



Sound propagation in forest and habitat desertion in the Western Capercaillie (*Tetrao urogallus* L.)

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Abstract

The Western Capercaillie *Tetrao urogallus* L. uses its calls for breeding, territorial and hierarchical purposes. We investigated whether changes in the vegetation structure of the forest might affect call transmission and contribute to Western Capercaillie's lek desertion in the Pyrenees, as predicted by the acoustic adaptation hypothesis. We measured forest structure and the sound propagation properties of the forest at nine occupied lek sites and eleven deserted lek sites in the *Alt Pirineu* Natural Park in Catalonia (NE Spain). We found similar values of forest Maturity Index (MI), Human Footprint Index (HFI) or Spatial Integrity Index (SII) in both groups of stands. Abandoned stands exhibited higher Dominant Tree Height (Ho), higher Basal Area (BA), higher Volume of Living Trees (FV) and higher Volume of Dead Trees (FM). Deserted sites exhibited higher values of Background Noise (N) and lower values of scattering of the sound on the vertical and horizontal plane (JLFH and JLFV), resulting in longer reverberation time (T20), higher sound pressure level (SIGC) and a slower decay curve (K) due to lower attenuation. We suggest that the background noise and the sound propagation characteristics of the deserted forest stands might be affecting the transmission of Capercaillies' calls, creating distortion and masking of the acoustic signal by excessive reverberation and noise. Our results suggest that changes in the acoustic properties of forests, partially driven by changes in the forest structure, may contribute to lek desertion. If confirmed, conservation-oriented forest management for Capercaillies should aim not only to maintain food and shelter resources, but also to preserve acoustic conditions that facilitate non-distorted and correct signal discrimination during display.

Resumen

El urogallo occidental (*Tetrao urogallus* L.) utiliza sus vocalizaciones con fines reproductivos, territoriales y jerárquicos. Investigamos si los cambios en la estructura del bosque podrían afectar a la transmisión de las llamadas y contribuir de este modo al abandono de los cantaderos por parte del urogallo occidental en los Pirineos, tal como predice la hipótesis de la adaptación acústica. Medimos la estructura forestal y las propiedades de propagación del sonido en nueve cantaderos ocupados y once cantaderos abandonados en el Parque Natural del Alt Pirineu, en Cataluña (noreste de España). Encontramos valores similares del Índice de Madurez Forestal (MI), del Índice de Huella Humana (HFI) o del Índice de Integridad Espacial (SII) en ambos grupos de rodales. Los rodales abandonados presentaron mayor altura dominante de los árboles (Ho), mayor área basal (BA), mayor volumen de árboles vivos (FV) y mayor volumen de árboles muertos (FM). Los sitios abandonados mostraron valores más altos de ruido de fondo (N) y menores valores de dispersión del

In memory of Angelo Farina.

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sonido en los planos vertical y horizontal (JLFH y JLFV), lo que resultó en un mayor tiempo de reverberación (T20), un mayor nivel de presión sonora (SIGC) y una curva de decaimiento más lenta (K), debido a una menor atenuación. Sugerimos que el ruido de fondo y las características de propagación del sonido en los rodales forestales abandonados podrían estar afectando la comunicación de los urogallos, generando distorsión y enmascaramiento de la señal acústica debido a una reverberación y ruido excesivos. Nuestros resultados sugieren que los cambios en las propiedades acústicas de los bosques, parcialmente impulsados por cambios en la estructura forestal, pueden contribuir al abandono de los leks por parte del urogallo occidental. Si se confirman estos resultados, la gestión forestal orientada a la conservación no solo debería centrarse en mantener los recursos alimenticios y de refugio, sino también en preservar condiciones acústicas que faciliten una correcta transmisión y discriminación de las señales durante el cortejo.

Highlights

- Background noise and sound propagation properties differ between occupied and deserted Capercaillie's lek forest stands in the Pyrenees.
- These differences, probably partially associated to changes in forest stand structure, might impair Capercaillie communication within deserted stands, suggesting that changes in call transmission might play a role in lek desertion.
- If these results were confirmed by further research, conservation-oriented management should consider, in addition to other factors, how to maintain adequate bioacoustic properties of the forest stands where Capercaillie's display takes place.

Keywords Bioacoustics · Bird calls · Bird conservation · Ambisonic recording · Forest management

Introduction

Animals use acoustic communication for territorial, social or reproductive purposes (Wegge et al. 2005). According to the acoustic adaptation hypothesis, species that use sound in their communication should try to adopt strategies to maximize their broadcast range and quality of the signal transmission (Boncoraglio and Saino 2007; Luther and Gentry 2013; Mullet et al. 2017) while trying to reduce the associated social and ecological costs of being detected at the same time (Brumm and Zollinger 2015). However, several factors can impair signal propagation and alter communication, which may have detrimental impacts at the individual, population or community level (Naguib 2003; Erbe et al. 2022). According to the principles of soundscape ecology, animal communication takes place in specific soundscapes, composed of sounds generated by animals (biophony), humans (anthropophony) or natural elements (geophony) (Pijanowski et al. 2011). The way animal calls transmit in such landscapes depends on background noises, as well as on the structural characteristics of the habitat (Ey and Fisher 2009) and meteorological factors (Ehrhardt et al. 2013), which has intra- and inter-specific communication consequences (Lohr et al. 2003; Luther and Gentry 2013).

Outdoor sound propagation suffers attenuation resulting from geometrical divergence and surface absorption. Surface scattering, temperature and wind can increase or decrease the intensity of the sound (White and Swearingen 2004; Tarrero et al. 2008). In birds, vocal learners, such as Passerines, Psittaciformes and Trochiliformes, can easily

vary the frequency (Hz), the duration (s), the intensity (dB) or the syntax (number and syllabic distribution) of their calls and songs, which can improve the transmission of their messages depending on the surrounding soundscape (Pohl et al. 2015; Roca et al. 2016). Most non-passerines, however, the so-called non-vocal learners, are not as capable of modulating their calls and have limited vocal plasticity (Francis et al. 2011; Robisson et al. 2010), so their communication performance can be seriously impaired in soundscapes that limit sound transmission in some way (Francis et al. 2011; Ríos-Chelén et al. 2012). Although some non-vocal learners have evolved tracheal and thorax characteristics that improve their aerobic capacity and minimize song attenuation (Robisson et al. 2010; Hart et al. 2020), these communication problems may lead to reduced mating and reproductive success (Schroeder et al. 2012) or the abandonment particular sites (Erbe et al. 2022).

