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Acoustic patterns of an invasive species: the Red-billed Leiothrix (*Leiothrix lutea* Scopoli 1786) in a Mediterranean shrubland

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The Red-billed Leiothrix (*Leiothrix lutea*) is an invasive species which has recently been found to be locally abundant in eastern Liguria (Italy). The song production of this bird was recorded over the course of an entire year (2011) and evaluated using both aural information and applying innovative automatic processing metrics. Our findings revealed that the Red-billed Leiothrix has loud vocalizations that are heard for most of the year, including in July and August when other birds are silent. Its song production has been estimated to amount to 37% of the sounds uttered by the entire bird community. The next most vocal species are the European Robin (36%), the Common Blackbird (18%), the Subalpine Warbler (5%) and the Sardinian Warbler (1%). The Red-billed Leiothrix can be seen as a new acoustically dominant species and, consequently, a potential modifier of the soundscape patterns of the indigenous bird community. The modification of acoustic traits in the repertoire of both indigenous species and the Red-billed Leiothrix is to be expected according to a co-evolution hypothesis.

Keywords: acoustic competition; acoustic complexity index; acoustic niche overlap; bird invasion; soundscape; timaliids

Introduction

The Red-billed Leiothrix (*Leiothrix lutea* Scopoli 1786), known also as the Japanese Hill-Robin, the Peking Robin or the Peking Nightingale, is a native species of Southeast Asia, southern China and the Indo-Himalayan regions. The species has also been introduced to the Hawaiian Islands, Japan and southern Europe, where it has colonized the wettest conditions of different vegetation types characterized by dense lower layers. In southern Europe, the Red-billed Leiothrix has been found in Italy, France and Spain (Lever 2005, pp. 174–176). From a recent study in Catalonia (northeast Iberian Peninsula), Herrando et al. (2010) confirmed this bird's rapid expansion and hypothesized that it could become common in many other parts of Europe in the near future. In Italy, its presence has been documented in the area north of Tuscany (Puglisi et al. 2009) since the early 1990s, and it has also recently been observed in eastern Liguria by Nardelli (pers. com).

The species' demography (Ralph et al. 1998), nest selection (Amano and Eguchi 2002a), foraging niches (Amano and Eguchi 2002b) and other life traits (Fisher and Baldwin 1947; Male et al. 1998; Basly 2007; Dubois 2007) outside its biogeographic range are only partially known and described.

Despite the fact that this species is characterized by a powerful and commonly used song repertoire, with high inter-individual variability associated with contact and social

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calls (Thielcke and Thielcke 1970; Basly 2007), no specific investigations have been carried out to characterize the song performances of the Red-billed Leiothrix, assess the amount of acoustic overlap with indigenous songbirds and evaluate the contribution of its acoustic performances to the overall soundscape. In this sense, the aim of this paper was as follows:

- Characterize the abiotic acoustic component and investigate the acoustic dynamics of the entire bird community, by applying recently developed *ad hoc* metrics.
- Describe, measure and characterize the seasonal and diurnal acoustic patterns of the Red-billed Leiothrix in a recently occupied area in eastern Liguria.
- Better understand the relationship of the acoustic performance of the Red-billed Leiothrix to the different abiotic and biotic components of the soundscape.
- Discuss the role of the rich acoustic repertoire of the species as a key factor that potentially contributes to its demographic success.

Study area

Acoustic data on the bird community were collected from a recording station that was exposed on the westerly side to a small hanging valley at the centre of a large secondary area of shrubland, close to Deiva Marina, eastern Liguria, Italy ($44^{\circ}13'27.6''\text{N}$, $9^{\circ}30'30.1''\text{E}$). This station stood at an elevation of 300 m and a distance of 600 m from the Tyrrhenian Sea (Figure 1). The area, which is away from main roads, is only crossed by a path utilized by tourists between late spring and early autumn and by hunters in autumn and early winter.

A dense secondary area of Mediterranean shrubland, dominated by *Erica scoparia* ($2.00\text{ m} \pm 0.03\text{ SE}$), *Quercus ilex* ($2.29\text{ m} \pm 0.11\text{ SE}$) and *Arbutus unedo* ($3.23\text{ m} \pm 0.13\text{ SE}$), covers this area, which was terraced and cultivated up to the 1950s. The foliage profiles are illustrated in Figure 2. Remnants of old scars testify that the area experienced wild fires in the woods before a recovery intervened over the course of the process of land abandonment. The percentage of open sky seen from beneath the forest canopy around the recording station was adopted as an estimator of vegetation cover by using the fisheye technique (Coolpix 990, Nikon, fisheye converter FC-e8 $0.21 \times$ Nikon). A total of 178 photos were taken at a distance of $2 \pm 0.3\text{ m}$ from each other along five transects of 100 m

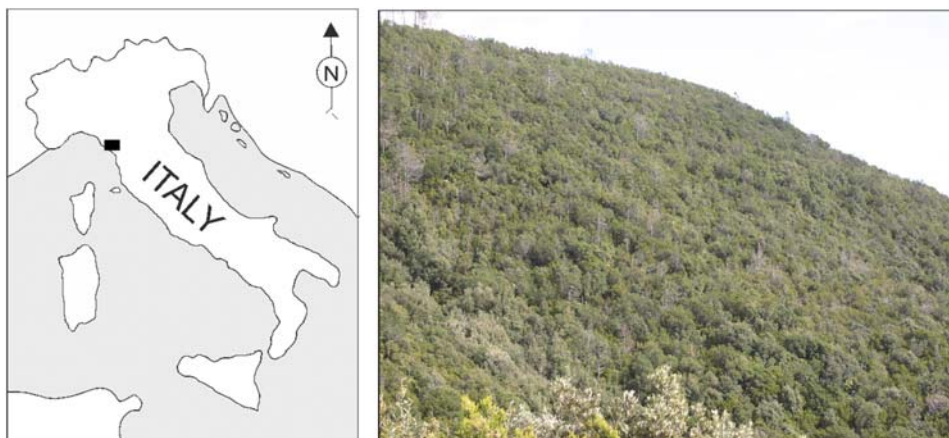


Figure 1. Location of the study area and a photograph thereof.

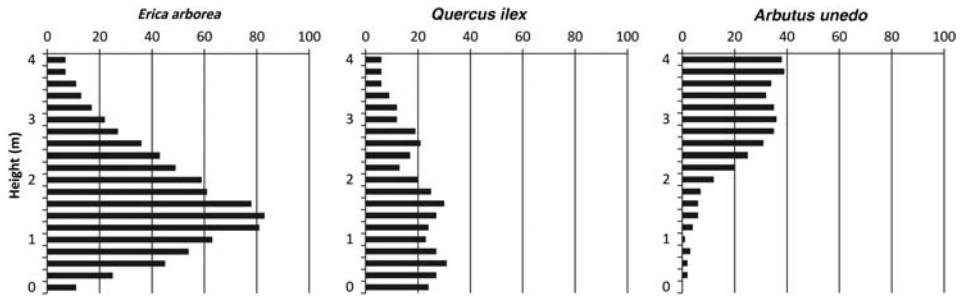


Figure 2. Foliage profile of the dominant shrubs and trees: *Erica arborea*, *Quercus ilex* and *Arbutus unedo*.

in length, 25 m apart and parallel to the maximum slope line. The Gap Light Analyzer 2.0 (Frazer et al. 1999) was used to calculate the Percentage of Canopy Openness, namely the percentage of open sky seen from beneath a forest canopy, which amounted to 21.01 ± 0.76 SE. The weather conditions (temperature mean/max/min, humidity, wind, rainy days, stormy days and foggy days) in 2011 at the Sarzana Luni climatic station, La Spezia, are set out in Table 1s (Supplementary Information).

