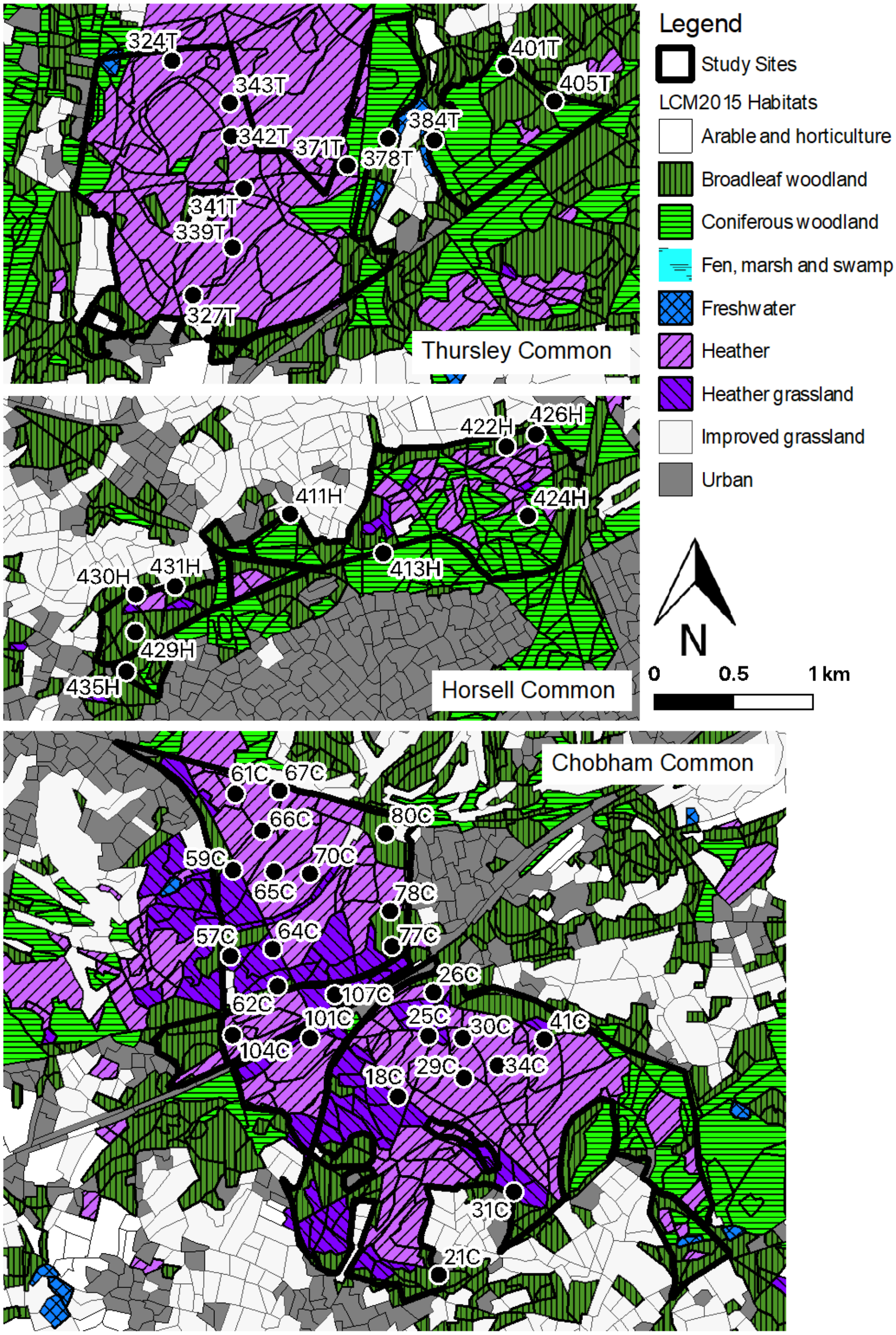

Figure 1. Land Cover Map 2015 habitat data and acoustic sampling site locations.

2.2 Acoustic Monitoring

We used Wildlife Acoustics SongMeter SM2 recorders, equipped with a single mono omnidirectional microphone to record audio data (see Supplementary Information: Appendix 1). These automated recording units were programmed to record a 1 minute audio sample every ten minutes (i.e. one minute on, nine minutes off), from two hours before sunrise, until three hours after, and then from one hour before sunset until two hours after. Daily sampling therefore took place within a 5 hour period at dawn, and 3 hours at dusk. The units were deployed at a single sample site for a period of six days during May-June 2018, so that each site had 288 minutes of recording. The audio samples were all recorded as .wav files onto an SD card, at 48kHz sampling rate and 16-bit depth (Abrahams, 2018). All microphones were calibrated to ensure comparable sensitivity and performance before deployment (Turgeon et al., 2017; Yip et al. 2017).