This problem is particularly important for woodland birds. Inside woodland, sound transmission can be affected by the dendrological and structural characteristics of the forest, as well as by the background noise (Tarrero et al. 2008; Muhlestein et al. 2018), which produce scattering and absorption (Swearingen and White 2007; Ehrhardt et al. 2013). To optimize sound propagation, some woodland animals shift the intensity (dB), the frequency (Hz) and the temporal structure (s) of their calls depending on the characteristics of the forest (Boncoraglio and Saino 2007). Several studies have analysed how habitat selection depends on the sound-scattering properties of the environment (Swearingen and White 2007; Mullet et al. 2017; García et al. 2022) and some other have stressed the need to consider the acoustical properties of

the forest in conservation oriented woodland management, which involves managing the forest to eliminate elements that impair sound transmission (Fang and Ling 2003; Boycott et al. 2019), as well as to promote the abatement of background noise (Tyagi et al. 2006; Iglesias-Merchán et al. 2019).

A good example of a non-learning woodland bird which might be subject to such communication constraints is the Capercaillie (*Tetrao urogallus* L.), which uses calls for individual recognition, territorial purposes and mating (Jahren et al. 2016; Hart et al. 2020). Thanks to its big ribcage, long trachea and optimal aerobic capacity, male Capercaillies produce a low-medium frequency band call which has optimal transmission characteristics in the coniferous forest habitat (Hart et al. 2020; Policht and Hart 2023). Each male produces a individual-specific call which probably encodes relevant information for mate choice and allows individual discrimination (Hart et al. 2020; Jordi et al. 2023). Changes in the characteristics of the forest might lead to sound distortion and reduced sound propagation, which could reduce the quality of the information transmitted and the subsequent mating success of males, making some specific forest patches less suitable for displaying.

The Pyrenees mountain range gives refuge, together with the Cantabrian mountains, to the southernmost Capercaillie populations in western Europe, where it occurs at the limits of its ecological tolerance (Canut et al. 2011). In the Pyrenees, the Capercaillie occurs mainly in coniferous forest, with Hook pine *Pinus uncinata* as the dominant tree species and Scots pine *Pinus sylvestris* or Silver fir *Abies alba* as accompanying trees (Sabaté et al. 2023). The occurrence of different phases of the sylvogenetic cycle gives those forest an irregular and heterogeneous structure, alternating clearings with denser forest, which contributes to the development of the understory (Canut et al. 2011; Sabaté et al. 2023). Capercaillie prefers mature, structurally diverse forests, characterized by canopy gaps with Bilberry *Vaccinium myrtillus* and Alpenrose *Rhododendron ferrugineum* on the undergrowth (Sitzia et al. 2019; Sabaté et al. 2023) and the presence of large live and dead trees, because they provide them with food and shelter (Montané et al. 2016; Sabaté et al. 2023; Plachyński et al. 2020). The management and conservation of such mature forests is key to maintaining the viability of Capercaillie populations (Quevedo et al. 2006b; Sirkia et al. 2011). Moreover, the presence of Capercaillie is associated to the presence of other forest specialist, so that it is considered as an umbrella species (Pakkala et al. 2003). Laiolo et al. (2011) showed that the characteristics of male's vocal display that advertise individual quality (low frequencies and rapid song rates) are significantly correlated with higher biodiversity values in the corresponding forest plots.

The Capercaillie is a species of conservation concern in many countries (Wegge et al. 2005; Sachot et al. 2006)

and it is ranked as threatened in Catalonia, our study region. Among other reasons, its poor conservation status in Catalonia is associated to the scarcity of mature forests, which still experiences deforestation and degradation (Pèlach et al. 2009; Palau and Garriga 2013). Several non-exclusive and synergistic factors have been postulated to explain the abandonment of leks and/or the reduction of Capercaillie's populations across its European range, including, climate change (Moss et al. 2001; Flousek et al. 2015), reduction of Bilberry production (Baines et al. 2004), excessive predation on adults or chicks (Baines et al. 2004; Moreno-Opo et al. 2015; Kämmerle and Storch 2019), habitat loss or fragmentation (Angelstam 2004; Suárez-Seoane et al. 2004; Quevedo et al. 2006a), excessive ungulate abundance (Quevedo et al. 2006a), or human disturbance (Suárez-Seoane et al. 2004; Thiel et al. 2008; Coppes et al. 2017). Gil et al. (2020) found that the decline in the number of males in the Central Pyrenees was faster at lower altitudes, suggesting that marginal habitats are deserted first, likely in association with an altitude shift of the forest quality caused by climate or land use changes. Paradoxically, Drozdowski et al. (2021, when comparing deserted and occupied Capercaillie lek sites in North-eastern Poland, showed that mature forests were being abandoned in favour of younger stands. This indicates that forest maturity per se might not be the only factor in place to ensure Capercaillies' persistence in a forest stand (Sirkia et al. 2011). However, the possibility that changes in the background noise or sound propagation properties of the forest might also play a role, as found in other species (García et al. 2022; Barbaro et al. 2023), has never been considered. In this study, we measured the dendrological characteristics and sound propagation profiles in forest stands occupied and deserted by the Capercaillies. By comparing the dispersion and persistence patterns of sound in both groups of forest stands, using acoustic impulse response analysis techniques (Farina 2007; Shelley et al. 2013), we aimed to establish whether changes in the acoustic variables of the forest stands may play a role in explaining the observed desertion patterns.

Materials and methods

Study area

The study was carried out in the Pyrenees, on the Natural Park *Alt Pirineu*, in Catalonia, NE Spain (Head Park office in Llavorsí, 42° 29' 45.530" N, 1° 12' 36.147" E) (Fig. 1). This area holds the largest population of Western Capercaillie on the Iberian Peninsula, but its population has declined from an estimate of 150 males in 2005 to 120 in 2015 (Servei de Biodiversitat i Protecció dels Animals 2015; Gil et al. 2020).