Methods

The acoustic repertoire of the bird community in which Red-billed Leiothrix has been found was collected over the course of an entire year (2011) by an automatic recording apparatus (Song Meter SM1, Wildlife Acoustics, Inc., Concord, MA, USA). This device, already used for evaluating acoustic diversity (e.g. Krause et al. 2011; Sueur et al. 2012), allows a researcher to capture the totality of the biophonies of most of the birdsong inside a radius of 30–40 m (pers. com.) in the dense Mediterranean maqui.

The equipment was configured with a daily schedule of 1 min of recording every 10 min from 4.00 am to 9.35 pm, which represents the starting and finishing limits of the singing activity of the bird community in late spring. Ninety-seven 1-min-long recordings were obtained per day, totalling 24,735 sound files ($255 \text{ days} \times 97 \text{ daily intervals of 1 min}$). The remaining days were not considered due to technical problems such as unexpected battery discharge or running out of storage space on flash cards. The Song Meter SM1 was set to collect sounds at a sampling rate of 44.1 kHz. Two 8-GB Secure Digital High Capacity cards were used to store sound files from recording sessions that each lasted for 2 weeks. The recording equipment, which was protected by a wooden roof to reduce the effects of bad weather on the microphone capsules, was placed at a height of 1.50 m inside the canopy of a small strawberry tree (*Arbutus unedo*).

The sound data were analysed according to two different procedures:

1. The aural identification of all of the downloaded sounds.
2. The measurement of the information content of the acoustic spectrograms.

The aural survey was conducted by listening to the sound files with WaveSurfer© software. Each distinct sound of geophysical (e.g. strong wind, thunder), biological (bird and insect sounds, human calls) and anthropogenic (airplanes and ship engines) origin was identified according to the source, noted on a form and later transferred to a spreadsheet. Of the biological sounds, the presence of each species was annotated for each minute and distinguished for acoustic typology (song, alarm and contact calls). The vocalizations of

the Red-billed Leiothrix were distinguished in terms of song, female contact calls, alarm calls and other social calls.

The amount of information present in each sound file was measured by converting the acoustic signals in the spectrograms by using the fast Fourier transform (FFT) procedure of WaveSurfer© software (Sjölander and Beskow 2000). In this way, it was possible to obtain the power spectrum of the recorded sounds, which is the relative table of power values divided into frequency bins and temporal steps (measured in W/Hz). Thereafter, the SoundscapeMeter© (Farina et al. 2012), a plug-in of WaveSurfer©, was used to calculate the Acoustic Complexity Index (ACI; Farina and Morri 2008) from the power spectrum data, which was renamed in the application as ACI_t. The SoundscapeMeter© plug-in was set by adopting a broadband filter to delete diffuse background noise and selecting a frequency interval from nought to 10,000 Hz.

The ACI_t (Farina, Pieretti, et al. 2011; Pieretti et al. 2011) is a measure of irregularities in the intensity values contained in a spectrogram across the different frequency bins. It is based on the assumption that structured sounds like bird song have variations in their intensity across the frequency bins. The difference between an intensity value and the one adjacent to it is calculated, and this value is then divided by the sum of the intensities according to the following algorithm:

$$ACI_t = \frac{\sum_{k=1}^{n-1} |I_k - I_{k+1}|}{\sum_{k=1}^n I_k},$$

where I_k is the sound intensity at the k th temporal resolution, k is set according to the selected purposes by fixing the FFT window, and n is the temporal dimension by which ACI_t is calculated and is selected using the <clumping> command of the SoundscapeMeter© plug-in.

Adopting an FFT window of 512 points, the sound files were sampled at a temporal resolution of 0.011 s. We used a clumping value of 1 s, which results in the processing of 86 (n) pieces of data per second. Over 1 min of recording, we obtained 60 ACI_t values for each of the 116 frequency bins, totalling 6960 ACI_t measures per minute.

The sound complexity obtained by adopting the ACI_t metric was coupled with the information collected by the aural identification process. The intersection with this last piece of information has primarily been utilized to assess the acoustic environment in which the Red-billed Leiothrix is living and to set its daily and seasonal singing repertoire.

All of the ACI_t values below 1500 Hz were considered to be the result of geophonies and anthrophonies, and were used to infer the temporal (daily and seasonally) distribution of environmental noise. A minor portion of the vocal acoustic cues of the Eurasian Jay (*Garrulus glandarius*) and the Carrion Crow (*Corvus corone cornix*) belongs to this frequency range. Meanwhile, the ACI_t values above 1500 Hz were principally regarded as the result of the sounds uttered by the entire bird community (biophonies).

Specifically, the song of the male Red-billed Leiothrix and the female contact calls ranges from approximately 1500 to 3800 Hz. This frequency range completely overlaps with the song of the Common Blackbird (*Turdus merula*) and partially overlaps with the song of other species like the European Robin (*Erithacus rubecula*) or the Subalpine Warbler (*Sylvia cantillans*). To measure the acoustic overlap between the Red-billed Leiothrix and the most acoustically active species, we calculated the probability of registering a co-occurrence of the song production of those species in the same recording minute. We therefore applied the Overlap Index of MacArthur and Levins (1967), which

was later adapted by Pianka (1986, p. 81), to the data obtained by aural identification:

$$O_{jk} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}},$$

where p_{ij} and p_{ik} represent the relative probability of song emission in the i th daily interval for species j and k , respectively. This index is usually adopted to investigate how different species use a resource matrix. In our case, such a matrix is represented by the 97 acoustic windows of 1 min recorded daily. The recorded probability of co-occurrences of songs of different species has been successively processed in order to obtain a mean value of overlap, both along the season and the hours of the day.

In order to represent the dynamisms of geophonies, anthrophonies, biophonies and the song production of the Red-billed Leiothrix over the course of the different months of the year, Surfer v.9.0 was used to interpolate the discrete data. The data distribution of all of the variables could not be interpreted as normal. Accordingly, a non-parametric statistical analysis was chosen to analyse the set of data. Using the values derived from the ACI_t results, a Spearman's rho correlation analysis was carried out to enable us to observe eventual correspondences between biophony (principally comprised over 1500 Hz) and noise (mainly under the 1500 Hz) in each 1-min file. The correlation was made for the entire year and also split for the two principal periods, spring–summer (April–September) and autumn–winter (October–December and January–March).