Sample locations were defined across the study area by using GIS to place a regular 250 m point grid across the three heathland sites. It was considered that this would be a sufficient distance for recordings to be independent of each other, and relevant to the territory sizes of the species being studied. From the 166 possible grid points, 48 were randomly selected, stratified to the relative area of each heathland site, to provide 9 sampling sites at Horsell Common, 15 at Thursley Common, and 24 at Chobham Common. As 16 recorders were available for the study, the 48 sampling sites were divided into three sessions of field recording: 26-31 May, 5-10 June, 16-21 June. The sites were randomly assigned to one of the three survey sessions, so that 3 sites at Horsell Common, 5 at Thursley Common, and 8 at Chobham Common would be sampled at each session. Despite differences in date, all site samples were treated equally as individual samples within a single season. A closure assumption was therefore made that bird distribution, population size and density did not change over the course of the three survey sessions.

All sites were given an identification code consisting of a number and site suffix of H, T or C (Figure 1). Field placements matched the GIS locations as closely as features on the ground would allow. During the deployments, one recorder failed to record evening sessions repeatedly (at three sampling sites), and another suffered battery failure on one occasion. These failures were all at Thursley Common (sites 315T, 319T, 332T, 391T) and the sites were removed from the dataset, leaving 44 sampling locations.

2.3 Audio Data

The audio recordings taken from the field were analysed using a semi-automated system to identify target species vocalizations (termed ‘phrases’) in the recordings. Kaleidoscope Pro 4.3.2 software (Wildlife Acoustics, 2017) was first employed, using its cluster analysis method with default settings (https://www.wildlifeacoustics.com/images/documentation/Kaleidoscope-Pro-5-User-Guide.pdf). This process analysed the time and frequency characteristics of the recorded audio files, using Hidden Markov Models, to search for sounds within a 1500-7000Hz frequency band and of 2-20 seconds duration, with a maximum inter-syllable gap of 1 second - creating each as an individual new .wav file. The analysis process grouped similar phrases in the recordings (e.g. the song of a particular bird species) into clusters based on their sound characteristics. After the automated clustering was complete, the phrases detected by the software were manually reviewed by listening to playback and by the visual inspection of spectrograms to classify the presence/absence of the target species in each phrase.

2.4 Environmental Data

In order to investigate the influence of habitat on occupancy and detectability at each of the study sites, we obtained data from a combination of satellite and terrestrial mapping sources. The proportion of Broadleaf trees, Coniferous trees, Heather and Heather grassland within 100m of each sample site was calculated from Land Cover Map 2015 (LCM2015) vector data, accessed from the Centre for Ecology and Hydrology (Rowland et al., 2017). Distance to the nearest road was calculated based on Ordnance Survey OpenMap-Local vector data (OS data © Crown copyright and database right 2018). We also used pre-processed satellite data from Copernicus Pan-European High Resolution Layers (HRL; https://land.copernicus.eu/pan-european/high-resolution-layers) representing Tree Cover Density (TCD), Water and Wetness (WAW) and Imperviousness (IMD) at a 20m resolution. The Tree Cover Density (forest) HRL provides the level of tree cover in a range from 0-100% for each pixel.. The Water and Wetness HRL shows the occurrence of water and wet surfaces over the period from 2009 to 2015, on a scale from (1) permanent water, to (4) temporary wetness. The Imperviousness degree IMD captures the spatial distribution of artificially sealed (i.e. urbanized/road) areas. We used Zonal Statistics to summarise these measures for each sampling site, to produce the sum of all pixel values within a 100m radius of the site. All spatial analyses were performed in QGIS (QGIS Development Team, 2018). Weather was represented in our environmental variables by 'derived 24hr sun duration' from the weather station at Wisley, Surrey (Ref. src_id 719/DCNN 5237, WGS84 51.3108, -0.47634), accessed from BADC (badc.nerc.ac.uk). Other weather variables were unavailable from this source as records for the survey period were sparse.

2.5 Occupancy Models

The occupancy of each of the three target species was modelled separately using a single-species, single-season modeling approach with observation and habitat covariates (Furnas & Callas, 2015; MacKenzie et al., 2002; MacKenzie et al., 2006; Stiffler et al., 2018), using established protocols with the 'Unmarked' package in R (Fiske & Chandler, 2011; R Core Team, 2013; RStudio Team, 2015). The acoustic data was summarised to day-level temporal resolution of presence/absence, to produce a detection history at each sampling site comprising six replicate surveys. The naive occupancy for each species was checked and confirmed to be >0.1, so that detection histories were not too sparse to fit single-species models. We first created null models, without covariates, to represent equal probability of detection and/or occupancy across all survey sites and days. We then developed models including covariates representing the areas of different habitat types within 100m of the sampling location (from LCM2015 and Copernicus data), and distance to the nearest road (as shown in Table 2). We anticipated that detection probability might change over the course of the survey period (Campos-Cerqueira & Aide, 2016; Furnas & McGrann, 2018) due to seasonal and weather reasons, and used Julian day of survey and 24-hour sun duration to represent this information. All variables were scaled and centered around zero prior to analysis. The broadleaf and coniferous covariates were excluded as these duplicated the TCDsum habitat type, and the LCM2015 data were more zero-inflated than the Copernicus data. IMDsum was also rejected as the data were very sparse. Covariates were applied first to the detection parameter, before the occupancy parameter. Each model was inspected to check estimates, standard errors and convergence. All models tested are listed in Table 2.

We assessed model fit using Akaike's Information Criterion (AIC), ranking and comparing models based on AIC relative differences between the top ranked model and each other model (ΔAIC) and AIC weights. We considered models with ΔAIC <2 to be equally supported (Burnham & Anderson, 2002) and combined these by applying model averaging using the MuMIn package in R (Barton, 2018), to estimate occupancy and detection for each species. Initially, models without occupancy covariates were fitted to select the most appropriate covariates for detection. These covariates were then retained for all candidate models when occupancy covariates were added. The models generated for each species were used to assess occupancy levels at the study sites, define potential habitat areas and calculate provisional population estimates.

3. RESULTS

3.1 Clustered Audio Segments

Kaleidoscope clustering of the complete audio dataset detected 28,775 phrases as individual .wav files, an average of 109 phrases per site/day. Each phrase included bird vocalizations and other sounds. With a mean duration of 6 seconds (range 2-20.9 sec), the clustered phrases comprised 48 hours of audio - 23% of the total recorded dataset. The phrases were grouped into 55 clusters by the software.

Manual review of all the clustered phrases identified the three target species in the dataset, with 757 phrases across 30 sites having vocalizations of nightjar, 327 of woodlark at 7 sites, and 115 of Dartford warbler at 14 sites. This gave a total of 1,199 phrases recorded for the three target species. Nightjar and

Dartford warbler were recorded at all three SPA sites, but woodlark was only recorded at Chobham and Thursley Commons.

3.2 Patterns in Activity

The total number of phrases recorded per day across all sampling sites varied from 1,974 on 30 May to 1,145 on 17 June. The daily number of phrases was relatively even between recording sessions 1 and 2, but declined for session 3 in mid-June. This pattern was matched somewhat by the daily numbers of target species vocalizations (Figure 2). Nightjar and Dartford warbler vocalizations were recorded throughout all three recording sessions, but woodlark was mostly confined to the early June session only - although this is likely to be related to presence at the sites being sampled at that time, rather than any reason to do with seasonal timing.

The most vocally active sites were 61C and 70C (north Chobham) for nightjar, 29C and 25C (south Chobham) for woodlark, and 339T and 343T (central Thursley) for Dartford warbler - see locations at Figure 1. Significant numbers of calls were not recorded for any species at the Horsell Common sites.

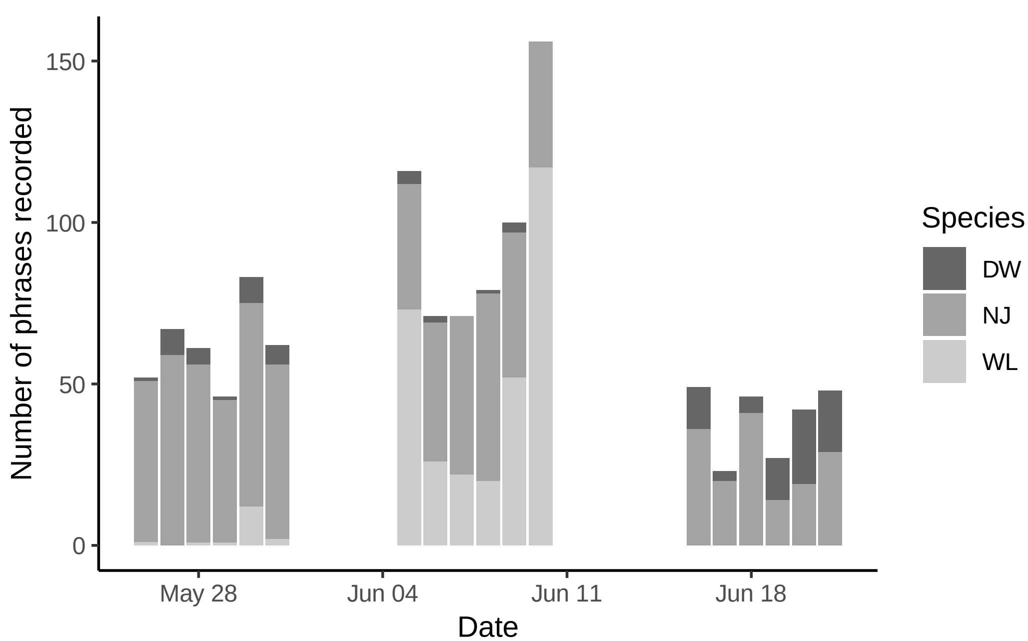

Figure 2. Number of target species recorded per day across all sampling sites, for Dartford warbler (DW), nightjar (NJ), and woodlark (WL).

3.3 Environmental Parameters

The recorders were placed in habitats that varied from open heath to mature forest (Figure 1). Thursley Common can be divided into a western part, dominated by Heather, with the eastern part being Coniferous and Broadleaved woodland. Chobham Common is a mosaic of Heather and Heather grassland, with Coniferous and Broadleaved woodland around its fringes. This site has a much larger cover of WAW than the two other sites. Horsell Common is mostly Coniferous and Broadleaved woodland, with patches of Heather at its eastern end. The means and ranges of the GIS-measured environmental parameters are listed in Table 1.

Habitat variable	Mean value	Range	Units
TCDsum	2570	0-6209	Sum of % per pixel
WAWsum	36.8	0-252	Sum of 1-4 index per pixel
Distance to Road (HubDist)	351	29-961	Metres
Heather	14459	0-31318	Sum of pixels
Heather grassland	4204	0-31060	Sum of pixels

Table 1. Measured habitat parameters (n=44 sampling sites)

3.4 Occupancy Modelling

Naive occupancy was calculated for each species, based on the presence of the species across all 44 sample sites in the study. The naive occupancy values, equal to the proportion of sites with positive detections, were 0.68 for nightjar, 0.32 for Dartford warbler and 0.16 for woodlark.

Models incorporating covariates on the detection and occupancy parameters were generated for each species (Table 2). Two models for nightjar had equal support (ΔAIC <2) and so were averaged to produce covariate estimates. The averaged model included Julian date (JULIAN), Tree Cover Density (TCDsum) and Water and Wetness (WAWsum) as detectability covariates with no covariates acting on occupancy. The best fit model for nightjar (NJmdet3), with an AICwt of 53%, indicates an occupancy of 0.684 (SE 0.071) with a detectability of 0.740 (SE 0.035), varying only slightly from the null model (Ψ=0.682, p=0.733).

There were four favoured models for Dartford warbler, including the null model, with TCDsum, WAWsum, and distance to road (HubDist) featuring on the detectability parameter. Heather grassland was the only indicator for occupancy. The averaged model for Dartford warbler used only distance to road as a detectability covariate, with no covariates acting on occupancy. The best-fit model for Dartford warbler (DWmdet5), with an AICwt of 36%, indicates an occupancy of 0.449 (SE 0.107), with a detectability of 0.196 (SE 0.053), an increase from the null model occupancy of 0.382 (SE 0.091), but decrease in detectability from 0.258 (SE 0.057).

Woodlark had two favoured models, sharing Julian date, WAWsum, distance to road, Heather and Heather grassland as detectability covariates, and WAWsum, Heather and Heather grassland for occupancy covariates. The averaged model for woodlark had five significant covariates, and again, these were all on the detection parameter. Julian date, WAWsum and Heather were all positively related to detectability, while distance to road and Heather grassland were negative indicators. For woodlark, the best-fit model (WLmocc2), with an AICwt of 59%, indicated an occupancy of 0.13 (SE 0.117), lower than the null model figure of 0.162 (SE 0.056), and a detectability of 0.996 (SE 0.012), which varied substantially from the null model detectability of 0.491 (SE 0.081).

Model	Formula	AIC	ΔAIC	AICwt
Nightjar				
NJmdet3	~JULIAN + TCDsum + WAWsum ~ 1	259.62	0.00	0.528
NJmocc3	~JULIAN + TCDsum + WAWsum ~ TCDsum	260.64	1.02	0.317
NJmocc2	~JULIAN + TCDsum + WAWsum ~ TCDsum + HubDist	262.33	2.70	0.136
NJmocc1	~JULIAN + TCDsum + WAWsum ~ TCDsum + WAWsum + HubDist + Heather + HeatherGrass	267.64	8.02	0.010
NJm0	~1 ~ 1	267.79	8.17	0.009
Dartford Warbler				
DWmdet5	~TCDsum + HubDist ~ 1	157.11	0.00	0.364
DWmocc3	~HubDist + TCDsum ~ HeatherGrass	158.19	1.08	0.212
DWmdet4	~TCDsum + WAWsum + HubDist ~ 1	158.40	1.29	0.191
DWm0	~1 ~ 1	159.00	1.89	0.142
DWmocc2	~HubDist + TCDsum ~ WAWsum + HeatherGrass	160.06	2.95	0.083
DWmocc1	~HubDist + TCDsum ~ TCDsum + WAWsum + HubDist + Heather + HeatherGrass	164.89	7.79	0.007
Woodlark				
WLmocc2	~JULIAN + WAWsum + HubDist + Heather + HeatherGrass ~ WAWsum + Heather + HeatherGrass	69.31	0.00	0.593
WLmocc3	~JULIAN + WAWsum + HubDist + Heather + HeatherGrass ~ WAWsum + HeatherGrass	70.75	1.44	0.288
WLmocc1	~JULIAN + WAWsum + HubDist + Heather + HeatherGrass ~ TCDsum + WAWsum + HubDist + Heather + HeatherGrass	73.10	3.79	0.089
WLmdet3	~JULIAN + WAWsum + HubDist + Heather + HeatherGrass ~ 1	75.29	5.98	0.030
WLm0	~1 ~ 1	100.55	31.24	0.000

Table 2 Model selection list for all species - with detectability and occupancy covariates

Predicted occupancy varied little between sampling sites for nightjar and Dartford warbler (Figure 3), as only single covariates were acting on these species - TCDsum and Heather grassland respectively. Woodlark occupancy predictions varied more widely due to the number of habitat covariates acting on the models for this species - including WAWsum, Heather and Heather grassland. Detectability predictions were sensible for nightjar and Dartford warbler, but highly polarised to 0-1 in the models for woodlark, due to the small number of positive sampling sites.

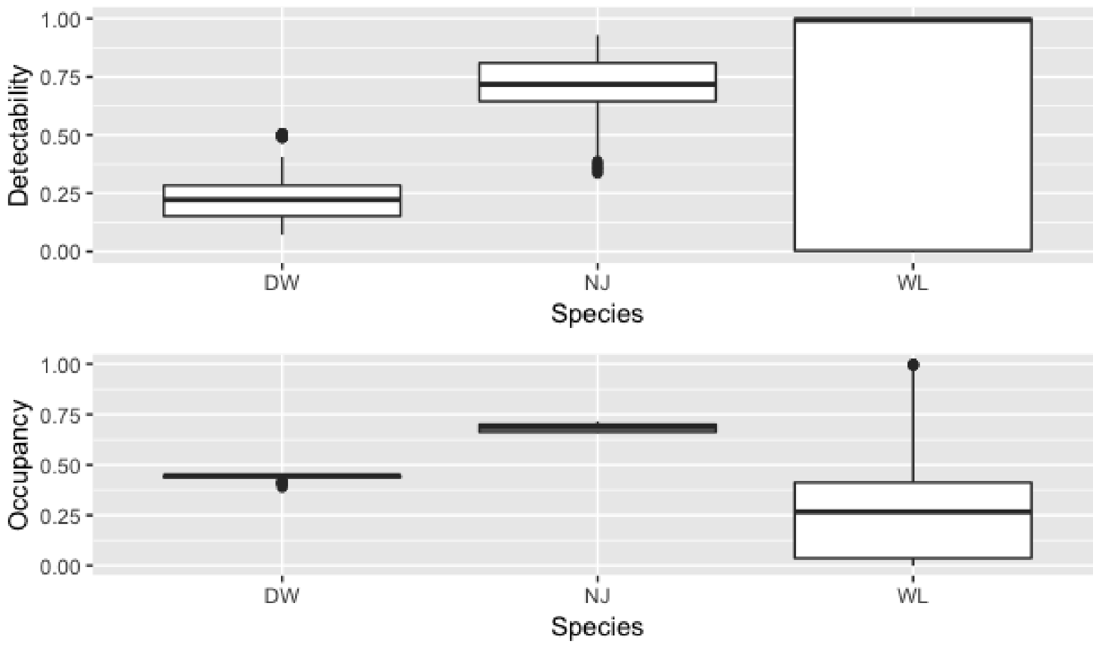

Figure 3. Model-averaged predicted occupancy and detectability across all sampling sites, for Dartford warbler (DW), nightjar (NJ), and woodlark (WL).

Our results can be used to provide a baseline for assessing the population of the three heathland bird species studied. We assumed that occupancy is a good surrogate for abundance (MacKenzie & Nichols, 2004) and that we could quantify the relative abundances of the bird species, based on the proportion of sampling sites in which they were recorded to be present. Given the separation distances between recorder locations in this study, it is considered reasonable to assume that each occupied sampling site represented a separate territory/pair. Using the occupancy estimates from the null models for the three species we can calculate that the areas of occupied habitat for each species, from a total 992 ha, are: nightjar 676 ha, Dartford warbler 379 ha, woodlark 161 ha (Table 3). Combining these habitat areas with published breeding densities of 0.074-0.078 males/ha for nightjar (Berry, 1979; Conway et al., 2007), 0.32-0.42 pairs/ha for Dartford warbler (Bibby & Tubbs, 1975), and 0.05 pairs/ha for woodlark (Langston et al., 2007; Sitters et al., 1996), gives estimated population levels of: nightjar 51 males, Dartford warbler 140 pairs, and woodlark 8 pairs (Table 3).

Species	Occupancy (SE)	Occupied habitat (90% CI)	Density ha^{-1}	Pairs (90% CI)
Nightjar	0.682 (0.0702)	676 ha (562-791)	0.075	51 (42-59)
Dartford warbler	0.382 (0.0914)	379 ha (230-528)	0.37	140 (85-195)
Woodlark	0.162 (0.0562)	161ha (69-252)	0.05	8 (3-13)

Table 3. Calculated areas of occupied habitat, based on intercept-only occupancy estimates

4. DISCUSSION

4.1 Bioacoustic Approach

To our knowledge, this is the first study in Europe to combine bioacoustic survey with occupancy modelling. It is also the first in the UK to undertake a large scale survey for multiple bird species using automated recorders. It therefore expands the geographic scope of case studies for these methods, and applies them in a new habitat, beyond the American forested ecosystems in which most previous studies have been located (Furnas & Callas, 2015; Campos-Cerqueira & Aide, 2016; Furnas & McGrann, 2018; Wood et al., 2019).

We used species detection data from six repeated days of recording at 44 sampling sites, combining this with environmental covariates to estimate occupancy and detectability for three bird species. Our results show that the bioacoustic approach can be used effectively for the survey and monitoring of heathland bird populations. Although we included models where habitat covariates could influence occupancy in our candidate sets, the 'best' models for each species suggested that the habitat variables were not important indicators of occupancy at the scale studied. This is possibly due to the fact that the study areas were all lowland heathland sites, generally suitable for the study species, and so the distribution of individuals was likely to relate to micro-habitat features that were not detectable at the scale of the field survey, satellite and map data applied. The satellite data used was at 20m pixel size, but the average size of the LCM polygons was 2.4 ha, equivalent to 87 m radius. Although the covariate data was sampled at a similar scale (100 m radius) to previous studies (Furnas & Callas, 2015; Campos-Cerqueira & Aide, 2016), these were landscape-scale surveys less dependent on small habitat features to differentiate plots. Thus, we would agree with the finding of Niedballa et al. (2015), that both the spatial scale of habitat covariate data, and the radius sampled around survey sites, can affect the fit of occupancy models. Higher resolution data is needed for a site-based scale of assessment, if habitat covariates are to be included in analyses. For future studies, this should be gained from either field survey or high-resolution aerial/satellite imagery, such as the 5m resolution RapidEye imagery used by Niedballa et al (2015).

Identification of species vocalizations is commonly done either by complete manual analysis or, increasingly, by the use of automated recognizers, which require the *a priori* compilation and analysis of a large library of known species vocalizations (Knight et al., 2017; Shonfield & Bayne, 2017). Our analysis workflow included automated clustering of the acoustic data set, followed by manual validation of candidate vocalizations of the target species (Abrahams & Denny, 2018). This process has two benefits. Firstly, the automated clustering identified signals, that may be target bird species, but filtered out noise. In the current study, this allowed 77% of the total acoustic dataset to be filtered out, before identifications were attempted, significantly reducing the later workload in manually reviewing data for target species vocalizations. The second benefit of the analysis approach taken here, was that the manual validation step helped to minimize false-positive detections (Campos-Cerqueira & Aide, 2016;), which are often a significant issue with automated species identification systems (Zwart et al., 2014; Salamon et al., 2016). Misclassification errors such as this violate a major assumption of most occupancy models, and can lead to substantial errors in occupancy estimates (MacKenzie et al., 2006; Banner et al., 2018). The issue can potentially be addressed by complete manual identification of all recordings, but this is highly time-consuming, while the hybrid automated/manual approach taken here reduced the workload in the manual review stage to less than a quarter of what it would have been. The corollary is that the data rejected by the automated clustering may contain target species vocalizations, and hence false-negatives may result. However, with the summation of the detailed call data down to daily presence/absence at each site, the potential loss of some target species phrases is considered unlikely to significantly affect the occupancy and detectability estimates derived from the modelling (Shonfield et al., 2018). The combined use of automated clustering and manual verification is therefore recommended as a valid approach for identification in bioacoustic studies.

4.2 Spatial Sampling Design

In bioacoustic studies with static sampling locations, the layout of recorder placements is of high importance. For occupancy modelling especially, the distance between sampling sites should be relevant to the territory size of the taxa being recorded (Niedballa et al., 2015), while also ensuring that the detection process is independent at each site by preventing overlap between the recording radius around each recorder. While this distance is variable, for many bird species the effective recording radius of most detectors is in the region of 50 m - although this is dependent on microphone model, variability and condition (Furnas & Callas, 2015; Turgeon et al., 2017; Yip et al., 2017). Within our study, the closest spacing between sampling sites was set by the ~250 m sampling grid. The mean nearest neighbour distances of the recorder sites were 316 m for Chobham, 346 m for Horsell, and 329 m for Thursley (range 202-703). Due to the sampling sites being spread across three survey sessions, the mean nearest neighbour distances between recorders in each session were 608 m, 466m and 508m.

For nightjar, a threshold of 350 m distance between registrations has been proposed to differentiate between male territories (Conway et al., 2007), while Stiffler et al (2018) applied a minimum spacing of 400 m for recording wetland birds. The spacing of the recorders within the current study related well to these studies, and as a result, there can be a reasonable confidence that there was no double-counting for the bird species being studied. A 250 m sampling grid, as set out in the draft protocol of Abrahams (2018) is therefore considered to be appropriate for future studies, although additional refinement of detector placement may be warranted to maximise coverage of sites, dependent on the vocal and territorial characteristics of the species being studied. For example, recent research has indicated that, for a desired threshold of detection efficiency, careful selection of optimised placements based on topography, vegetation and weather patterns, may be most efficient (Piña-Covarrubias et al., 2018).

4.3 Temporal Sampling Design

In any occupancy study, the balance between the number of sites and number of sampling events differentially affects the accuracy and precision of the occupancy and detectability estimates. We recorded for six days at 44 sites, which we considered likely to balance fieldwork resourcing with sufficient sample site density. This was a longer deployment time than the two-three days used by Furnas & Callas (2015) and Stiffler et al. (2018), and equivalent to that employed by Campos-Cerqueira & Aide (2016) and Wood et al. (2019). For rare species with a high probability of detection (i.e. woodlark for this study) the required survey effort should maximize the number of sites covered, while for common species with low detection (i.e. Dartford warbler) the most efficient sampling approach is to increase the number of survey occasions (Mackenzie & Royle, 2005). With the low occupancy for woodlark found here, it is likely that an increased number of sampling sites (and lower number of survey days if necessary) would be likely to improve the modelling results (Mackenzie & Royle, 2005; Banner et al., 2018). This modified sampling approach would, however, have to be considered in terms of its costs/benefits, taking into account the potential effects on Dartford warbler modelling and increased fieldwork time or equipment requirements.

4.4 Detectability

Using the null models, without covariates, we estimated detectability as 0.73 for nightjar, 0.49 for woodlark and 0.26 for Dartford warbler. The national Breeding Bird Survey (BBS) (Johnston et al., 2014) found a much lower detectability of 0.30 for nightjar, which is perhaps unsurprising, due to the difficulties with surveying this species within a standard (mostly daytime) survey method. However, the

BBS detectability estimates of 0.47 for woodlark and 0.37 for Dartford warbler are similar to those found in this bioacoustic study. In this comparison, nightjar is much better detected by acoustic recorders (as found by Zwart et al., 2014), but Dartford warbler less so, while detectability for woodlark is matched.

Taking detectability into account during traditional bird surveys requires repeated visits across the season. The time often occurring between site visits may then invalidate the assumption that detection probability remains constant across the survey events. The protocol used in this study enabled six days of back-to-back recording, simultaneously at 16 sites, minimising the risk that detection probability would change between sampling events. This would have been difficult to achieve without the use of automated recorders. The greater number of survey replicates achievable with the bioacoustics approach is therefore able to improve occupancy and detection estimates (MacKenzie et al., 2006; Stiffler et al., 2018).

We found that survey date, combined with habitat characteristics, explained detectability and improved the performance for some of the species models generated here, similar to the finding of Furnas & Callas (2015). Wetland (WAWsum) was a positive parameter on detectability for all three species, and woodland (TCDsum) was also positive for nightjar, as was Heather for woodlark. The probability of detecting a species during a bioacoustic survey is a function of both the probability of it vocalizing and the recorder detecting the call. The vocalization rates of many birds vary due to age, sex, breeding status, time of day, and seasonal variation (Campos-Cerqueira & Aide, 2016; Furnas & McGrann, 2018). As a consequence, both survey timing and the number of visits need to accommodate species vocalizing behavior to ensure accurate detection, particularly for species with sporadic vocalization patterns (La & Nudds, 2016). Age and sex-specific variation in vocalization rates cannot be accounted for easily when using automated recorders, but our methods allowed for the other variation factors, as we sampled over a relatively short period of time during the breeding season, and sampled over a wide timeframe every day, thereby minimising the potential for seasonal and diurnal variation in call rates. Our results, together with those of Johnston et al. (2014), showing how detection probability varies by species, should be considered in decisions about study design when planning to survey birds using automated recorders or traditional methods.

4.5 Occupancy

We calculated occupancy as 0.682 for nightjar, 0.382 for Dartford warbler and 0.162 for woodlark, showing that nightjar is widespread across the study sites, while woodlark has a much more restricted distribution. This is in line with other survey data for the sites, collected by traditional survey methods (J.Eyre & J.Clark; D. Boyd pers. comms.), and previous occupancy studies (Furnas & Callas, 2015; Campos-Cerqueira & Aide, 2016; Wood et al. 2019). Although the occupancy figures provide a population estimate in themselves, they could potentially be used to generate an estimate of the number of pairs, as the common measure for population size. We did this provisionally, using a combination of habitat area and previously recorded breeding densities to give the following numbers: Dartford warbler 140, nightjar 51 and woodlark 8.

The occupancy modelling indicated a positive relationship between nightjar and TCDsum. This corresponds to associations with woodland found in previous studies (Bright et al., 2007; Conway, 2010]. The negative relationship between Dartford warbler and Heather Grassland was surprising, as this species is generally associated with dry-humid heath, and gorse, sometimes with a grassy component (Bibby & Tubbs, 1975). Woodlark occupancy was positively related to Heather Grassland, and negatively to WAWsum and Heather. These results are more expected, as nest sites for this species are generally found in tall/dense heather or grass (Mallord et al., 2007), while foraging sites have short grass and bare ground (Conway et al., 2009).

5. CONCLUSION

Our study demonstrates the suitability of the bioacoustics approach to identify the distributions and assess the populations of target bird species on heathland study areas. Occupancy and detectability estimates were produced, taking into account imperfect detection. If carried out on a regular basis, this method could provide a valuable new approach for monitoring of population levels and favourable conservation status. For future studies in this setting, and with these species, methods might be improved by increasing the number of sample sites at which recording takes place. This approach would be likely to improve the modelling for woodlark, but would need to be balanced against potential effects on models for the other two species studied.

The field of conservation biology is continuously adopting improved, cheaper and more easily available technologies. In the near future, automated interpretation of recordings using machine learning methods will become increasingly viable, allowing effective identification of a range of bird species (Brandes, 2008; Acevedo & Villanueva-Rivera, 2009; Knight et al., 2017; Shonfield & Bayne, 2017, Stowell et al., 2019). The permanent nature of bioacoustic recordings will allow these ongoing developments in call analysis and automated identification to be used to re-analyse previously collected data, perhaps alongside new recordings (Shonfield & Bayne, 2017; Stiffler et al., 2018). The use of bioacoustics will, therefore, be indispensable for conducting long-term and potentially continuous monitoring over large spatial scales, aiding understanding of the ongoing effects of threats and management practices on bird populations on heathland and in other environments.

AUTHORS' CONTRIBUTIONS

CA conceived the ideas, designed methodology; collected and analysed the data. CA led the writing of the manuscript, with MG contributing to establishment of occupancy modelling methods and development of the text. Both authors contributed critically to the drafts and gave final approval for publication.

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DATA ACCESSIBILITY

Data, metadata and R script will be archived at Zenodo.org (DOI tbc)

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SUPPLEMENTARY INFORMATION: APPENDIX 1

Kaleidoscope 4.3.2 software settings

File parameters:

- No subdirectories
- No split to max duration
- Split channels—yes.

Signal parameters:

- Signal of interest 1500–7000 Hz

- Duration 2–20 s
- Maximum inter syllable gap 1 s

Scan and cluster recordings:

- Max distance 1.0
- FFT window 5.33 ms
- Max states 12
- Max distance for building clusters 0.5
- Max clusters 500

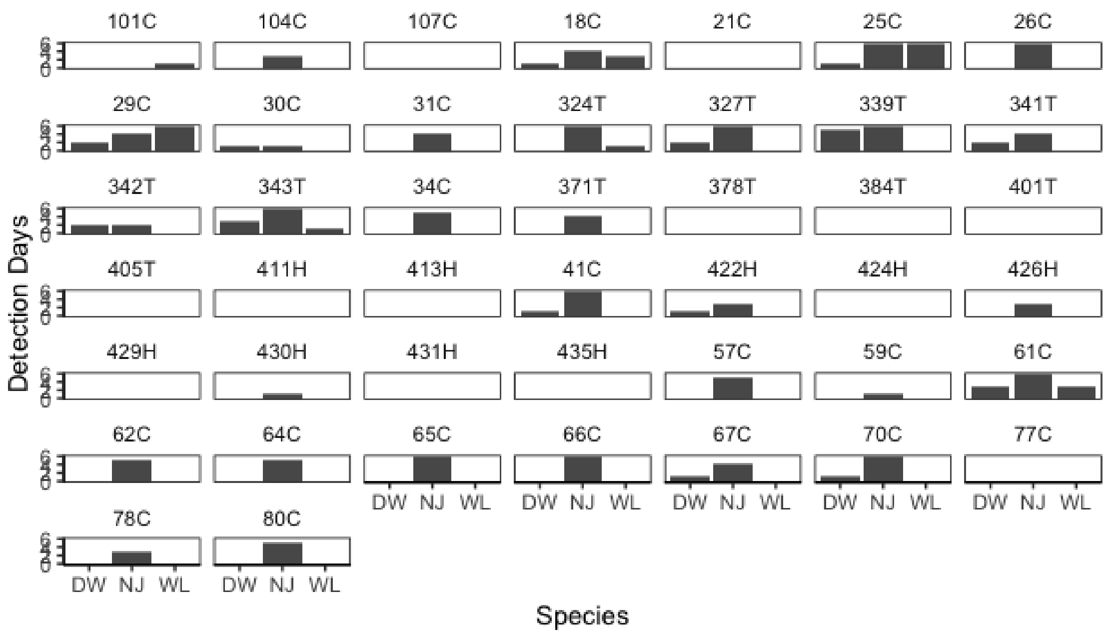

Figure 4. Number of detection days for each species at each site.