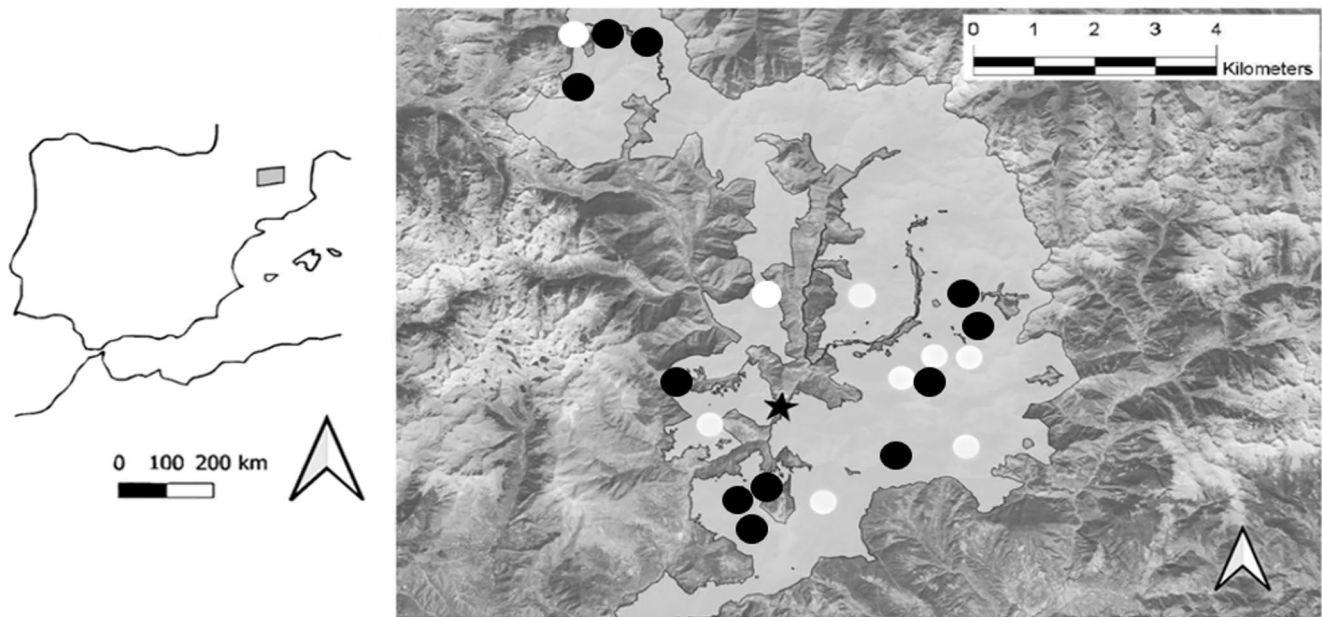


Fig. 1 Study area in Natural Park Alt Pirineu. White circles indicate the location of the nine occupied Capercaillie lek sites and the black dots indicate the eleven non-occupied lek sites. The star indicates the village of Llavorsí, where the head office of the natural park is located

Sampling design

We selected 20 forest stands of an average size of 14 ± 8 hectares (min=5 ha, max=31.1 ha). Nine of these stands were occupied lek-sites and eleven were former leks that have been deserted by Capercaillies since the last 10 years (Servei de Biodiversitat i Protecció dels animals 2015) (Fig. 1). The average altitude above sea level of all these stands was 2055 ± 159.60 m above sea level (min=1700, max=2300 m) and consisted on mixed forests dominated by Hook pine, with Bilberry, Alpenrose, Bearberry *Arctostaphylos uva-ursi*, and Common juniper *Juniperus communis* in the underground (Pèlachs et al. 2009).

Forest structure description

To characterize the forest structure of each stand, a series of dendrometric variables were measured (Table 1). At each of the 20 forest stands, we randomly selected three plots separated a minimum of 100 m from each other. On a 25 m radius around each of these points, we measured all the dead or alive standing and fallen trees greater than 17.5 cm diameter. We measured tree diameters and heights using a force pod and a laser meter respectively. These field measurement data were entered into the spreadsheets provided by the RedBosques forest monitoring protocol (Fungobe 2024), thereby yielding the values for the dendrometric

Table 1 Forestry indices and dendrometric variables measured on each study plot following the RedBosques protocol (see methods)

Variable name, acronym and units	Meaning
Maturity Index, MA	Low values correspond less heterogeneous forest due to the less structural and composition complexity reflected by dendrometric values.
Human Footprint Index, HFI	Based on historical data, low values correspond to low trace of human presence, which means less alteration of the forest.
Spatial Integrity Index, SII	Low values correspond to low spatial integration with the surrounding forest due to the spatial continuity, connectivity, and border effect characteristics.
Dominant tree height, Ho (m)	The average for each stand of the measured values of the tree height using a digital distance meter (laser).
Basal area, BA (m ² /ha)	It is a forest indicator that measures the degree of spatial occupancy. A high value indicates that the forest is dense and lush and that shaded conditions dominate below the canopy. Is the sum of the normal diameter sections (measured at 1.3 m from the ground) of the feet of all trees of normal diameter greater than or equal to 17.5 cm in each plot expressed in m ² /ha.
Monumental Trees, MON (n°)	The number of trees that have a diameter (cm) three times greater than their height (cm) /100.
Volume of living trees, VLT (m ³ /ha)	Is used to calculate the indicator the proportion of live wood. Is the sum of the values of the volume of the dead feet expressed in m ³ /ha.
Volume of dead trees, VDT (m ³ /ha)	Is used to calculate the indicator the proportion of dead wood. Is the sum of the values of the volume of the dead feet expressed in m ³ /ha.

variables and indices (ranging from 0 to 10 each, Table 1) for each of the 20 stands. Forest description was conducted during the non-breeding season from June to November in 2020 and 2021.

Moreover, each plot was also described by means of the three indices, as described in the RedBosques protocol (Fungobe 2024). The Forest Maturity Index (MA) uses several dendrological parameters of each plot, such as n° of tree species, basal area, live-tree volume, n° of diametrical classes, n° of vertical strata and density of old trees to deliver an indication of the maturity of the stand. Secondly, the Human Footprint Index (HFI) evaluates the human uses on the forest stand in the last 50–60 years, based on the evidence of the presence of agro-pastoral and forestry uses, invasive species, hunting, herbivory or browsing and paths or roads within <100 m of the plot. And finally, the Spatial Integrity Index (SII) characterizes the spatial context in which a stand is located by measuring its size, spatial continuity, connectivity, and border effect. This was automatically calculated introducing the stand polygon on the main application RedBosques protocol.

Forest bioacoustic description

Within each of the 20 forest stands, we also randomly selected three points 100 m apart from each other, different from the points considered for the forest description. A series of acoustic parameters were measured (Table 2). On each of the three selected plots within a stand, we placed a microphone on a central point, at 1.5 m height, from which two transects lines parallel to the terrain contour line departed in opposite directions. On each transect, five sound impulses (separated by 30 s of silence each) were generated at 10, 20, 40 and 60 m from the central point, to measure the effect of distance on the sound pressure level (SIGC) and reverberation time (T20) (Farina 2007; Tarrero et al. 2008). A wooden clapper, stuck at 1.5 m height, was used as a 100 dB sound source (Papadakis and Stavroulakis 2019) containing the octave frequency bands of 250 Hz, 500 Hz, 1000 Hz and 2000 Hz, which are those that encompass the frequency range of the audible spectrum of sound used by Capercaillie during display (Laiolo et al. 2011; Hart et al. 2020). On each clap, the sound was recorded with a microphone located at the central point, obtaining 120 recorded claps at each forest stand. On that way, for each octave band, eight measurements of each of the acoustical variables were obtained per plot, except for the attenuation factor K, where only two were obtained (one on each transect line, resulting from the linear regression of sound pressure level SIGC between all the distances at each transect described in the statistical analysis) (Table 2).

Table 2 Acoustical parameters measured on each study plot in this study

Variable name, acronym and units	Meaning
Reverberation time, T20 (s)	Describes de temporal structure of the sound. The time required for a 60 dB decay after a steady sound source is switched off. According to ISO 3382-2 standard, this is obtained by multiplying the time required for the decay between -5 and -25 dB below the steady-state initial level by 3. This is extracted automatically by the Aurora Plugin
Sound pressure level, SIGC (dB)	The sound pressure level (dB) value at each measurement point $L_p(d)$, extracted automatically by the Aurora Plugin, corrected for each distance d (m) from the source, using the formula: $SIGC = L_p(d) + 20 * \log_{10}(d)$
Attenuation factor, K	K is estimated by performing a linear regression over the 4 data points of each transect, at the 4 measured distances. Defined by the formula $L_p(d) = L_p(1\text{ m}) - K * \log_{10}(d)$, where $L_p(d)$ is the sound pressure level (dB) value at each distance, $L_p(1\text{ m})$ is the sound pressure level (dB) value at 1 m from the sound source and d is the value of each distance (10, 20, 40 and 60 m) Two K values were obtained per plot (one for each transect).
Background noise, NOISE (dB)	This parameter measures all sound that is not considered as the study target. The sound pressure level of the natural background noise recorded at each measurement point when there was no extraneous noise caused by the experimenter. This is extracted automatically by the Aurora Plugin.
Lateral horizontal fraction, JLFH (dB)	Defines how much the sound is scattered around in the horizontal. The measure of the ratio between the reflected lateral sound and the omnidirectional sound captured by the sound pressure microphone. This is extracted automatically by the Aurora Plugin.
Lateral vertical fraction, JLFV (dB)	Defines how much the sound is scattered around in the vertical plane. The measure of the ratio between the reflected vertical sound and the omnidirectional sound captured by the sound pressure microphone. This is extracted automatically by the Aurora Plugin

We used a Neveaton VR ambisonic microphone, 80 Hz high-pass filtered and covered with a windshield Boya-WS1000 to eliminate wind noise, connected to a Zoom F6 recorder set to 48 kHz, 32 bits float and 32 dB. Ambisonic microphones record in a so-called A-format, which has to be converted to B-format before formal analysis. We did this conversion using the Soundfield plugin on the host software Adobe Audition (Adobe Systems Incorporated 2023). In terms of acoustic behaviour, a forest can be considered of as a very large room—for example, an opera house—and can therefore be characterized using the same acoustic parameters that are used to characterize such spaces, in accordance with the ISO 3382:1 standard (Campanini and Farina 2008; Shelley et al. 2013). Because of that, the acoustical parameters were calculated automatically according to the

above-mentioned standard, employing the Aurora Plugin named “ISO3382 Acoustical Parameters” running inside Adobe Audition 3.0 and by the formula defined in Table 2 (Campanini and Farina 2008).

At a distance of less than 100 m from the sound source and at height less than 5 m above the ground, the effect of air absorption, temperature and wind may be neglected. For this reason, we were fairly confident that the variability on sound measurements should be directly correlated with the vegetation structure on each stand. Recording was conducted between 08:00–13:00 h (official time) during July 2022.

Statistical analysis

For each variable recorded at every point, the mean values of the three points was recorded at each stand and the average, standard deviation and range subsequently computed for occupied (lek) and deserted (nolek) stands. Prior to modelling, collinearity among the maturity, human footprint and integrity indices was assessed using the Pearson correlation coefficient and the variance inflation factors (VIF) (Dormann et al. 2013; Zuur et al. 2010). A t-student’s test for independent samples was performed to compare the elevation of occupied and deserted sites. To test for differences in the remaining characteristics of occupied and deserted stands, non-parametric Kruskal-Wallis tests were used. To describe the behaviour of the sound across all octaves, we plotted the average values of background noise (N), horizontal and vertical lateral fraction (JLFH and JLFV) and the attenuation factor (K) at each octave band for occupied and for deserted sites. We also plotted the distance profiles for reverberation time (T20) and sound pressure level (SIGC), to compare the sound propagation profiles between both groups of sites at each different octave band. The differences between occupied and deserted sites in reverberation time (T20), sound pressure level (SIGC), attenuation factor (K), background noise level (N), horizontal and vertical lateral fraction (JLFH and JLFV), at each octave band and at each distance, were tested by means of Generalized Linear Mixed Model (GLMM), assuming a gamma distribution. As fixed categorical factors we included the occupied/deserted variable (two levels), the distance to the microphone (four levels) and the frequency band (four levels). To account for the spatial correlation and non-independence of the samples, a random factor variable was created to identify the claps belonging to the same point. In order to uncover potential relationships between forest structural parameters and sound propagation parameters at forest scale, we conducted a bivariate Spearman correlation analysis between the average values of the dendrometric variables and the acoustic parameters obtained at each forest stand ($n=20$).

All analyses were performed using R Statistical Software (v4.0.4; R Core Team 2021).

Results

We found no statistically significant difference in the elevation above sea level between occupied (2089 ± 110 m, range: 1900–2300, $n=9$) or deserted (2027 ± 186 m, range 1700–2300, $n=11$) sites (t -student=0.41, $p>0.05$). No significant differences were detected neither in the Maturity Index (MI), the Spatial Integrity Index (SII) or the Human Footprint Index (HFI) between occupied and deserted sites (Table 3). Pairwise correlations between the three indices were low ($|r| < 0.55$), as well as all VIF values (< 2.0), indicating no evidence of problematic multicollinearity. Abandoned sites had significantly higher Dominant Tree Height (Ho), higher Basal Area (BA), higher Volume of Living Trees (FV) and higher Volume of Dead Trees (FM) than occupied sites. Deserted sites also had significantly higher levels of Background Noise (N), both globally and for each of the octaves analysed (Tables 4 and 5, and Fig. 2).

Table 3 Average \pm standard deviation (min and max) for the LIFE-Redbosques protocol forestry indexes for occupied and deserted stands

Forestry indices	Occupied $N=9$	Deserted $N=11$	Kruskal-Wallis test
Maturity	5.13 \pm 0.80 (2.8–5.4)	5.60 \pm 1.55 (5.6–8.2)	$\chi^2=1.481$ df=1 p-value=0.22
Human Footprint	3.03 \pm 0.39 (1.4–3.9)	2.74 \pm 1.19 (1.7–4.7)	$\chi^2=0.032567$ df=1 p-value=0.85
Spatial Integrity	4.93 \pm 1.98 (1.4–6.8)	5.27 \pm 2.25 (1.6–9.6)	$\chi^2=0.14595$ df=1 p-value=0.70

Table 4 Average \pm standard deviation (min and max) of the dendrometric variables for occupied and deserted sites

Dendrometric variables	Occupied $N=9$	Deserted $N=11$	Kruskal-Wallis test
Dominant tree height (m)	13 \pm 3 (9–18)	18 \pm 3 (13–26)	$\chi^2=13.062$, df=1, p-value<0.001
Basal area (m ² /ha)	19.58 \pm 10.98 (5.31–58.09)	37.54 \pm 10.55 (16.20–60.73)	$\chi^2=9.9408$, df=1, p-value=0.001
Monumental Trees (n°)	46 \pm 44 (0–128)	27 \pm 24 (0–83)	$\chi^2=1.5738$, df=1, p-value=0.209
Volume of living trees (m ³ /ha)	109.07 \pm 56.95 (22.82–204.60)	281.06 \pm 87.09 (83.65–448)	$\chi^2=13.023$, df=1, p-value<0.001
Volume of dead trees (m ³ /ha)	34.37 \pm 26.81 (0.87.50)	113.87 \pm 68.66 (12.10–277.56)	$\chi^2=8.1169$, df=1, p-value=0.004

Table 5 Average ± standard deviation (min and max) of the acoustical parameters in occupied and deserted sites

	Occupied N=9	Deserted N=11	Kruskall-Wallis test
Reverberation time (s)	0.72±0.09 (0.53–0.82)	0.74±0.07 (0.65–0.85)	$\chi^2=0.11688$, df=1, p-value=0.732
Sound pressure level (dB)	113.79±2.55 (108.89–117.60)	114.36±1.05 (113.02–115.95)	$\chi^2=0.070707$, df=1, p-value=0.790
Distance attenuation factor	25.98±2.02 (22.89–28.64)	24.51±3.76 (19.35–30.75)	$\chi^2=0.90188$, df=1, p-value=0.342
Background noise (dB)	31.53±3.61 (26.59–37.30)	37.19±5.57 (29.60–46.85)	$\chi^2=5.3694$, df=1, p-value=0.020
Lateral horizontal fraction (dB)	0.08±0.2 (0.03–0.41)	0.07±0.19 (0.02–0.54)	$\chi^2=2.9221$, df=1, p-value=0.087
Lateral vertical fraction (dB)	0.17±0.06 (0.09–0.28)	0.16±0.05 (0.06–0.23)	$\chi^2=0.001443$, df=1, p-value=0.969

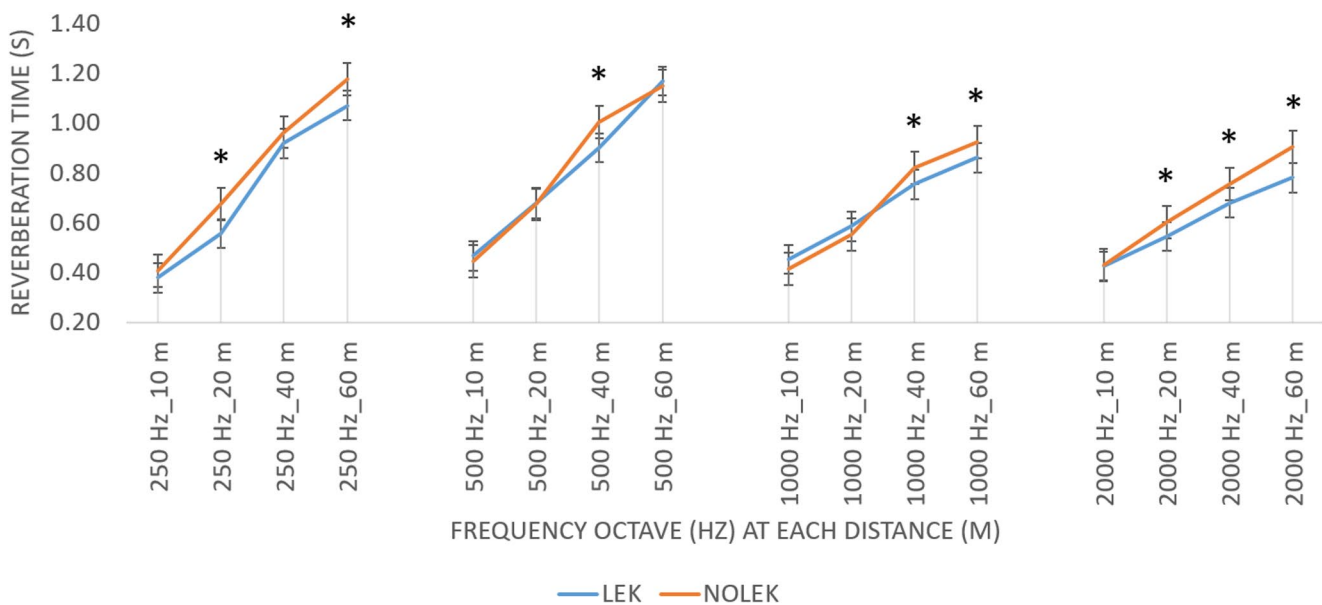


Fig. 2 Means ± sd of Reverberation Time T20 (s) values at different distances (10 m, 20 m, 40 m and 60 m) and octave bands for lek sites and non-lek sites. Significant (P<0.05) differences between lek and non-lek sites are indicated by *

Reverberation time (T20) increased with distance to the sound source and decreased for each octave band. Deserted sites had significantly higher Reverberation time at all frequency octaves between 20 m and 60 m (Fig. 3). Sound Pressure Level (SIGC) values decreased with distance and remained similar between octaves (Fig. 4). Deserted sites had significant higher Sound Pressure Level (SIGC) at all frequency octaves, except at 1000 kHz between 20 m and 60 m. The Attenuation Factors (K) were lower on deserted sites than in occupied sites at all frequencies, excepting at 1000 kHz. This meant that these frequencies were attenuated more gradually, persisting for longer in deserted sites than in occupied sites (Fig. 5). Both groups of sites showed different sound propagation profiles of the Lateral Fraction in horizontal (JLFH) and vertical (JLFV) plane. At deserted sites, the Lateral Fraction in the Horizontal Plane (JLFH) showed significantly lower values at 250 Hz and 500 Hz, and the Lateral Fraction in the Vertical Plane (JLFV) showed

significantly lower values at 250 Hz and 2000 Hz but significantly higher values at 500 Hz (Fig. 6). The Background Noise (N) was significantly and positively correlated with the Dominant Tree Height (Ho), the Volume of Living Trees (FV) and the Volume of Dead Trees (FM) of the stands, while the Attenuation Factor (K) was significantly negatively correlated with the volume of Dead Trees (FM) of the stands (Table 6).

Discussion

According to the Acoustic Adaptation Hypothesis, animals that use sounds in their communication should avoid occupying sites with sub-optimal sound propagation (Lohr et al. 2003; Naguib 2003; Luther and Gentry 2013). Our results show that deserted forest stands exhibit similar elevation, maturity, human footprint or spatial integrity than occupied

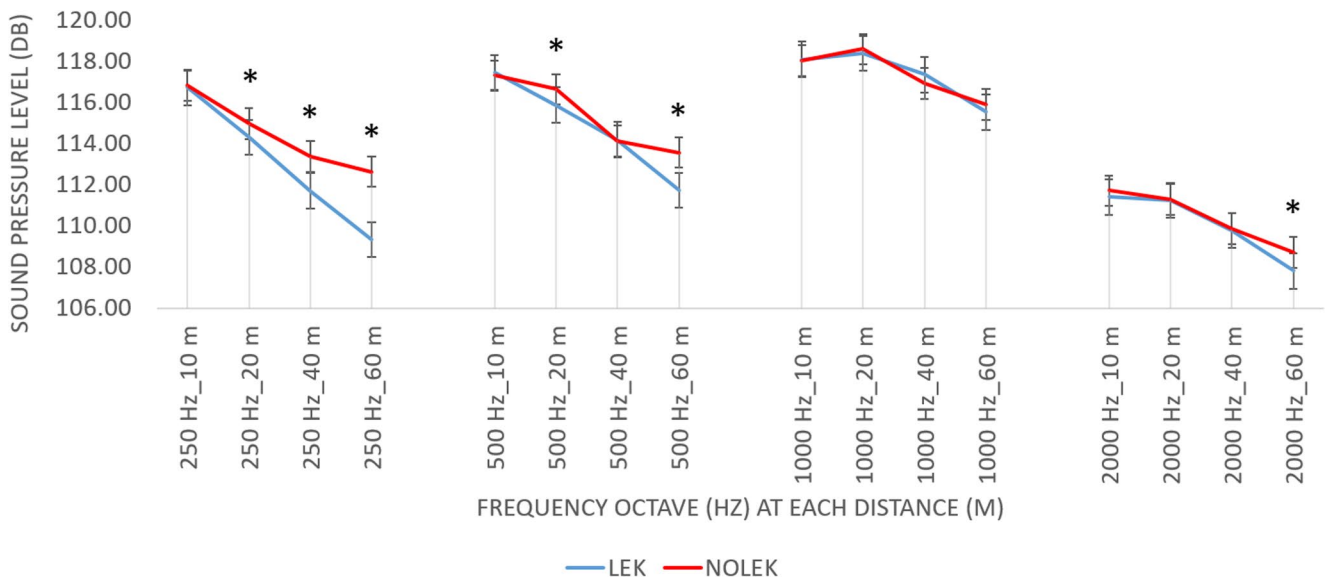


Fig. 3 Means ± sd of Sound Pressure Level SIGC (dB) values at different distances (10 m, 20 m, 40 m and 60 m) and octave bands for lek sites and non-lek sites. Significant ($P < 0.05$) differences between lek and non-lek sites are indicated by *

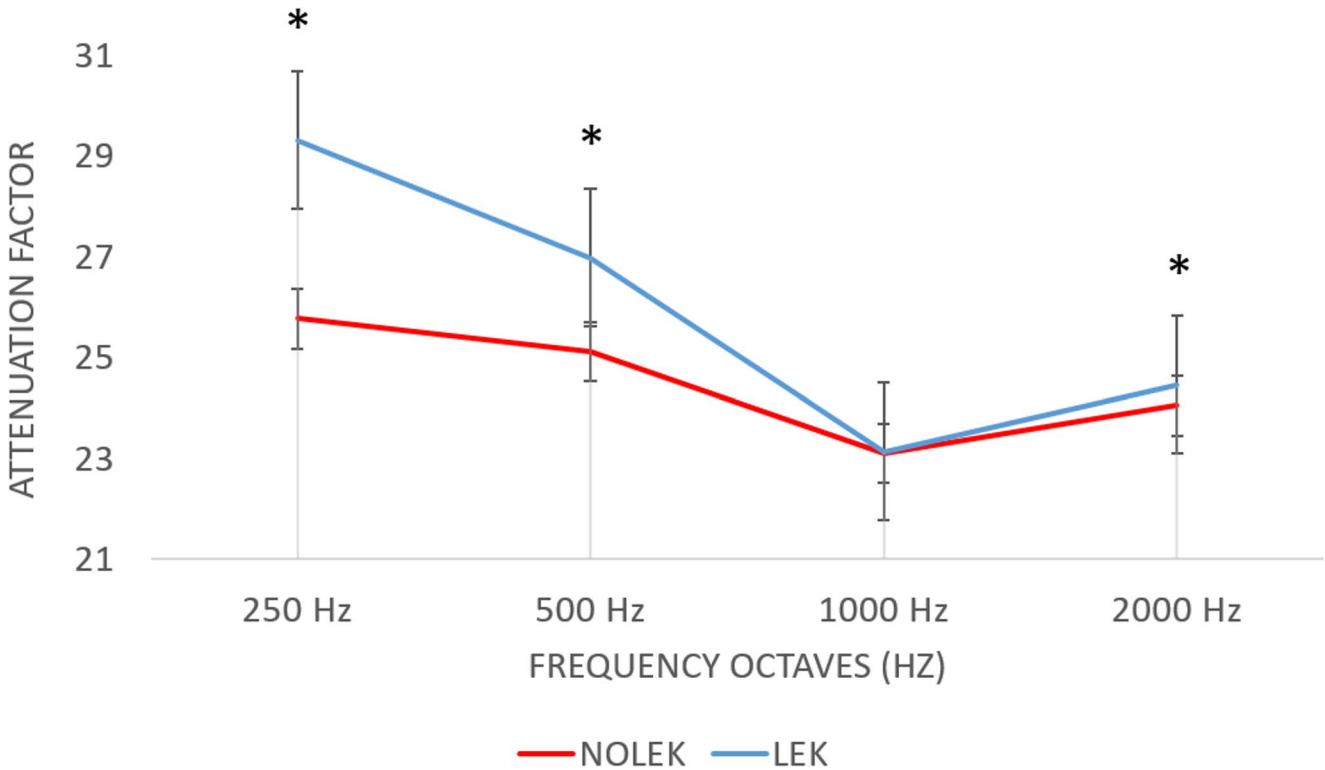


Fig. 4 Means ± sd of Attenuation Factor K values for lek sites and non-lek sites at each octave band. Significant differences ($P < 0.05$) between lek and non-lek sites are indicated by *

stands, but slightly different forest structure, as well as differences in sound propagation properties. Deserted stands showed higher levels of noise and reverberation of the sound, which might impair the transmission and discrimination of display calls of Capercaillie within the stands and, eventually, promote desertion.

Capercaillie *Tetrao u. aquitanicus*, the subspecies inhabiting the Pyrenees, uses the upper limit of the forest, but we did not find that lek desertion was associated to an elevation gradient, as Gil et al. (2020) found in a previous study in Central Pyrenees. This suggests that, although historical altitudinal treeline shifts due to the combination of climate

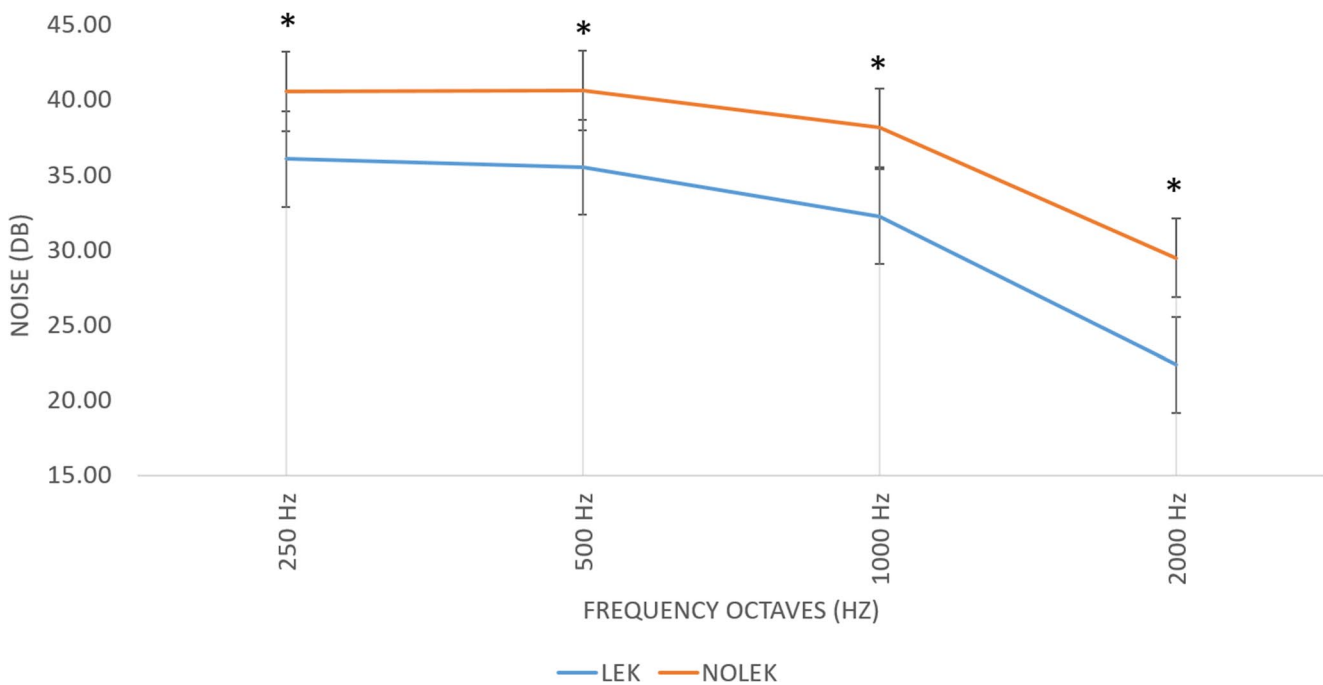


Fig. 5 Comparison of Background Noise (db) at difference frequencies between lek sites and non-lek sites. Significant differences ($P < 0,05$) between lek and non-lek sites are indicated by *

and land use changes in the Pyrenees (Feuillet et al. 2020; Ameztegui et al. 2016) may be relevant at a large spatial scale in explaining the abandonment of leks, this didn't appear as a relevant factor to explaining desertion in our study area and temporal scale.

Several studies have stressed the importance of human disturbance or distance to roads in explaining occupancy of Capercaillie lek sites (Summers et al. 2007; Storch 2013; Coppes et al. 2017). Proximity to roads or tracks can produce noise and have negative impact on bird communication (Summers et al. 2007; Barrero et al. 2020; Barbaro et al. 2023). We did not find differences between deserted or occupied sites in the Human Footprint index (HFI), which includes a qualitative assessment of proximity to roads and tracks, but we found higher background noise levels in deserted sites. Although we have no information on the potential origin of this noise (and cannot preclude an anthropogenic origin), we observed that the level of background noise was associated to the structural characteristics of the forest, suggesting that this can probably be amplified or attenuated depending on the characteristics of the forest vegetation. A more detailed study on the origin and transmission of background noise within the forest would be necessary for better understanding on how forest vegetation structure can be managed to absorb or reduce background noise.

The absence of significant differences between deserted and occupied sites in the Spatial Integrity Index suggests that habitat fragmentation didn't play a role in explaining desertion process in our case, which is consistent with the fact

that, in the Pyrenees, rural abandonment during the last century has promoted the increase of the area covered by forest, instead of fragmenting it: on average, forests in the Pyrenees are more extensive, store more biomass, and display more advanced structural development than they did a century ago (Vicente-Serrano et al. 2004; Lasanta-Martínez et al. 2005).

In spite of being similarly mature, as revealed by similar maturity indices (MI), deserted sites were structurally different from occupied sites, featuring higher values of Dominant Tree Height (Ho), higher Basal Area (BA), higher Volume of Living Trees (FV) and higher Volume of Dead Trees (FM) than occupied sites. These changes are consistent with the possibility that some mature forest have developed a secondary layer of trees in the undergrowth that makes them less suitable for lekking males, in agreement with the results of Drozdowski et al. (2011) or Sirkiä et al. (2011) when comparing deserted and occupied Capercaillie lek sites in North-eastern Poland or in Finland. Several non-exclusive factors might explain why these old-growth forests might be less appropriate to Capercaillies. The additional layer of trees may render visual contact more difficult (Schwendtner et al. 2005) or reduce the amount of Bilberry available for food and shelter (Montané et al. 2016). Our aim was not to rule out such alternatives, but rather to explore the possibility that changes in the acoustic properties of the stands might impair communication during display and also play a role.

Our findings, while not excluding other alternatives, are consistent with this possibility. The global shape of the

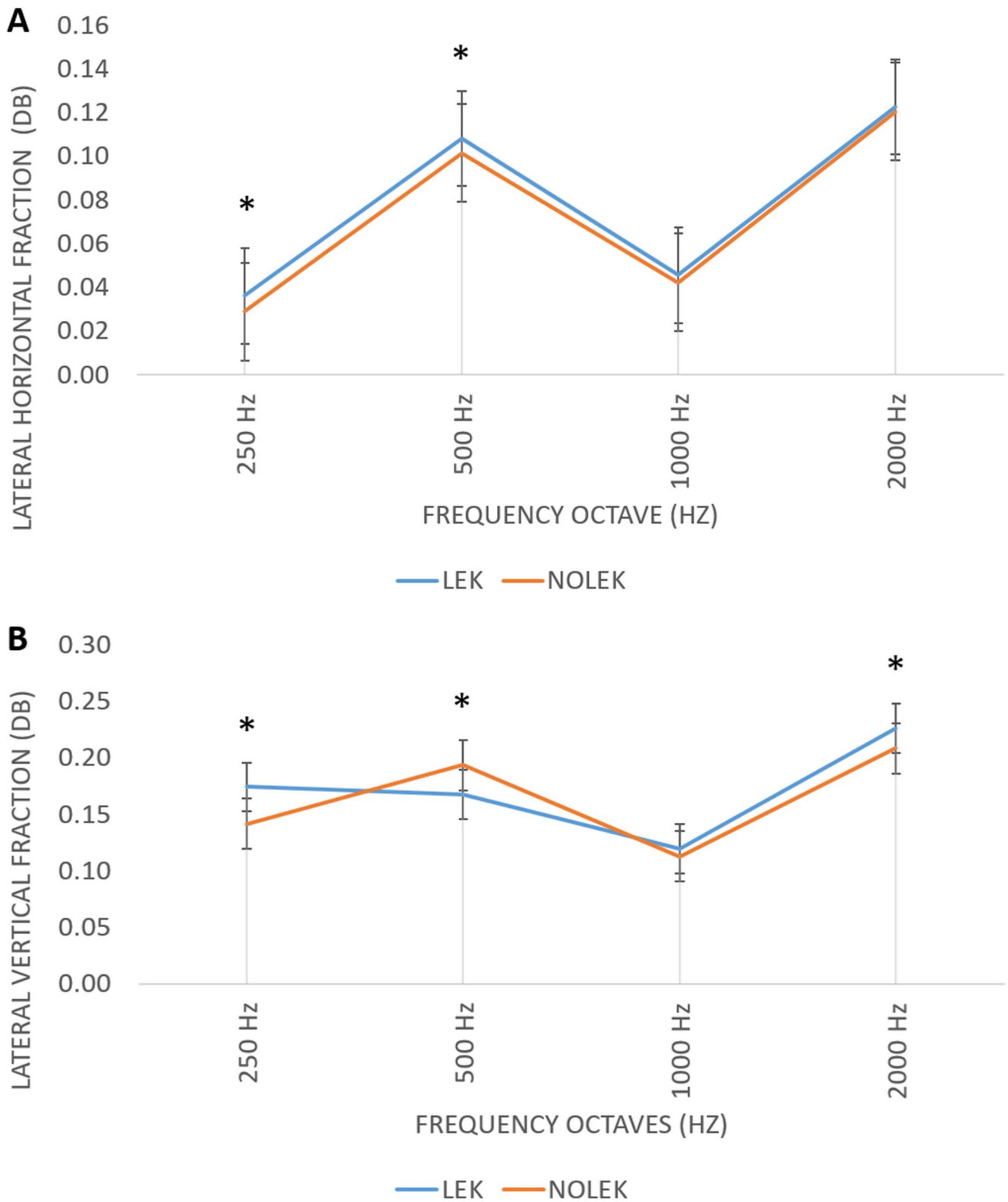


Fig. 6 Means of the Lateral Horizontal Fraction (**A**) and Lateral Vertical Fraction (**B**) values (dB) for lek sites and non-lek sites at each octave band

Table 6 Pearson correlation coefficients (r) between the acoustical parameter and the dendrometric variables of the 20 stands. Significant correlations ($p < 0.05$) are shown in bold

	Reverberation time (s)	Dominant tree height (m)	Basal area (m ² /ha)	Volume of living trees (m ³ /ha)	Monumental Trees (n)	Volume of dead trees (m ³ /ha)
	0.14	0.001		0.20	-0.009	0.10
Sound pressure level (dB)	0	0.076		0.001	0.11	0.056
Distance attenuation factor	0.13	-0.14		0.04	-0.26	-0.40
Background noise (dB)	0.39	0.15		0.41	0.002	0.68
Lateral horizontal fraction (dB)	0.001	-0.16		0.001	-0.18	-0.11
Lateral vertical fraction (dB)	0.001	-0.15		-0.15	-0.02	-0.22

sound propagation in our stands between the 125 Hz–2 kHz octaves was that expected for a heterogeneous coniferous forest (Tarrero et al. 2008; Muhlestein et al. 2018; Europarc-España 2019; Fungobe 2024). However, background Noise (N) was higher in deserted stands. Any sound emitted by a bird will be masked by background noise when there is a difference of less than 25 dB between them (Fang and Ling 2003; Lohr et al. 2003; Berger-Tal et al. 2019). As male Capercaillies call at less than 68–70 dB (Laiolo et al. 2011; Hart et al. 2020; Jordi et al. 2023), background noise levels over 33–35 dB, as those found on average on deserted sites, may already impair communication. Moreover, reverberation time (T20) and Sound Pressure Level (SIGC) were higher in abandoned sites, while the Attenuation Factor (K), Vertical Lateral Fraction (JLFV) and Horizontal Lateral Fraction (JLFH) showed lower values. This indicates that in deserted sites sound experiences less attenuation and scattering, allowing it to persist for longer. Combined with higher background noise, this may impair and distort Capercaillie call transmission due to the boosting effect of vegetation (Slabbekoorn et al. 2002; Swearingen and White 2007; Luther and Gentry 2013). Interestingly, the most relevant differences were detected on the lower frequency octave bands which is consistent with the results of Hart et al. (2020), who found the importance of low frequencies in the Capercaillie display call. However, because our profiles did not include the low frequencies analysed by Hart et al. (2020), future research is needed to see whether the differences between deserted and occupied sites persists on this lower infrasound band.

Although our study does not demonstrate that forest acoustic characteristics are a determining factor in site desertion, our results are consistent with the possibility that the acoustic properties of deserted sites could interfere with the effective transmission of male display calls. In support of this idea some previous research has shown how forest vegetation structure can eliminate the negative effects of background noise on forest bird biodiversity (Barbaro et al. 2023). Male Capercaillie voice is composed by a rapidly repeated elements with a modulated broad band frequency pattern, resulting in a signal more susceptible to be degraded during transmission in the forest (Naguib 2003; Policht and

Hart 2023; Jordi et al. 2023). Because of this, excess background noise, sound pressure level and reverberation might lead to the distortion of the call message (Slabbekoorn et al. 2002; Naguib 2003; Erbe et al. 2022). Experiments with real display call records, to check how they are transmitted in different forest types and sites could help to clarify these issues. Moreover, more detailed research on land-use history, forest structure, food availability, and human disturbance within and around both deserted and occupied lek sites is needed to disentangle whether communication constraints, if any, play a role in the desertion process, and if so, to assess their relative importance compared with other factors previously discussed. Forest management for Capercaillie has traditionally concentrated on the management on the undercover to provide shelter and food and to maintain a heterogeneous underground woodland cover (Hancock et al. 2011; Broome et al. 2014). If our results are confirmed, attention should also be given to forest structure management to enhance Capercaillie call transmission and reduce the impact of background noise.

Conclusions

Our study shows that changes in the structure of the forest stands could induce differences in sound transmission properties that might lead to an impairment of the communication of Capercaillie during display, which may eventually lead to desertion. Although more research is needed to confirm or reject our hypothesis, these results highlight the importance of considering aspects other than resources (food, shelter...), such communication constraints, when trying to explain the mechanisms behind habitat selection in birds.

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Author contributions olga jordi is the corresponding author and has been in charge of the design of the theoretical framework, field experiments, statistics and writing of the document.santiago mañosa is the supervisor of the biology part and has been in charge of the supervision of the writing and the experimental and statistical design.adriano farina and angelo farina have been the supervisors of the acoustic engineering part and have been in charge of the supervision of the acoustic field sampling and the acoustic logistics.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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