The Kruskal–Wallis test was successively utilized to investigate if singing activity or noise levels varied over the 12 months of the year, and to compare the different probability of overlap among the diverse species. We used the Mann–Whitney U -test to assess if noise or the biophony differed between the two periods of the year (spring–summer and autumn–winter), and to consider their differences each month at dawn and over the course of the rest of the day. In order to reduce uncertainty about the singing activity linked to the light intensity that changes according to daily weather conditions, the files recorded before dawn and after sunset were not considered. This was achieved by looking at the first and last biophonies of the day. The Mann–Whitney U -test was also used to investigate whether a species overlapped more with the Red-billed Leiothrix in the April–September period, or whether they sang together preferentially in the first few hours of the day (from 4 to 8 am).

All of the statistical analyses were carried out using the statistical software Statistica™ v.8.0.

Results

The abiotic component of the acoustic context

The amount of acoustic complexity produced by geophonies and anthrophonies (combined) over the year, and calculated by applying the ACI_t metric, is set out in Figure 3(a). Wind, rain and sea waves represent the majority of the geophonies, whereas airplanes, helicopters and boats are the main source of the anthrophonies. The noise level, which was heterogeneously distributed through the year (Kruskal–Wallis test: $H = 711.69$, $df = 11$, $p < 0.001$), appears to be especially intense outside the breeding season, showing a significant decrease in the period April–September when compared to the rest of the year (Mann–Whitney U -test: $U = 16,539$, $p < 0.001$), coupled with a coincident increase in the acoustic activity of birds. The noise level is significantly lower

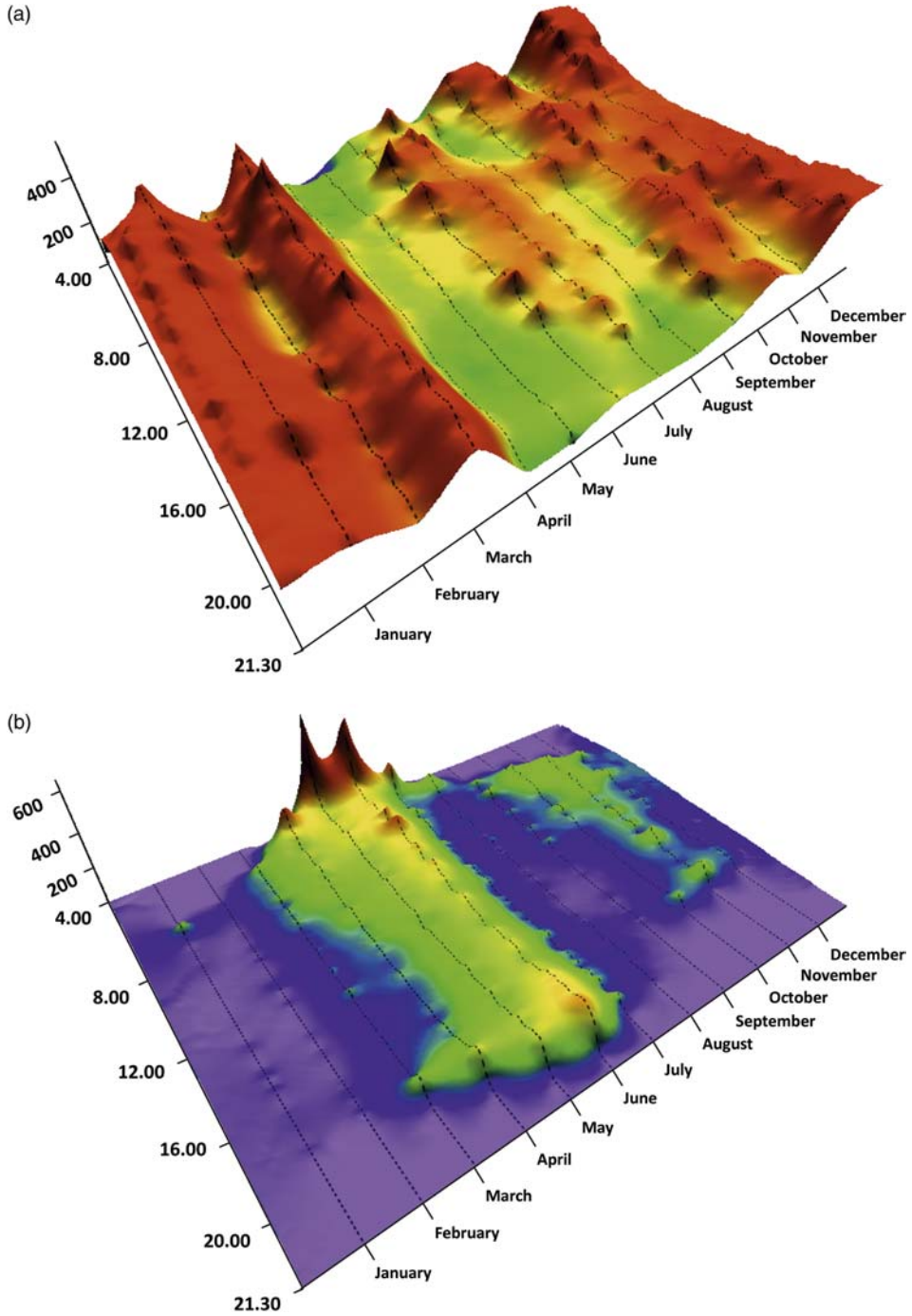


Figure 3. (a) A 3D representation of the ACI_t values (z -axis) applied to the frequency bins < 1500 Hz and interpreted as geophonies and anthrophonies (combined) over the year (x -axis) and across the day (y -axis). (b) A 3D representation of the ACI_t values (z -axis) applied to the frequency bins > 1500 and $< 10,000$ Hz and interpreted as biophonies (the entire bird community) over the year (x -axis) and across the day (y -axis).

at dawn (2 h after the first biophony and the rest of the day) in April (Mann–Whitney U -test: $U = 251$, $p = 0.02$), May (Mann–Whitney U -test: $U = 114$, $p < 0.001$), June (Mann–Whitney U -test: $U = 65$, $p < 0.001$), July (Mann–Whitney U -test: $U = 59$, $p < 0.001$) and August (Mann–Whitney U -test: $U = 92$, $p < 0.001$). In March (Mann–Whitney U -test: $U = 180$, $p < 0.001$) and September (Mann–Whitney U -test: $U = 59$, $p < 0.001$) the noise is greater at dawn.

The biotic component of the acoustic context

A total of 39 species of bird were identified over the year using aural identification. The Red-billed Leiothrix, European Robin, Common Blackbird and Subalpine Warbler are dominant (with a relative importance of $>5\%$ of the entire collection), whereas the Sardinian Warbler, Common Firecrest, Eurasian Jay, Dartford Warbler and Chaffinch are the sub-dominant species (1–5%; see Table 1). The Subalpine Warbler, European Nightjar, European Bee-eater, European Turtle Dove, Eurasian Wryneck, European Serin, Common Swift, Pallid Swift, Common House Martin, Nightingale, Common Chiffchaff and Short-toed Snake Eagle are migratory breeders. The amount of information expressed by the biophonies uttered by the entire community and estimated by applying the ACI_t metric is summarized in Figure 3(b). In this case, we only took into consideration the ACI_t values corresponding to the 1-min samples in which one or more species were identified during the aural screening.

As expected, the distribution of biophonies varies significantly over the course of the year (Kruskal–Wallis test: $H = 583.89$, $df = 11$, $p < 0.001$), with several peaks observed from April to September. This corresponds to a significant difference when this period is compared to the rest of the year (Mann–Whitney U -test: $U = 64,237$, $p < 0.001$) and reveals an interesting pattern: a ridge-like shape, with a gentle slope moving from March to April, and a steeper slope at the end of June. This asymmetry demonstrates how the song activity starts gradually at the end of winter and ends abruptly in early summer. Moreover, the maximum acoustic activity of the entire community is performed early in the morning, in particular during the first 2 h of the day from the first biophony in respect of the rest of the daylight hours (Mann–Whitney U -test: $U = 41,911$, $p < 0.001$). However, in January (Mann–Whitney U -test: $U = 196$, $p < 0.06$), July (Mann–Whitney U -test: $U = 312$, $p < 0.051$) and November (Mann–Whitney U -test: $U = 215$, $p < 0.11$), there are no significant differences between dawn and the rest of the day. In July, this is probably due to the acoustic activity of cicadas in the late morning and the afternoon. From October to December, a moderate amount of the acoustic activity is probably caused by the presence of stopover migratory birds.

The biophonies are weakly and negatively correlated with noise across the year (Spearman rho: $r = -0.17$, $n = 20,265$, $p < 0.05$), and this does not change significantly when dividing the year into two semesters: the most canorous period (April–September; Spearman rho: $r = -0.10$, $n = 10,648$, $p < 0.05$) and the less canorous period (October–March; Spearman rho: $r = -0.17$, $n = 9690$, $p < 0.05$).

The Red-billed Leiothrix acoustic activity over the year

The Red-billed Leiothrix has been confirmed as a loud bird all year long, with its maximum acoustic performance taking place from March to September (Figure 4(a)). Its song peaks in July and has a typical bell-shaped distribution, with a maximum that ranges from April to August. Female contact calls present a bimodal form of distribution with two

Table 1. List of species identified using the aural procedure applied to 24,735 files of 1 min in length each.

Species		Samples with vocalizations	%
<i>Erithacus rubecula</i>	European Robin	7926	34.54
<i>Leiothrix lutea</i>	Red-billed Leiothrix	6596	28.74
<i>Turdus merula</i>	Common Blackbird	4068	17.73
<i>Sylvia cantillans</i>	Subalpine Warbler	1158	5.05
<i>Sylvia melanocephala</i>	Sardinian Warbler	631	2.75
<i>Regulus ignicapillus</i>	Common Firecrest	595	2.59
<i>Garrulus glandarius</i>	Eurasian Jay	547	2.38
<i>Sylvia undata</i>	Dartford Warbler	357	1.56
<i>Fringilla coelebs</i>	Chaffinch	338	1.47
<i>Parus caeruleus</i>	Blue Tit	222	0.97
<i>Corvus corone cornix</i>	Hooded Crow	99	0.43
<i>Parus major</i>	Great Tit	58	0.25
<i>Picus viridis</i>	European Green Woodpecker	53	0.23
<i>Caprimulgus europaeus</i>	European Nightjar	50	0.22
<i>Apus apus</i>	Common Swift	39	0.17
<i>Sylvia atricapilla</i>	Blackcap	29	0.13
<i>Aegithalos caudatus</i>	Long-tailed Tit	28	0.12
<i>Phylloscopus collybita</i>	Common Chiffchaff	25	0.11
<i>Troglodytes troglodytes</i>	Eurasian Wren	18	0.08
<i>Buteo buteo</i>	Common Buzzard	17	0.07
<i>Prunella modularis</i>	Duncock	15	0.07
<i>Phylloscopus trochilus</i>	Willow Warbler	11	0.05
<i>Parus cristatus</i>	European Crested Tit	10	0.04
<i>Luscinia megarhynchos</i>	Nightingale	8	0.03
<i>Corvus corax</i>	Common Raven	7	0.03
<i>Falco tinnunculus</i>	Common Kestrel	6	0.03
<i>Dendrocopos major</i>	Great Spotted Woodpecker	6	0.03
<i>Delichon urbica</i>	Common House Martin	5	0.02
<i>Motacilla alba</i>	White Wagtail	5	0.02
<i>Streptopelia turtur</i>	European Turtle Dove	4	0.02
<i>Chloris chloris</i>	European Greenfinch	4	0.02
<i>Strix aluco</i>	Tawny Owl	3	0.01
<i>Jinx torquilla</i>	Eurasian Wryneck	3	0.01
<i>Apus pallidus</i>	Pallid Swift	2	0.01
<i>Serinus serinus</i>	European Serin	2	0.01
<i>Circaetus gallicus</i>	Short-toed Snake Eagle	1	0.00
<i>Motacilla flava</i>	Yellow Wagtail	1	0.00
<i>Pica pica</i>	Eurasian Magpie	1	0.00
<i>Merops apiaster</i>	European Bee-eater	1	0.00
Unidentified vocalizations		99	0.43
		22,949	100.00

Note: Each typology of species-specific vocalization was recorded only once per minute.

peaks, the first (minor) in March and the second in October (Figure 4(b)). Alarm calls are clearly present from April to September, but other social calls (males, juveniles, etc.) are only heard in a few months and particularly in September. Song is the dominant acoustic activity (84.55%), followed by female contact calls (9.40%), alarm calls (5.40%) and other social calls (0.65%; see 2).

The Red-billed Leiothrix acoustic activity over the course of the day

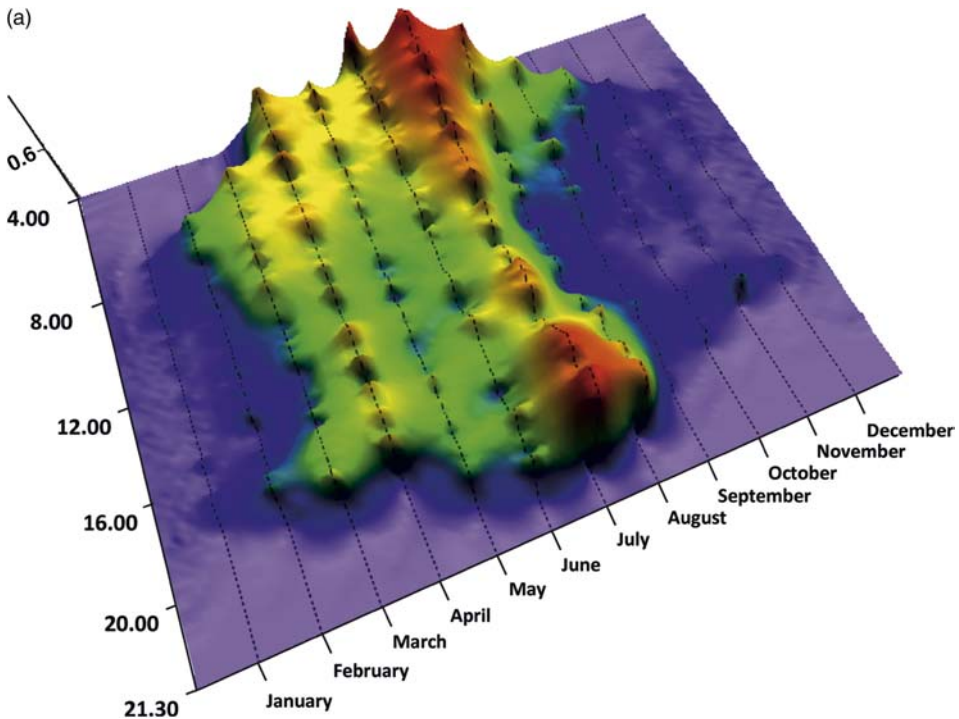
The Red-billed Leiothrix sings in the early morning, in particular immediately after sunrise, with this activity decreasing over the course of the day, with the minimum activity being in the middle of the day (Figure 4(c)). The birds start to sing soon after dawn (a few minutes after the Common Blackbird), but their singing activity falls significantly in the late afternoon and at dusk. Despite the fact that some authors report that this bird sings particularly at roost (Male et al. 1998), our data confirm that this habit is noticeable only in July and August (Figure 4(a)).

The female contact calls are distributed bimodally over the course of the day, with peaks in the early morning and in the afternoon, which is similar to the trend of the song of the males. Alarm calls have a similar trend to the female calls, with a peak in the morning. The “other social calls” do not seem to have recognizable patterns across the day.

Nevertheless, when observing Figure 4(c), it is important to consider that this refers to the sum of the overall song production of the entire year. Indeed, it is not possible to see the predominance of the singing activity in the first few hours of the day, since it shows the result of the overlap of all of the different dawns of the year, which clearly occur at different times of the day depending on the season.

The Red-billed Leiothrix and species' associations

In order to evaluate the potential role of the Red-billed Leiothrix in the acoustic context of the entire bird community, we compared the song activity of this species with that of the entire community, the dominant species (European Robin, Common Blackbird and Subalpine warbler) and the first of the sub-dominant species (the Sardinian Warbler).



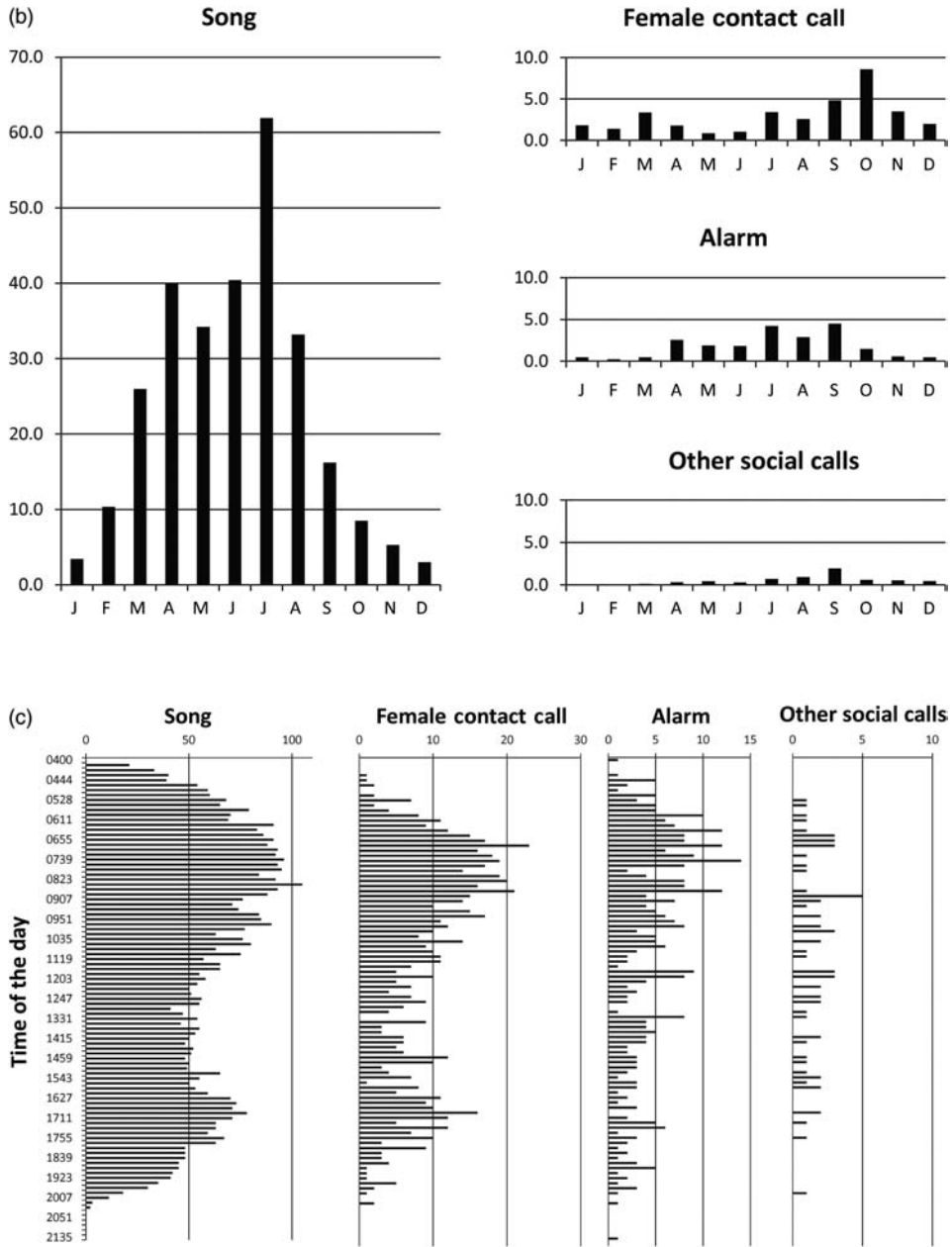


Figure 4. (a) A 3D representation of the acoustic activity of the Red-billed Leiothrix as the result of the aural identification of male song, female contact calls, alarm calls and other social calls. (b) Annual distribution of the songs, the female contact calls, the alarm and other social calls of the Red-billed Leiothrix. (c) Daily distribution of the songs, the female contact calls, the alarm and other social calls of the Red-billed Leiothrix. The reported values are relative to the overall song production of the year, so they are affected by a diverse beginning and ending (dawn and dusk) of the day.

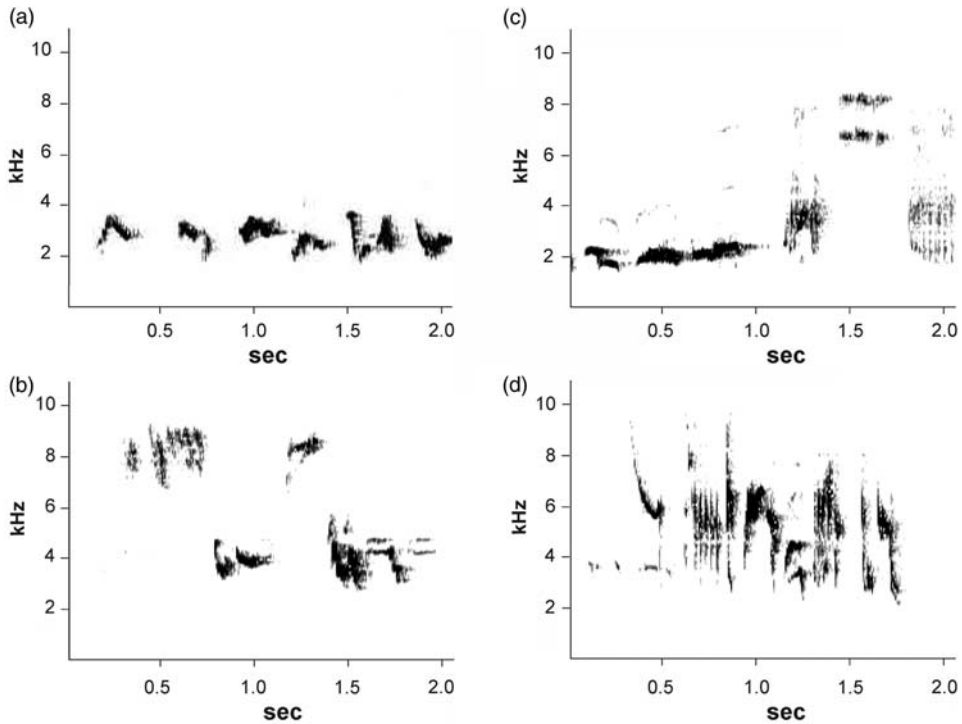


Figure 5. A spectrogram of the typical song of Redbilled Leiothrix (a), European Robin (b), Common Blackbird (c), Subalpine Warbler (d) as an example of potential frequency masking with the song of the Red-billed Leiothrix.

Figure 5 sets out the spectrograms of the songs of these species to provide a visual comparison. As summarized in Table 2, 84% of all of the songs produced by the community (Red-billed Leiothrix excluded) are concentrated in the April–June period. However, with the Red-billed Leiothrix included, the song activity is distributed over a longer period (this species is active all year round, in particular singing from March to August).

The song of the Red-billed Leiothrix comprises 37% of the singing produced by the entire community, and is a strong indicator of the importance of its song there. The monthly and hourly song overlap between the Red-billed Leiothrix and all other species is reported in Tables III and IV and Figure 6(a). The song of the European Robin represents 36% of the singing activity of the entire community. In particular, 87% of this bird's song is concentrated in the period from March to June, with a total seasonal overlap of 2.52 with the Red-billed Leiothrix (Table 3 and Figure 6(b)). The Common Blackbird (which comprises 18% of the singing activity of the entire community) is the third most canorous species, with 90% of its song being concentrated in the period from April to June. The total seasonal overlap with the Red-billed Leiothrix is 1.30 (Table 3 and Figure 6(c)). The Subalpine Warbler is a breeding visitor, and its brief song period is determined by its late arrival in April. Its maximum song activity is in May, with 85% of its singing being concentrated between May and June. The total seasonal overlap with the Red-billed Leiothrix is 0.75 (Table 3 and Figure 6(d)).

Table 3. The values of the mean acoustic overlap \pm SE between the Red-billed Leiothrix and the most common species along the different months (see "Methods" section).

	January	February	March	April	May	June	July	August	September	October	November	December
	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE
European Robin	0	0.02 \pm 0.02	0.31 \pm 0.06	0.61 \pm 0.03	0.59 \pm 0.02	0.62 \pm 0.02	0.06 \pm 0.06	0.01 \pm 0.01	0.07 \pm 0.02	0.08 \pm 0.02	0.10 \pm 0.02	0.05 \pm 0.02
Common Blackbird	0	0	0.14 \pm 0.04	0.38 \pm 0.02	0.36 \pm 0.02	0.38 \pm 0.02	0.04 \pm 0.04	0	0	0	0	0
Subalpine Warbler	0	0	0	0.05 \pm 0.03	0.36 \pm 0.02	0.17 \pm 0.02	0.16 \pm 0.03	0	0	0	0	0
Sardinian Warbler	0	0	0.02 \pm 0.01	0.23 \pm 0.05	0.05 \pm 0.02	0	0	0	0	0	0	0
Common Firecrest	0	0.05 \pm 0.02	0.17 \pm 0.04	0.10 \pm 0.02	0.08 \pm 0.02	0.03 \pm 0.02	0	0	0	0	0	0.01 \pm 0.01
Eurasian Jay	0.02 \pm 0.01	0.06 \pm 0.02	0.11 \pm 0.03	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.05 \pm 0.02	0.10 \pm 0.02	0.15 \pm 0.03	0.05 \pm 0.02	0.10 \pm 0.04	0.04 \pm 0.02
Dartford Warbler	0	0.01 \pm 0.01	0.04 \pm 0.02	0.04 \pm 0.02	0.01 \pm 0.01	0	0.01 \pm 0.01	0	0	0	0	0
All species	0	0.08 \pm 0.02	0.38 \pm 0.06	0.64 \pm 0.03	0.61 \pm 0.02	0.63 \pm 0.02	0.21 \pm 0.06	0.01 \pm 0.01	0.08 \pm 0.02	0.08 \pm 0.02	0.11 \pm 0.02	0.06 \pm 0.02

Table 4. The values of acoustic overlap \pm SE between the Red-billed Leiothrix and the most common species along the hours of the day (see "Methods" section).

	04:00	05:00	06:00	07:00	08:00	09:00	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	
Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	
European Robin	0.65 \pm 0.11	0.56 \pm 0.02	0.48 \pm 0.03	0.52 \pm 0.02	0.46 \pm 0.01	0.45 \pm 0.01	0.43 \pm 0.02	0.39 \pm 0.02	0.38 \pm 0.01	0.37 \pm 0.02	0.32 \pm 0.02	0.38 \pm 0.02	0.36 \pm 0.01	0.37 \pm 0.02	0.42 \pm 0.02	0.42 \pm 0.02	0.33 \pm 0.02	0.15 \pm 0.06
Common Blackbird	0.57 \pm 0.11	0.34 \pm 0.03	0.24 \pm 0.01	0.32 \pm 0.02	0.24 \pm 0.01	0.22 \pm 0.01	0.23 \pm 0.02	0.18 \pm 0.03	0.20 \pm 0.02	0.23 \pm 0.03	0.21 \pm 0.02	0.24 \pm 0.03	0.22 \pm 0.03	0.30 \pm 0.03	0.37 \pm 0.01	0.30 \pm 0.01	0.30 \pm 0.02	0.09 \pm 0.06
Subalpine Warbler	0.29 \pm 0.06	0.31 \pm 0.02	0.24 \pm 0.03	0.22 \pm 0.01	0.24 \pm 0.02	0.22 \pm 0.03	0.18 \pm 0.03	0.12 \pm 0.03	0.14 \pm 0.02	0.11 \pm 0.03	0.11 \pm 0.02	0.09 \pm 0.03	0.10 \pm 0.04	0.09 \pm 0.04	0.07 \pm 0.04	0.10 \pm 0.04	0.10 \pm 0.04	0.00
Sardinian Warbler	0.03 \pm 0.03	0.09 \pm 0.03	0.13 \pm 0.02	0.13 \pm 0.02	0.10 \pm 0.04	0.09 \pm 0.03	0.10 \pm 0.02	0.02 \pm 0.02	0.10 \pm 0.03	0.06 \pm 0.03	0.12 \pm 0.01	0.09 \pm 0.03	0.09 \pm 0.04	0.06 \pm 0.03	0.00	0.00	0.00	0.00
Common Firecrest	0.19 \pm 0.05	0.14 \pm 0.02	0.05 \pm 0.03	0.09 \pm 0.05	0.09 \pm 0.03	0.12 \pm 0.03	0.12 \pm 0.01	0.10 \pm 0.05	0.05 \pm 0.02	0.02 \pm 0.02	0.02 \pm 0.02	0.09 \pm 0.03	0.03 \pm 0.03	0.06 \pm 0.03	0.13 \pm 0.03	0.03 \pm 0.03	0.03 \pm 0.03	0.00
Eurasian Jay	0.00	0.05 \pm 0.03	0.15 \pm 0.03	0.12 \pm 0.03	0.12 \pm 0.02	0.08 \pm 0.02	0.08 \pm 0.02	0.07 \pm 0.02	0.04 \pm 0.02	0.04 \pm 0.02	0.03 \pm 0.02	0.04 \pm 0.02	0.04 \pm 0.02	0.07 \pm 0.03	0.05 \pm 0.04	0.00	0.00	0.00
Dartford Warbler	0.00	0.00	0.00	0.00	0.00	0.08 \pm 0.03	0.06 \pm 0.03	0.08 \pm 0.03	0.04 \pm 0.03	0.04 \pm 0.04	0.00	0.05 \pm 0.03	0.02 \pm 0.02	0.02 \pm 0.02	0.02 \pm 0.02	0.00	0.00	0.00
All species	0.67 \pm 0.11	0.58 \pm 0.02	0.50 \pm 0.02	0.53 \pm 0.02	0.48 \pm 0.01	0.47 \pm 0.01	0.46 \pm 0.02	0.41 \pm 0.02	0.41 \pm 0.01	0.41 \pm 0.02	0.35 \pm 0.02	0.39 \pm 0.02	0.39 \pm 0.01	0.41 \pm 0.02	0.45 \pm 0.01	0.34 \pm 0.02	0.15 \pm 0.06	

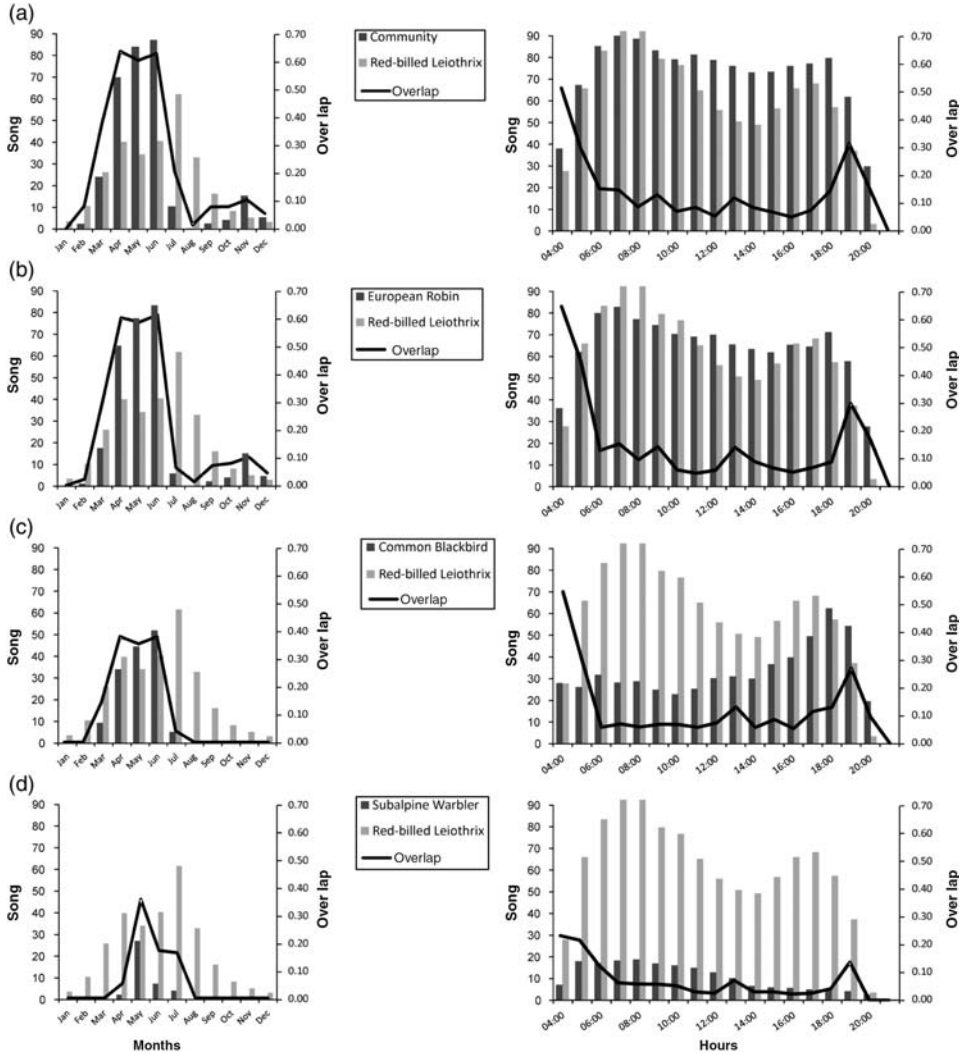


Figure 6. The song distribution of the Red-billed Leiothrix and its overlap with the song of (a) the entire community, (b) the European Robin, (c) the Common Blackbird and (d) the Subalpine Warbler along the season (left figure) and along the different hours of the day (right figure).

The singing activity of the Sardinian Warbler, meanwhile, is concentrated in April, when 86% of all of its songs can be heard. It has a total seasonal overlap with the song of the Red-billed Leiothrix of 0.31 (Table 3).

The acoustic overlap with the Red-billed Leiothrix is different according to the species selected (Kruskal–Wallis test: $H = 313$, $df = 8$, $p < 0.001$), and this variability is maintained on a monthly scale. Moreover, from April to September, the overlap is significantly greater than during the period October–March (see Table 3) for the following species: European Robin (Mann–Whitney U -test: $U = 5224$, $p < 0.001$), Common Blackbird (Mann–Whitney U -test: $U = 4805.5$, $p < 0.001$), Sardinian Warbler (Mann–Whitney U -test: $U = 7831$, $p < 0.001$) and Subalpine Warbler (Mann–Whitney U -test: $U = 4800$, $p < 0.001$). This is not the case for the Common Firecrest (Mann–Whitney U -

test: $U = 8755$, $p < 0.34$), Dartford Warbler (Mann–Whitney U -test: $U = 8952$, $p < 0.35$) and Eurasian Jay (Mann–Whitney U -test: $U = 8779.5$, $p < 0.46$).

For all of the species mentioned, the different levels of overlap over the course of the hours of the day were also considered. It is possible to note from Table 4 that the Red-billed Leiothrix overlaps with some species, especially during the dawn chorus. In particular, the European Robin, the Common Blackbird, the Subalpine Warbler and the Dartford Warbler overlap significantly more during the first few hours of the day, in the period 4 to 8 am, than during the rest of day (Mann–Whitney U -test, respectively: $U = 0.00$, $p < 0.01$; $U = 7.00$, $p = 0.03$; $U = 2.00$, $p = 0.01$; $U = 8.00$, $p = 0.03$). The other investigated species did not significantly overlap during this period of the day: the Sardinian Warbler (Mann–Whitney U -test: $U = 13.00$, $p = 0.14$), the Common Firecrest (Mann–Whitney U -test: $U = 12.00$, $p = 0.11$) and the Eurasian Jay (Mann–Whitney U -test: $U = 18.00$, $p = 0.36$).

Discussion

The study area is characterized by low acoustic disturbance from human activity due to the peculiar position of the hanging valley, which is located far from permanent settlements and road infrastructures. The level of background noise that appears to be higher outside the breeding season seems to be connected with more intense levels of bad weather in winter and autumn according to the Mediterranean climate. The moderate peak observed in noise distribution in June and July, particularly during the second part of the day, can be attributed to local breezes, summer thunderstorms and boat engines. In autumn, some of the noise caused by shooting during hunting activities was reported, especially in the early morning. Dawn was the period with the lowest background noise due to fewer breezes and less human activity. In turn, the higher noise levels in March and September could be connected to the presence of boats fishing along the coast. The slightly negative correlation between biophonies and environmental noise seems to confirm the influence of the latter on the communication mechanisms of animals, but further investigations and more data are required to better interpret this finding.

Relatively few species have been found to be resident throughout the year (four dominant and five sub-dominant), but others are migratory breeders and/or winter visitors dispersed over a wider area, confirming that the Mediterranean maqui supports a very restricted number of specialized species, as reported in the relevant literature (Blondel 1969; Cody and Walter 1976). The acoustic activity of the entire community is concentrated in the spring, with a gradual increase over the course of the season and a sharp decrease at the end of June that is coincident with the end of the breeding period for the majority of species.

The Red-billed Leiothrix is one of the loudest birds over the course of the year, with the longest period of acoustic activity (mainly song) when compared with all of the other species comprising this bird community. The acoustic pattern of this species during the day seems to be similar to that of one of the other indigenous species. However, in July and August, when the weather conditions are hot and dry, its sound activity persists throughout the day, including at dusk. This characteristic differentiates the Red-billed Leiothrix from all of the indigenous species and confirms its alien origins as a sub-tropical bird.

In the study area, the demographic success of the Red-billed Leiothrix may be due to its high foraging plasticity, as hypothesized by Eguchi and Amano (2004). However, this bird's strong acoustic activity, which is highlighted by our results, enables us to consider that this alien species has significantly modified the soundscape in the study area. Its song

overlaps with those of the indigenous species only during the part of its acoustic activity (April–June), and this is mainly concentrated at dawn. The fact that it sings alone, despite the silence of potential indigenous competitors from July onwards and before April, is an important factor that probably allows this bird to better delimit the breeding territory and to consolidate the acoustic communication network among the members of its population, especially outside the breeding season when it forms flocks of several individuals (Male et al. 1998). At the same time, this habit probably permits the species to occupy and defend new territories by using acoustic signals without the masking or overlapping effects of sounds from other acoustically competitive species along the different hours of both the day and the season.

We have no data about the learning processes that may be used by the Red-billed Leiothrix to take advantage of information about its surroundings, but from a theoretical point of view, this could be possible. The soundtope hypothesis (Farina, Lattanzi, et al. 2011; Farina, Pieretti, et al. 2011) is largely based on the notion that birds have a detached acoustic representation (*sensu* Gärdenfors 1995), which could bring this species to the fore when it comes to researching a very informative acoustic pattern. Moreover, the hetero-specific habitat copying hypothesis (Parejo et al. 2004) could be invoked to explain how the Red-billed Leiothrix, which probably is a competitor of most of the species in the Mediterranean shrubland, can use the acoustic information of these other species to establish territories in more favourable areas (see Mönkkönen and Forsman 2002; Redmond et al. 2009).

The high density of the Red-billed Leiothrix may cause “apparent competition” (*sensu* Martin and Martin 2001), as also argued by Eguchi and Amano (2004). Indeed, loud songs, alarm calls and social calls uttered during and outside the breeding season could have potentially negative effects on the indigenous community, as they may attract nest predators like Carrion Crow or Jay. This effect could reduce the density of the indigenous community or lead to the disappearance of some species, as observed in Japan by Shigeo (2006). In this sense, the rarity of the Blackcap (*Sylvia atricapilla*) in the study area, a species that is expected to be commonplace, especially in the wettest and most densely covered slopes, is unexplained. The long-term studies of bird dynamics are necessary to verify the presence of an excluding mechanism between the Blackcap and the Red-billed Leiothrix, and could follow the experimental approaches outlined in this study.

As reported by Shigeo (2006), due to the overlapping of different life traits, the Red-billed Leiothrix has led to a reduction in the abundance of the Bush Warbler (*Cettia diphone*) and probably the Japanese Robin (*Erithacus akahige*) and the Great Tit (*Parus major*) in Japanese habitats. The lack of historical data on the study area herein currently prevents us from making a similar comparison. However, the methodology adopted will allow us to make an inter-annual comparison of the acoustic activity of potentially competitive species in the future, which is a life trait that is rich in valuable information due to its plasticity.

It is reasonable to expect adaptations in the temporal song patterns of the Red-billed Leiothrix as a consequence of the influence of other birds’ songs. For instance, the variation of song amplitude is a dynamic regulating mechanism that is activated according to the ecological demands of signal transmission and the social context in which birds are living (Brumm 2004). Indeed, this effect has been demonstrated by Brumm (2006) with playback experiments on the nightingale (*Luscinia megarhynchos*). Luther (2009), meanwhile, has observed that the species that sing at the same time and in the same space disperse the acoustic signal more to reduce acoustic overlap and masking, while species that sing randomly in space and time have a less dispersed song. According to this

hypothesis, we can expect a remodelling of the acoustic activity of the bird community in this Mediterranean shrubland after a consistent number of Red-billed Leiothrix individuals have become established there. From April to June, the song activity of the Red-billed Leiothrix overlaps extensively with that of the Common Blackbird, European Robin, Subalpine Warbler and Sardinian Warbler, and this should have consequences for these species, at least in terms of communication performance. