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Vocal individuality of male Western Capercaillie *Tetrao urogallus* calls, an ambisonic bio-acoustic approach

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ABSTRACT

Capsule: Male Western Capercaillies *Tetrao urogallus* use their vocalizations during the breeding season for territorial and reproductive purposes, and these have genetically predefined characteristics that confer each bird with a unique and distinguishable vocal signature.

Aims: To investigate whether call components allow discrimination between different individual Western Capercaillie males.

Methods: We used ambisonic technology, capable of recording in closed forests and at long ranges, to record and analyse the calls of 12 male Western Capercaillies during the courtship season on seven lek areas of the Alt Pirineu Natural Parc, in north-east Spain. We measured call variables relative to the fundamental frequency and the duration of the song components. A supervised cluster analysis evaluated the power of call characteristics for inter-individual discrimination and correct classification of vocalizations to each individual.

Results: All measured characteristics of vocalizations showed significant differences between males. Supervised cluster analysis showed that audio recordings were identifiable to individual males.

Conclusion: Calls of male Western Capercaillies could be individually identified and differentiated from each other through their bioacoustic characteristics. This may have applications in improving the monitoring and management of the species, allowing for the future development of non-invasive bioacoustic tools for the identification of individual males.

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For decades, scientists have focused their attention on individual variability of bird vocalizations (Fox *et al.* 2008, Průchová *et al.* 2017), because this can provide reliable information about the identity and characteristics of the sound emitter, and do so over long distances in open or cluttered environments (Slabbekoorn *et al.* 2002, Benedict & Warning 2017). Previous research has found a vocal signature unique to each individual in some vocal and non-vocal learner bird species, which is important for understanding how individual identity (Rebbeck *et al.* 2001, Tibbetts & Dale 2007), body condition (Juola & Searcy 2011, Cramer 2013, Wang *et al.* 2019) or social status are communicated through the duration, number, ordination or frequency peaks of the syllabic components of songs and calls (Favaro *et al.* 2015, Elie & Theunissen 2018).

Whereas vocal learning is critical for the normal development of song in most passerines and some

non-passerines (Wada 2010, Liu *et al.* 2013, Logue *et al.* 2019), in most non-passerines song appears to develop innately and is mainly genetically fixed (Fujiwara & Tobari 2021, Ten 2021). For that reason, the structure of the vocalizations of non-vocal learners may exhibit, in general, less intra-individual variation (Robisson *et al.* 2010) and is more likely to be correlated with other genotypic and phenotypic traits. This is particularly important in lekking birds, in which males do not provide any sort of parental care or resources for the female and the brood (Shelly 2018). In these birds, the only benefit females would obtain from mate selection is an improved genetic quality of their offspring (Westcott 1992, Shelly 2018). In this context, the use of calls as honest signalling of genetic quality would be highly selected for, and one would expect the existence of consistent individual variation in male calls that is correlated with genetic traits (Gil & Gahr 2002).

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One such lekking species is the Western Capercaillie *Tetrao urogallus* (hereafter ‘Capercaillie’). This is the largest grouse species in Europe, which inhabits boreal and temperate forests, predominantly coniferous habitats consisting of *Pinus* spp., *Picea* spp. and *Abies* spp., from south-western Europe to eastern Siberia (Sirkia *et al.* 2011). Despite the Capercaillie being widespread with healthy populations in northern Europe and Russia, populations in central and western Europe steadily declined throughout the twentieth century, with their viability being seriously compromised in many areas (Gonzalez *et al.* 2016, Jähren *et al.* 2016).

Capercaillies exhibit a dispersed lek mating system in which males loosely aggregate to display in particular areas of the forests, which are visited by females solely for mating (Castroviejo 1975). Male calls may have an important role in the choices made by females, which express an active preference for males with certain syntax, frequency and duration features within their calls (Liu *et al.* 2013, Fujiwara & Tobari 2021, Gémard *et al.* 2021). Accordingly, Laiolo *et al.* (2011), by relying on registration in the audible range using directional microphones at very close range (*c.* 15 m), found consistent inter-individual variation between calls of male Capercaillies, which correlated with habitat quality. Hart *et al.* (2020) also found consistent variation between male calls emitted at very low-frequency (<20 Hz), which they argued could be used by females to assess male quality.

The recording of low-frequency calls, as in Hart *et al.* (2020), requires relatively expensive and sophisticated equipment and is limited to a very close range. However, recording wild birds in the audible range using cheaper directional equipment is also challenging, due to microphone noise or the distortion caused by sound attenuation, dispersion, reverberation or ambient noise, impairing the quality of recordings. This is especially so for species like the Capercaillie, which vocalize at frequencies below 4 kHz at low intensity and in forest environments, with lots of sound attenuation (Slabbekoorn *et al.* 2007). This limits the application of conventional equipment to relatively short ranges, as in Laiolo *et al.* (2011).

A potential way to overcome some of these limitations is the use of ambisonic technology (Moreau *et al.* 2006, Mattioli *et al.* 2017), which can detect signals coming from all directions over long distances, avoiding the distorting effects of dense vegetation without loss of signal from the effect of sound propagation in the forest (Tarrero 2002). Moreover, if more than one individual is calling at the same time, their corresponding vocalizations can be

split from each other in signal pre-processing using virtual super-directional microphones (Farina *et al.* 2010).

Bioacoustic monitoring allows the study of the population trends of breeding (Buxton & Jones 2012, Marques *et al.* 2013) or migratory birds (Van Doren *et al.* 2024, Weisshaupt *et al.* 2024). A bioacoustic index can be developed to reflect population changes that can be associated with environmental changes (Marques *et al.* 2013, Van Doren *et al.* 2024). Acoustic data have been used for monitoring species living in remote and forested environments, such as high mountains, where methods other than passive acoustics are difficult to implement (Serrurier *et al.* 2024, Southwell *et al.* 2024). This is especially important in the case of endangered and sensitive species, such as the Capercaillie (Jähren *et al.* 2016, Gil *et al.* 2020), where non-invasive acoustic monitoring, even at the individual scale, can provide detailed information on population declines, identify threats and measure the effectiveness of conservation management (Fagerlund 2012, Abrahams 2019, Hart *et al.* 2020).

Beyond the population level, some research has evidenced the possibility of identifying individual animals by their vocalizations, opening the possibility of applying passive acoustic monitoring techniques to individual monitoring (Kondo *et al.* 2010, Cheng *et al.* 2012, Martin *et al.* 2022). This allows a shift from monitoring at the population scale (Abrahams 2019, Braun *et al.* 2019, Serrurier *et al.* 2024) to the individual level, recording individual activity patterns, movement and behaviour (Favaro *et al.* 2015, Marin-Cudraz 2019, Martin *et al.* 2022), increasing the possibilities to understand the behavioural and demographic processes that underlie population dynamics or species evolutionary changes (Clutton-Brock & Sheldon 2010, Bocaccio *et al.* 2023).

The aim of our research was to use ambisonic technology to record individual male Capercaillies and to investigate whether the recorded calls could allow males to be individually differentiated from each other on the basis of the acoustic characteristics of their calls.

Methods

Ethical considerations

The Capercaillie in Spain (*T. urogallus aquitanicus*) is an endangered and declining subspecies (Servei de Biodiversitat i Protecció dels animals 2015, Gil *et al.* 2020), and access to male arenas is strictly controlled by regional administrations. This study was conducted

under permission from the *Generalitat de Catalunya*, was not invasive, and the animals were not handled or disturbed.

Study area

The study was carried out in the Natural Park Alt Pirineu in Spain (Head Office of the park at Llavorsí, 42° 29' 45.530" N, 1° 12' 36.147" E), which is a refuge for the largest population of Capercaillies in the Iberian Peninsula. The population is subject to a severe decline from an estimated 150 males in 2005 to only 120 in 2015 (−20%) (Servei de Biodiversitat i Protecció dels Animals 2015). We selected seven forested study plots, averaging 11 ± 4.1 ha (minimum 6 ha, maximum 18 ha), which were permanently inhabited by Capercaillies according to a census conducted by the Department of Territory and Sustainability of the Generalitat de Catalunya (Servei de Biodiversitat i Protecció dels Animals 2015; Figure 1). The plots were 1,700–2,300 m above sea level and consisted of mixed forests of *Pinus nigra* as the dominant species, with *Betula* spp. and *Abies alba* as companion species, and *Vaccinium myrtillus*, *Rhododendron ferrugineum*, *Arctostaphylos uva-ursi* and *Juniperus communis* in the understorey (Pèlach et al. 2009).

Sound recording and acoustic analyses

In May 2021 we sampled each plot on a single one-night-session, recording seven different males on five plots (two males on two plots and one male in three plots). In May 2022 we sampled the two negative plots from the previous year during six consecutive night-sessions at each one and obtained six recordings of two males and five recordings of three males.

During the breeding season, male Western Capercaillies behave in a very territorial manner and move no more than 2 km from their lek area (Hjeljord et al. 2000, Eliassen & Wegge 2007, Wegge et al. 2009). Because the average nearest-neighbour distance between our plots was 12 ± 2.7 km (range 2–22 km), and sampling was carried out during the peak of courtship (May), we were fairly confident that the recorded males within each season did not move between our studied lek sites (Storch 1997, Wegge et al. 2005) and were different from each other.

Male Capercaillies also exhibit a high fidelity to lek sites from year to year. According to Bañuelos et al. (2024), the probability of a male moving to a different lek area from one year to the next is only 0.33, and the median distance of these movements is only

483 m, with very few greater than 4,000 m. The sites where we recorded males in 2022 were 4 and 10 km away from the nearest sites where we recorded males in 2021, and separated by high mountains and valleys, so there is a very low possibility that the calls recorded in 2022 belonged to a bird already recorded in the previous year. Recording was conducted between 20:00 and 23:00 hours and between 5:00 and 11:00 hours (local time) from a hide installed on each study plot during the peak of the first fortnight of the breeding season.

To minimize disturbance, we entered the hides at 18:30–19:00 hours (1.5 h before the usual display start time) and left at 12:00 hours, after the end of the display time (Servei de Biodiversitat i Protecció dels Animals 2015). No recordings were made on rainy or windy days (Budka et al. 2015). We used a Neve VR ambisonic microphone connected to a Zoom F6 recorder set to 48 kHz sampling rate, 32 bits float, with 32 dB of gain and 80 Hz high pass filter, obtaining signals from birds up to 180 m away. A windshield Boya-WS1000 was used to eliminate wind noise.

Ambisonic microphones record in a so-called A-format, which has to be converted to B-format before formal analysis of the calls. We did this conversion using the Soundfield plug-in on the host software Adobe Audition (Adobe Systems Incorporated 2003). We also used Adobe Audition to create virtual super-directive microphones to discriminate simultaneous calls coming from different individuals in the lek (Moreau et al. 2006). We analysed each song and manually extracted the sound values on the spectrogram using Avisoft-SASLab Pro software (Specht 2016) with setting of FFT length 1,024, frame size 100%, overlap 87.5%, Hamming window, time resolution 5.8 ms, frequency resolution 22 Hz and sampling rate 22.05 kHz.

The display call of male Capercaillies is formed by a series of preliminary syllables that lead into the main call, which is formed by a characteristic initial single syllable – the ‘click’, followed by a trill (a quick repetition of syllables) that is immediately followed by a characteristic single syllable – the ‘cork’ and sounding like pulling a cork from a bottle, which then gives rise to the ‘whetting’ – a sequence of syllables sounding like a scraping noise (Figure 2) (Castroviejo 1975, Hart et al. 2020). Besides the duration of some vocal components, previous studies have already shown the importance of the fundamental frequency of the ‘cork-pop’ note in discriminating between individuals (Laiolo et al. 2011, Hart et al. 2020), so here we have also taken this syllable into account.

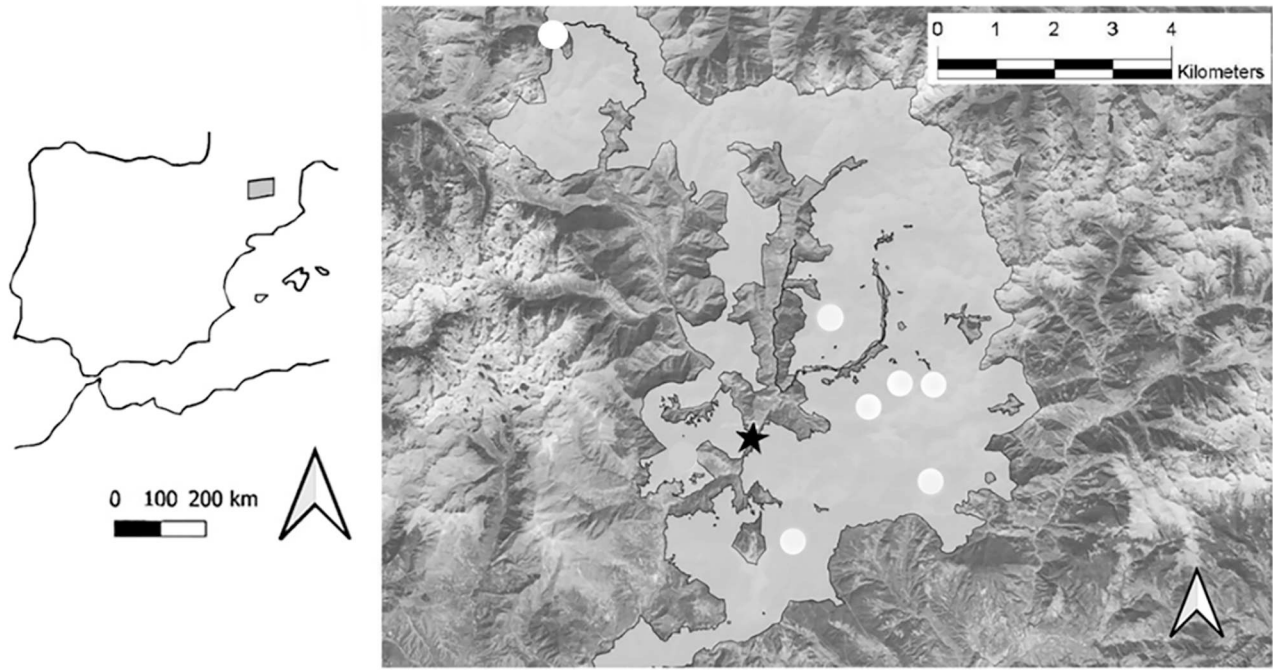


Figure 1. Study area in the Alt Pirineu Natural Park, Catalonia. Circles indicate the location of the seven Capercaillie lek sites sampled. The star indicates the village of Llavorsí.

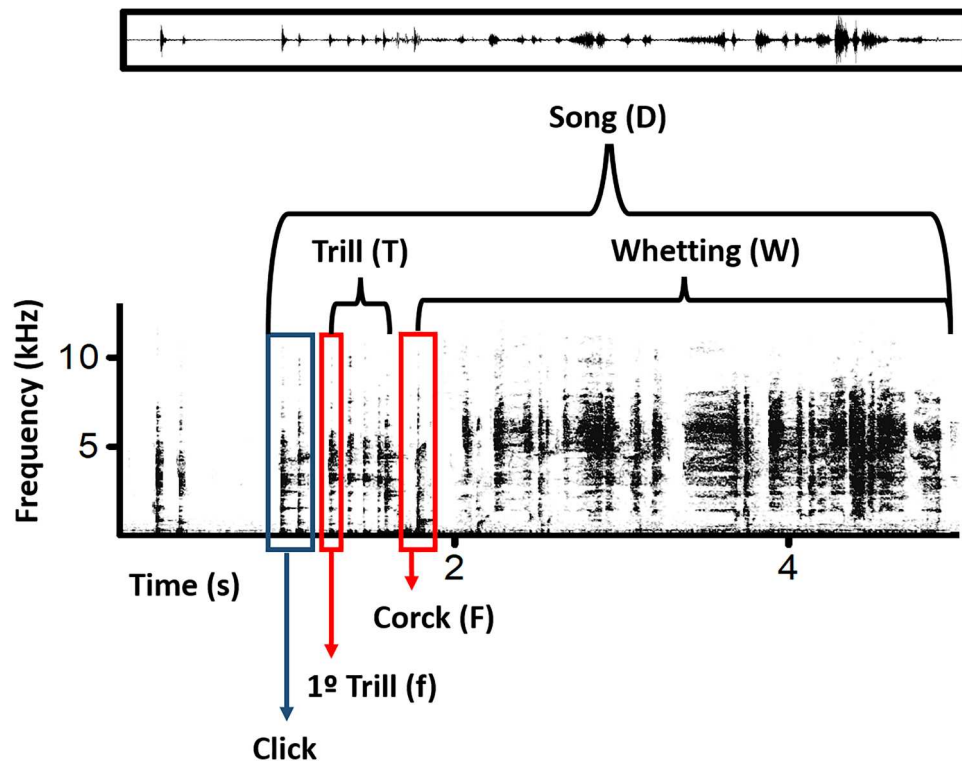


Figure 2. Spectrogram of a Capercaillie song showing the four phases: 'Click', Trill, 'Cork' and 'Whetting'. The variables measured are: D = song duration (s); f = fundamental frequency of the first component of the Trill phase (Hz); F = fundamental frequency of the 'cork-pop' note (Hz); T = duration of the Trill phase (s); and W = duration of 'whetting' (s). The start of each phase or component was defined by the peak in the amplitude spectrum.

The first syllable of the trill has been used in analyses because the following syllables of the trill phase are a 'shadow' of the first, and the intensity peaks are less marked and do not give as much information as the first syllable. Contrary to Laiolo *et al.* (2011), we did not use the mean of the entire trill phase for this reason. We defined a sample call as the sequence of sounds produced from the first individual syllable until the last syllable of the 'whetting' phase. We recorded 90 sample calls of every male at each night session.

On each sample call, we measured the following acoustic variables on the spectrogram and on the amplitude spectrum (Figure 2): (1) the call duration (D) as the number of seconds from the start of the syllable 'click' till the start of the last syllable of the wetting phase; (2) the duration of the trill phase (T) as the number of seconds from the start of the first syllable of the trill until the start of the last syllable of the trill; (3) The duration of the 'whetting' (W) as the number of seconds from the start of the 'cork' syllable until the start of the last syllable of the 'whetting' phase; (4) the fundamental frequency of the first syllable of the trill (f) in Hz, which is the frequency where we find the first peak of highest intensity on the amplitude spectrum of the spectrogram; (5) the fundamental frequency of the 'cork-pop' note (F) in Hz, which is the frequency of the first peak of highest intensity on the amplitude spectrum of the spectrogram.

Each syllable is a pulse in the spectrogram. Its beginning was defined by a peak amplitude profile measured in the amplitude frequency domain from the amplitude spectrum. The duration of each sound component was measured on the time domain of the spectrogram in seconds (s) (Hart *et al.* 2020).

Statistical analysis

Medians, means and minimum–maximum ranges were computed for all variables. Most variables showed some Heteroscedasticity between birds and also some outliers. Therefore, differences in each variable between individual birds were tested by means of non-parametric Kruskal–Wallis tests (Hollander & Wolfe 1973) and Dunn's post-hoc tests, with Holm's P -adjustment method for pairwise comparisons (Siegel & Castellan 1988). We used a supervised cluster analysis (Alloghani *et al.* 2020.) to find out whether it was possible to classify the different calls obtained, according to the male that produced them. We compared two well-known methods of supervised cluster analysis, the K-nearest-neighbour algorithm (K-NN) (Venables & Ripley 2013) and quadratic

discriminant analysis (QDA) (Starzacher & Rinner 2009).

K-NN is a non-parametric method, where no data distribution is assumed. For the implementation of K-NN, the min–max normalization of variables has been used so that they all take values between 0 and 1, and a Euclidean distance is used. Each test sample observation is classified into the most common group among the closest K neighbours of training data. This K value must be specified by the user and depends on the problem and the data. In our case, the values of K have been varied from 1 to 30 and the optimum has been obtained for $K = 2$.

The QDA-supervised cluster analysis assumes that the variables of each group are distributed according to a multivariate normal distribution, where the mean and matrix of covariances can be different between groups. The probabilities of belonging to each group have been considered equiprobable, considering a priori that the call of an individual may come with the same probability as any other individual. Some of the variables did not exhibit variability, especially the 'cork-pop' frequency (Figure 3), which arose from the technology's difficulty in measuring low frequencies accurately. In order to apply QDA, it was necessary to estimate the variance of each variable for each male, and, computationally, this value cannot be zero. Therefore, we introduced a negligible white noise (from a normal distribution with a mean of zero and a deviation of 0.01) to enable the analysis. However, adding noise to the data made it more challenging to detect the signal.

To evaluate the predictive properties of each method and compare them, an ad hoc cross-validation was performed (Gelman *et al.* 1996). By aligning the validation process with the specific objectives, we ensured that the model's performance was evaluated in a manner that directly addressed the intended use and requirements. Training data were first created by excluding from the original dataset the sample call of a same-day Capercaillie (session) and the excluded sample calls became the test data. On each day 90 calls were recorded, so we classified all the songs of the session into the Capercaillie (cluster) where most of the calls were classified. For the Capercaillie where only one session was recorded, the 90 calls were divided into three groups of 30 calls and we then proceeded in the same way, as if we had three sessions of 30 calls. Thus, in total, 48 pairs of training and test datasets were created (2 Capercaillies with 6 sessions, 3 birds with 5 sessions and 7 had their only session divided into 3 sub-sessions, $2 \times 6 + 3 \times 5 + 7 \times 3 = 48$).

Finally, for each method we evaluated how well the test data were classified, using the percentage of well-

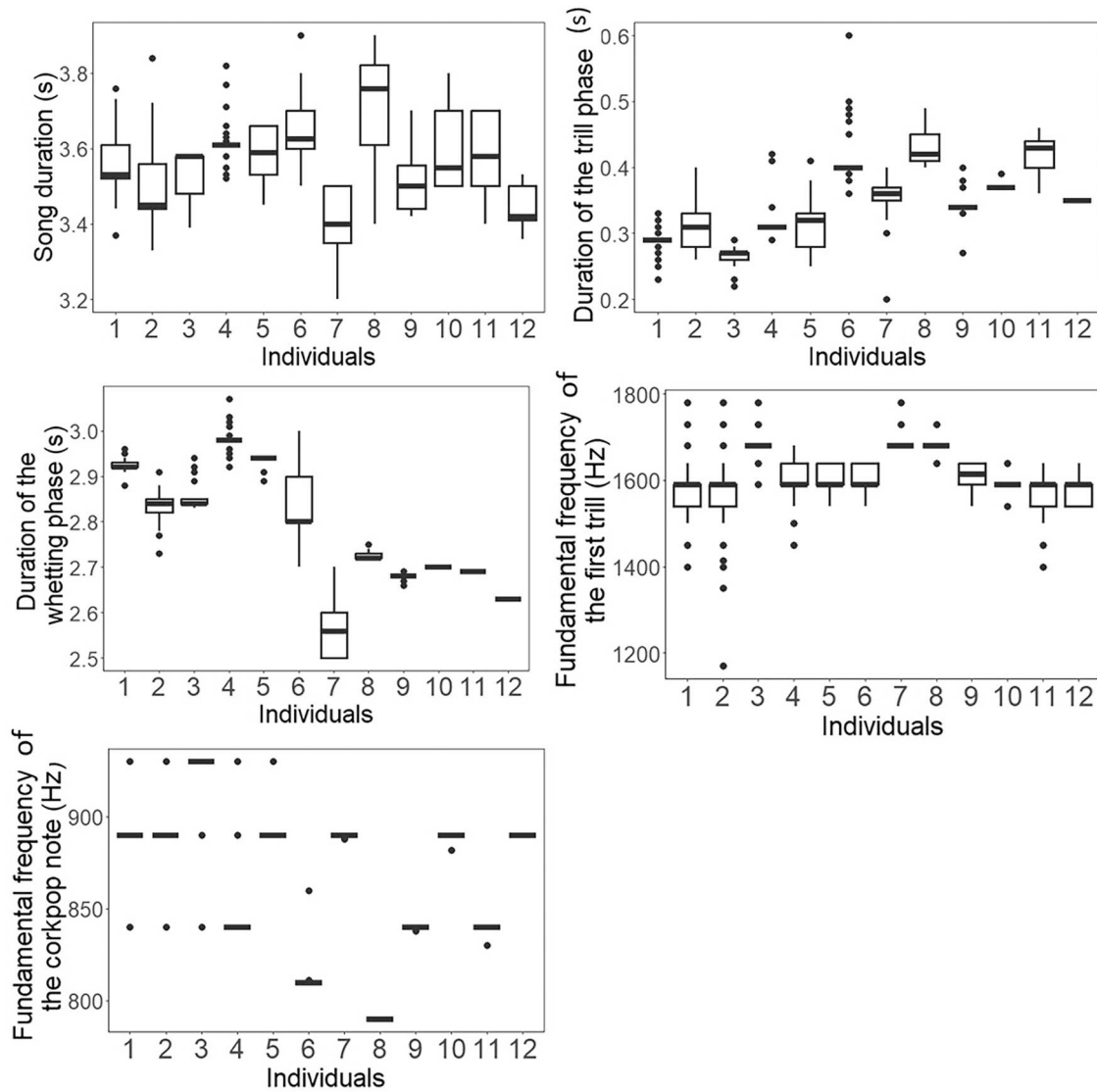


Figure 3. Box plots showing the median (horizontal line), the Q1 and Q3 quartiles (the box), the maximum and minimum values (vertical lines) and the outliers (points) for the variables characterizing each call. D = song duration (s); T = duration of the trill phase (s); W = duration of ‘whetting’ (s); f = fundamental frequency of the first component of the trill phase (Hz); and F = fundamental frequency of the ‘cork-pop’ note (Hz).

classified sessions or sub-sessions. Descriptive analyses were performed using R Statistical Software (v. 4.0.4; R Core Team 2021). We performed post-hoc analysis using the R package PMCMRplus (Pohlert 2023) for identifying significant differences between groups. The QDA was conducted using the R package MASS (Venables & Ripley 2013, Ripley 2024), and the K-NN analysis was implemented using the R package ‘class’ (Venables & Ripley 2013, Ripley 2023).

Results

The descriptive analysis showed inter-individual variability in the five acoustic variables analysed (Figure 3, Table 1). Kruskal–Wallis tests showed

significant differences among birds in each variable (all P -values < 0.001). Post-hoc tests showed significant inter-individual differences in most of the possible 66 pairwise comparisons for each variable. Specifically, 59 of the 66 pairs were significantly different for the variable D , 53 for T , 48 for W , 47 for f and 49 for F (details of all pairwise comparisons are in the supplementary material).

Both the K-NN and QDA methods correctly classified 100% of the sessions or sub-sessions of the test data (Table 2), meaning that call sessions of previously recorded males could be assigned to the correct individual with almost total certainty. When considering individual calls the percentages were lower, but, in practice, we did not aim to classify

Table 1. Descriptive analysis (median and minimum–maximum range) for the calls of the 12 recorded male Capercaillies over their recording sessions, and the global corresponding average and standard deviation. Kruskal–Wallis test results (H score and *P*-value) are reported in all of the variables of the call structure: *D* = full call duration; *T* = duration of the trill phase; *W* = duration of ‘whetting’ phase; *f* = fundamental frequency of the first syllable of the trill; *F* = fundamental frequency of the ‘cork-pop’ note (see Methods for details).

Individual	Sessions	<i>D</i> (s)	<i>T</i> (s)	<i>W</i> (s)	<i>f</i> (Hz)	<i>F</i> (Hz)
1	6	3.53 (3.37–3.76)	0.29 (0.23–0.33)	2.92 (2.88–2.96)	1,590 (1,400–1,780)	890 (840–930)
2	6	3.45 (3.33–3.84)	0.31 (0.26–0.40)	2.84 (2.73–2.91)	1,590 (1,170–1,780)	890 (840–930)
3	5	3.58 (3.39–3.58)	0.27 (0.22–0.29)	2.84 (2.83–2.94)	1,680 (1,590–1,780)	930 (840–930)
4	5	3.61 (3.52–3.82)	0.31 (0.29–0.42)	2.98 (2.92–3.07)	1,590 (1,450–1,680)	840 (840–930)
5	5	3.59 (3.45–3.66)	0.32 (0.25–0.41)	2.94 (2.89–2.94)	1,590 (1,540–1,640)	890 (890–930)
6	1	3.63 (3.50–3.90)	0.40 (0.36–0.60)	2.80 (2.70–3.00)	1,590 (1,540–1,640)	810 (810–860)
7	1	3.40 (3.20–3.50)	0.36 (0.20–0.40)	2.56 (2.50–2.70)	1,680 (1,680–1,780)	890 (888–890)
8	1	3.76 (3.40–3.90)	0.42 (0.40–0.49)	2.72 (2.72–2.75)	1,680 (1,640–1,730)	790 (790–790)
9	1	3.50 (3.42–3.70)	0.34 (0.27–0.40)	2.68 (2.66–2.69)	1,615 (1,540–1,640)	840 (838–840)
10	1	3.55 (3.50–3.80)	0.37 (0.37–0.39)	2.70 (2.70–2.70)	1,590 (1,540–1,640)	890 (882–890)
11	1	3.58 (3.40–3.70)	0.43 (0.36–0.46)	2.69 (2.69–2.69)	1,590 (1,400–1,640)	840 (830–840)
12	1	3.42 (3.36–3.53)	0.35 (0.35–0.35)	2.63 (2.63–2.63)	1,590 (1,540–1,640)	890 (890–890)
Total		3.58 (3.20–3.90)	0.31 (0.20–0.60)	2.86 (2.50–3.07)	1590 (1,170–1,780)	890 (790–930)
Kruskal–Wallis’ <i>H</i>		2,051.1 <i>P</i> < 0.001	2,806.8 <i>P</i> < 0.001	2,806.8 <i>P</i> < 0.001	1,872.2 <i>P</i> < 0.001	2,190.4 <i>P</i> < 0.001

individual calls but rather a sequence of calls from the same bird.

Discussion

Our results support previous research (Laiolo *et al.* 2011, Hart *et al.* 2020) showing that the calls of male Capercaillies can be individually discriminated by their acoustic characteristics. However, previous research was based either on the low-frequency components of the vocalizations (Hart *et al.* 2020), which was only possible in captivity using very expensive equipment logistics (Florkowski *et al.* 2023, Sagasti *et al.* 2023, Wilson *et al.* 2023), or with the use of shot gun or omnidirectional microphones that properly detect and record sounds only when the source is directly pointed at (Farina *et al.* 2010, Farina & Tronchin 2013). These latter methods do not record the entire signal due to the outdoor dispersal and attenuation of sound (Slabbekoorn *et al.* 2007, Schreiber & Beckenbauer 2013), and thus limit the recording of wild birds to very close range (<15 m in Laiolo *et al.* 2011). The ambisonic technology used in this project allowed us to record the audible calls from several males at once, from up to 150 m distance (Moreau *et al.* 2006, Mattioli *et al.* 2017, Jordi *et al.*

2023), avoiding the potential distortion and attenuation problems associated with standard omnidirectional or shotgun microphones when used outdoors (Slabbekoorn *et al.* 2007).

The supervised cluster analysis showed that such recordings of individual male Capercaillies could be individually distinguished from each other on the basis of a few acoustic variables. In this study, supervised cluster analysis QDA and the non-parametric K-NN method were compared and both showed good behaviour by correctly classifying 100% of sessions and sub-sessions. These similar results add robustness to the final conclusions. The individual discrimination of the calls was possible thanks to the combined effect of its several components. However, future research should analyse in more detail which are the best classification techniques, including not only those implemented in this work but also other methods, such as classification trees (Naufal *et al.* 2023).

We found little or no intra-individual variation in the fundamental frequencies of the recorded sounds, which agreed with the expectation that these frequencies are closely linked to the individual characteristics of each bird, such as body size or characteristics of the respiratory system, which are largely genetically determined (Brumm 2009, Kriesell *et al.* 2020). The

Table 2. Percentage of sessions or sub-sessions correctly classified by each of the two supervised cluster analysis methods employed (k-NN and QDA, respectively) and minimum and maximum percentage of calls within each session or sub-session correctly classified. For Capercaillies with 5 or 6 recording sessions (Capercaillies 1–5), % of well-classified sessions are presented. For Capercaillies with a single session (Capercaillies 6–12 with), this was split into 3 sub-sessions.

Capercaillie	K-NN			QDA		
	Well-classified sessions or sub-sessions % (number)	Min. calls correctly classified %	Max. calls correctly classified %	Well-classified sessions or sub-sessions % (number)	Min. calls correctly classified %	Max. calls correctly classified %
1	100 (6)	84.4	97.8	100 (6)	68.9	78.9
2	100 (6)	80.0	100	100 (6)	72.2	100
3	100 (5)	98.9	100	100 (5)	97.8	100
4	100 (5)	96.7	100	100 (5)	93.3	100
5	100 (5)	86.7	100	100 (5)	88.9	98.9
6	100 (3)	93.3	100	100 (3)	93.3	100
7	100 (3)	90	100	100 (3)	96.7	100
8	100 (3)	100	100	100 (3)	100	100
9	100 (3)	76.7	96.7	100 (3)	76.7	100
10	100 (3)	96.7	100	100 (3)	96.7	100
11	100 (3)	86.7	96.7	100 (3)	83.3	96.7
12	100 (3)	100	100	100 (3)	100	100
Global	100 (48/48)	76.79	100	100 (48/48)	68.9	100

few intra-individual deviations of the values of these variables were considered acoustically normal since it occurred approximately within the same third of the octave frequency (Weiss 2023). In line with this result, the inter-individual differences found in the post-hoc analysis for the fundamental frequency of the trill, and the fundamental frequency of the ‘cork’, probably convey relevant information about the size or other general and phenotypic characteristics of the male. This agreed with the results of Laiolo *et al.* (2011), who found that males singing at lower frequencies (indicative of a larger body size) settle in apparently better habitat plots.

However, given the limited body-size variation that exists between individual grouse (Castroviejo 1975), little more inter-individual variation of the fundamental frequencies could be expected unless the number of grouse in our sample was increased (Brumm 2009, Shelly 2018). Despite this, fundamental frequencies by themselves were not the only variables involved in individual discrimination. The ability to emit calls of longer duration and at lower frequencies is associated with larger birds of greater body condition (Juola & Searcy 2011), which probably confers a higher capacity for territorial defence and sexual attraction (Benedict & Warning 2017, Wang *et al.* 2019). In this way, the duration and frequencies of the call may be indicative of male condition and status, conferring a recognizable individual signature that remains constant (Favaro *et al.* 2015, Hart *et al.* 2020).

Increasing the number of leks and Capercaillies recorded in the future would probably reduce the percentage of good classification, as there is a greater

likelihood that two individuals would have similar songs (Brumm 2009, Shelly 2018). This potential problem can be mitigated by weighting the classification probabilities so that it considers a recording is more likely to come from the same individual if the recordings have been obtained at the same lek site, and less likely when the lek sites are further away. With QDA analysis this can be incorporated easily, since the a priori probability of belonging to a cluster (one male Capercaillie selected) can be defined so that it depends on the distance between lek sites (Starzacher & Rinner 2009). Moreover, including new variables, such as syllabic composition, spectral shape or time elapsed between song components of the calls (Mandiwana *et al.* 2014, Bregman *et al.* 2016, Templeton 2016) could also help to optimize correct classifications with larger sample sizes. Capercaillie leks in Catalonia are quite small, with most containing fewer than four males, and the maximum number counted in a single lek is 10 (Servei de Biodiversitat i Protecció dels Animals 2015). Therefore, this technique of considering further variables in analyses may be useful in Catalonia but perhaps not elsewhere when leks include more males and the probability of finding similarly calling males could be greater. In order to evaluate the robustness of the proposed methodology when the number of males increases, we intend to carry out a larger sampling, including tagged males, so that we can clearly check for consistency in the calls of more individual birds, and also for consistency of the calls during their lifespan.

Our results are a first step for the development of techniques allowing the identification of different

males from their call, by developing an algorithm to assign any Capercaillie call to a previously registered call or as belonging to a previously unregistered male, using a similar approach to Puig *et al.* (2016) in the analysis of attribution of texts to different authors. Being able to identify male Capercaillies by their calls, over long distances and in closed forest environments, would provide a relatively easy way to monitor the annual composition and hierarchies of leks (Abrahams 2019), as well as the movements between leks within the metapopulation (Sachot *et al.* 2006, Wegge *et al.* 2009). However, to achieve this objective, future research should also address whether the individual signatures are maintained in successive years, which would be key in developing such monitoring programmes.

The usual method for estimating population size and trends of Capercaillie populations is direct lek surveys through observations and listening by researchers in the field. However, this human disturbance may reduce the number of birds actually calling. Moreover, the results may be subject to between-observer biases, and the limited availability of people and funding to conduct the counts often results in the impossibility of surveying the whole population (Abrahams 2019, Baines & Aebischer 2023). Acoustic monitoring can overcome such limitations by being non-invasive, free of between-observer biases, easily standardized and a less resource-demanding technique (Farina *et al.* 2010, Mattioli *et al.* 2017).

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References

- Abrahams, C. 2019. Comparison between lek counts and bioacoustic recording for monitoring Western Capercaillie (*Tetrao urogallus* L.). *J. Ornithol.* **160**: 685–697.
- Adobe Systems Incorporated. 2003. *Adobe Audition* (13.0.6). Windows. Adobe, San Jose, CA.
- Alloghani, M., Al-Jumeily, D., Mustafina, J., Hussain, A. & Aljaaf, A.J. 2020. A systematic review on supervised and unsupervised machine learning algorithms for data science. In Berry, M. W., Mohamed, A. & Yap, B. W. (eds) *Supervised and Unsupervised Learning for Data Science*, 3–21. Springer, Cham, Switzerland.
- Baines, D. & Aebischer, N. 2023. Estimating Capercaillie *Tetrao urogallus* population size in Scotland from annual leks and counts of broods over the period 2010–2020. *Wildl. Biol.* **2023**: e01104.
- Bañuelos, M., Morán-Luis, M., Mirol, P. & Quevedo, M. 2024. Tracking movements in an endangered Capercaillie population using DNA tagging. *Wildl. Biol.* **2024**: e01121.
- Benedict, L. & Warning, N. 2017. Rock Wrens preferentially use song types that improve long distance signal transmission during natural singing bouts. *J. Avian Biol.* **48**: 1254–1262.
- Bocaccio, H., Domínguez, M., Mahler, B., Reboreda, J. & Mindlin, G. 2023. Identification of dialects and individuals of globally threatened Yellow Cardinals using neural networks. *bioRxiv*.
- Braun, C., Taylor, W., Ebbert, S. & Spitler, L. 2019. Monitoring Rock Ptarmigan (*Lagopus muta*) populations in the Western Aleutian Islands, Alaska. *Can. Field-Nat.* **133**: 49–55.
- Bregman, M.R., Patel, A.D. & Gentner, T.Q. 2016. Songbirds use spectral shape, not pitch, for sound pattern recognition. *Proc. Natl. Acad. Sci. U.S.A.* **113**: 1666–1671.
- Brumm, H. 2009. Song amplitude and body size in birds. *Behav. Ecol. Sociobiol.* **63**: 1157.
- Budka, M., Wojas, L. & Osiejuk, T.S. 2015. Is it possible to acoustically identify individuals within a population? *J. Ornithol.* **156**: 481–488.
- Buxton, R. & Jones, I. 2012. Measuring nocturnal seabird activity and status using acoustic recording devices: applications for island restoration. *J. Field Ornithol.* **83**: 47–60.
- Castroviejo, J. 1975. El urogallo en España. Monografías de la Estación Biológica de Doñana, 3. *Consejo Superior de Investigaciones Científicas, Madrid* **84**: 546.
- Cheng, J., Xie, B., Lin, C. & Ji, L. 2012. A comparative study in birds: call-type-independent species and individual recognition using four machine-learning methods and two acoustic features. *Bioacoustics* **21**: 157–171.
- Clutton-Brock, T. & Sheldon, B. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *TREE* **25**: 562–573.
- Cramer, E.R. 2013. Physically challenging song traits, male quality, and reproductive success in House Wrens. *PLoS One* **8**.
- Eliassen, S. & Wegge, P. 2007. Ranging behaviour of male Capercaillie *Tetrao urogallus* outside the lekking ground in spring. *J. Avian Biol.* **38**: 37–43.
- Elie, J.E. & Theunissen, F.E. 2018. Zebra finches identify individuals using vocal signatures unique to each call type. *Nat. Commun.* **9**: 4026.

- Fagerlund, S. 2012. Acoustic monitoring of Capercaillie courting display. In Ciplys, D. (ed) *19th International Congress on Sound and Vibration 2012*, Vol. 2, 1681–1688. International Institute of Acoustics and Vibration, Vilnius, Lithuania.
- Farina, A., Capra, A., Chiesi, L. & Scopece, L. 2010. A spherical microphone array for synthesizing virtual directive microphones in live broadcasting and in post production. In *Proceedings of the AES 40th International Conference: Spatial Audio: Sense the Sound of Space*, 1–11. Audio Engineering Society, Tokyo, Japan.
- Farina, A. & Tronchin, L. 2013. 3D sound characterisation in theatres employing microphone arrays. *Acta Acust. United. Acust.* 1: 118–125.
- Favaro, L., Gamba, M., Alfieri, C., Pessani, D. & McElligott, A. 2015. Vocal individuality cues in the African Penguin (*Spheniscus demersus*): a source-filter theory approach. *Sci. Rep.* 5: 17255.
- Florkowski, M.R., Hamer, S.A. & Yorzinski, J.L. 2023. Brief exposure to captivity in a songbird is associated with reduced diversity and altered composition of the gut microbiome. *FEMS Microbiol. Ecol.* 99: fiad096.
- Fox, E.J.S., Roberts, D. & Bennamoun, M. 2008. Call-independent individual identification in birds. *Bioacoustics* 18: 51–67.
- Fujiwara, H. & Tobari, Y. 2021. Courtship vocalizations in non-songbirds: auditory and neuroendocrine mechanisms in intersexual communication. In Rosenfeld, C. (ed) *Neuroendocrine Regulation of Animal Vocalization*, Vol. 10: 327–334. Academic Press, San Diego, CA.
- Gelman, A., Meng, X. & Stern, H. 1996. Posterior predictive assessment of model fitness via realized discrepancies. *Stat. Sin.* 6: 733–807.
- Gémard, C., Aubin, T., Reboud, E. & Bonadonna, F. 2021. Call rate, fundamental frequency, and syntax determine male-call attractiveness in Blue Petrels *Halobaena caerulea*. *Behav. Ecol. Sociobiol.* 75: 1007.
- Gil, D. & Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* 17: 133–141.
- Gil, J., Gómez-Serrano, M. & López-López, P. 2020. Population decline of the Capercaillie *Tetrao urogallus aquitanicus* in the Central Pyrenees. *Ardeola* 67: 285.
- Gonzalez, M., Garcia-Tejero, S., Wengert, E. & Fuertes, B. 2016. Severe decline in Cantabrian Capercaillie *Tetrao urogallus cantabricus* habitat use after construction of a wind farm. *Bird Conserv. Int.* 26: 256–261.
- Hart, V., Policht, R., Jandák, V., Brothánek, M. & Burda, H. 2020. Low frequencies in the display vocalization of the Western Capercaillie (*Tetrao urogallus*). *PeerJ.* 8: e9189.
- Hjeljord, O., Wegge, P., Rolstad, J., Ivanova, M. & Beshkarev, A. 2000. Spring-summer movements of male Western Capercaillie: a test of the 'landscape mosaic' hypothesis. *Wildlife. Biol.* 6: 251–256.
- Hollander, M. & Wolfe, D.A. 1973. *Nonparametric Statistical Methods*. John Wiley & Sons, New York.
- Jahren, T., Storaas, T., Willebrand, T. & Fosslund, M.P. 2016. Declining reproductive output in Capercaillie and Black Grouse – 16 countries and 80 years. *Anim. Biol.* 66: 363–400.
- Jordi, O., Farina, A. & Mañosa, S. 2023. Sound amplitude (dB) of male Western Capercaillie *Tetrao urogallus* calls. *RCO* 39: 60–64.
- Juola, F. & Searcy, W. 2011. Vocalizations reveal body condition and are associated with visual display traits in Great Frigatebirds (*Fregata minor*). *Behav. Ecol. Sociobiol.* 65: 2297–2303.
- Kondo, N., Izawa, E.-I. & Watanabe, S. 2010. Perceptual mechanism for vocal individual recognition in Jungle Crows (*Corvus macrorhynchos*): contact call signature and discrimination. *Behaviour* 147: 1051–1072.
- Kriesell, H.J., Le Bohec, C. & Cerwenka, A.F. 2020. Vocal tract anatomy of King Penguins: morphological traits of two-voiced sound production. *Front. Zool.* 17: 1–11.
- Laiolo, P., Bañuelos, M.J., Blanco-Fontao, B., García, M. & Gutiérrez, G. 2011. Mechanisms underlying the bioindicator notion: spatial association between individual sexual performance and community diversity. *PLoS One* 6: e22724.
- Liu, W., Wada, K. & Jarvis, E. 2013. Rudimentary substrates for vocal learning in a suboscine. *Nat. Commun.* 4: 2082.
- Logue, D., Sheppard, J., Walton, B., Brinkman, B. & Medina, O. 2019. An analysis of avian vocal performance at the note and song levels. *Bioacoustics* 2: 709–730.
- Mandiwana, T., Bowie, R., Hausberger, M., Henry, L. & Crowe, T. 2014. Taxonomic and phylogenetic utility of variation in advertising calls of francolins and spurfowls (Galliformes: Phasianidae). *Afr. Zool.* 49: 54–82.
- Marin-Cudraz, T. 2019. *Potentialité de la bioacoustique comme outils de dénombrement d'espèces d'accès difficile: Cas du Lagopède alpin (Lagopus muta)*. PhD thesis, University of Lyon, France.
- Marques, T.A., Thomas, L., Martin, S., Mellinger, D.K., Ward, J.A., Moretti, D.J., Harris, D.V. & Tyack, P.L. 2013. Estimating animal population density using passive acoustics. *Biol. Rev. Camb. Philos. Soc.* 88: 287–309.
- Martin, K., Adam, O., Obin, N. & Dufour, V. 2022. Rookognise: acoustic detection and identification of individual Rooks in field recordings using multi-task neural networks. *Ecol. Inform.* 72: 101818.
- Mattioli, T., Farina, A., Armelloni, E., Hameau, P. & Díaz Andreu, M. 2017. Echoing landscapes: echolocation and the placement of rock art in the Central Mediterranean. *J. Archaeol. Sci.* 83: 12–25.
- Moreau, S., Daniel, J. & Bertet, S. 2006. 3D sound field recording with higher order ambisonics – objective measurements and validation of a 4th order spherical microphone. Paper presented at Audio Engineering Society 120th Convention, Paris, France.
- Naufal, H., Efendi, A. & Sumarminingsih, E. 2023. Bayesian additive regression trees for classification of unbalanced class of credit collectability data. *Asian J. Probab. Stat.* 23: 16–27.
- Pélachs, A., Tersa, J., Soriano, J.M., Molina, D. & Cunill Artigas, R. 2009. Changes in Pyrenean woodlands as a result of the intensity of human exploitation: 2,000 years of metallurgy in Vallferrera, northeast Iberian Peninsula. *Veg. Hist. Archaeobot.* 18: 403–416.
- Pohlert, T. 2023. *PMCMRplus: calculate pairwise multiple comparisons of mean rank sums extended*. R package version 1.9.10.

- Průchová, A., Jaška, P. & Linhart, P. 2017. Cues to individual identity in songs of songbirds: testing general song characteristics in Chiffchaffs *Phylloscopus collybita*. *J. Ornithol.* **158**: 911–924.
- Puig, X., Font, M. & Ginebra, J. 2016. A unified approach to authorship attribution and verification. *Am. Stat.* **70**: 232–242.
- R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rebbeck, M., Corrick, R., Eaglestone, B. & Stainton, C. 2001. Recognition of individual European Nighthawks *Caprimulgus europaeus* from their song. *Ibis* **143**: 468–475.
- Ripley, B. 2023. *Class: functions for classification*. R package version 7.3-22.
- Ripley, B. 2024. *MASS: support functions and datasets for Venables and Ripley's MASS*. R package version 7.3-60.0.1.
- Robisson, P., Aubin, T. & Bremond, J.C. 2010. Individuality in the voice of the Emperor Penguin *Aptenodytes forsteri*: adaptation to a noisy environment. *Ethology* **94**: 279–290.
- Sachot, S., Perrin, N. & Neet, C. 2006. Viability and management of an endangered Capercaillie (*Tetrao urogallus*) metapopulation in the Jura Mountains, Western Switzerland. *Biodivers. Conserv.* **15**: 2017–2032.
- Sagasti, A., Pietrzak, A., Martin, R. & Eguinoa, R. 2023. Localization of sound sources in binaural reproduction of first and third order ambisonics. *Vib. Phys. Syst.* **33**: Article 2022214.
- Schreiber, L. & Beckenbauer, T. 2013. Sound propagation outdoors. In Müller, G. & Möser M. (eds) *Handbook of Engineering Acoustics*, 125–136. Springer, Berlin, Germany.
- Serrurier, A., Zdroik, P., Isler, R., Kornienko, T., Peris Morente, E., Sattler, T. & Pradervand, J. 2024. Mountain is calling – decrypting the vocal phenology of an alpine bird species using passive acoustic monitoring. *Ibis* **166**: ibi.13314.
- Servei de Biodiversitat i Protecció dels animals. 2015. *Direcció General de Polítiques Ambientals*. Departament de Territori i Sostenibilitat. Resultats dels censos de cantaders de Gallfer a Catalunya.
- Shelly, T.E. 2018. Sexual selection on Leks: a fruit fly primer. *J. Insect Sci.* **18**: 9.
- Siegel, S. & Castellan Jr, N.J. 1988. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.
- Sirkia, S., Helle, P., Lindén, H., Nikula, A., Norrdahl, K., Suorsa, P. & Valkeajarvi, P. 2011. Persistence of Capercaillie (*Tetrao urogallus*) lekking areas depends on forest cover and fine-grain fragmentation of boreal forest landscapes. *Ornis Fenn.* **88**: 14–29.
- Slabbekoorn, H., Ellers, J. & Smith, T. 2002. The benefits of reverberations: birdsong and sound transmission. *Condor* **104**: 564–573.
- Slabbekoorn, H., Yeh, P. & Hunt, K. 2007. Sound transmission and song divergence: a comparison of urban and forest acoustics. *Condor* **109**: 67–78.
- Southwell, D., Smart, A., Merson, S., Selwood, K. & Macgregor, N. 2024. Using power analysis and spatial prioritization to evaluate the design of a forest bird monitoring programme. *Oryx* **1**: 10.
- Specht, R. 2016. *Avisoft-SASLab Pro Version 5.2.15. Sound Analysis and Synthesis Laboratory Software for MS-Windows*. Avisoft Bioacoustics, Berlin.
- Starzacher, A. & Rinner, B. 2009. Evaluating KNN, LDA and QDA classification for embedded online feature fusion. In *Proceedings of the 2008 International Conference on Intelligent Sensors, Sensor Networks and Information Processing*, 85–90. IEEE, Piscataway, NJ.
- Storch, I. 1997. Male territoriality, female range use, and spatial organisation of Capercaillie *Tetrao urogallus* leks. *Wildlife. Biol.* **3**: 149–161.
- Tarrero, A. 2002. *Propagación del sonido en bosques. Análisis comparativo de las medidas insitu, en laboratorio y de los valores predichos por un modelo*. PhD thesis, Universidad de Valladolid, Spain.
- Templeton, C.N. 2016. Name that tune: melodic recognition by songbirds. *Learn. Behav.* **44**: 305–306.
- Ten, C. 2021. Re-evaluating vocal production learning in non-oscine birds. *Phil. Trans. Royal Soc. B* **376**: 1836.
- Tibbetts, E. & Dale, J. 2007. Individual recognition: it is good to be different. *Trends Ecol. Evol.* **22**: 529–537.
- Van Doren, B., Farnsworth, A., Stone, K., Osterhaus, D., Drucker, J. & Horn, V. 2024. Nighthawk: acoustic monitoring of nocturnal bird migration in the Americas. *Methods Ecol. Evol.* **15**: 329–344.
- Venables, W. & Ripley, B. 2013. *Modern Applied Statistics with S-PLUS*. Springer, New York.
- Wada, H. 2010. The development of birdsong. *Nat. Educ. Knowl.* **3**: 86.
- Wang, J., Liu, J. & Zhang, Z. 2019. Male condition corrected with song features in Dusky Warblers (*Phylloscopus fuscatus*). *Avian Res.* **10**: 18.
- Wegge, P., Eliassen, S., Finne, M. & Odden, M. 2005. Social interactions among Capercaillie *Tetrao urogallus* males outside the lek during spring. *Ornis Fenn.* **82**: 147–154.
- Wegge, P., Finne, M. & Rolstad, J. 2009. GPS satellite telemetry provides new insight into Capercaillie *Tetrao urogallus* brood movements. *Wildlife. Biol.* **13**: 87–94.
- Weiss, Z. 2023. Tuning the octave bands: a history of dividing the spectrum for acoustical measurements in the 20th century. *J. Acoust. Soc. Am.* **153**: A183–A183.
- Weissaupt, N., Saari, J. & Koistinen, J. 2024. Evaluating the potential of bioacoustics in avian migration research by citizen science and weather radar observations. *PLoS One* **19**: e0299463.
- Westcott, D. 1992. Inter- and intra-sexual selection: the role of song in a lek mating system. *Anim. Behav.* **44**: 695–703.
- Wilson, T., Petrin, C. & Elbing, B. 2023. Infrasound and low-audible acoustic detections from a long-term microphone array deployment in Oklahoma. *Remote Sens.* **15**: 1455.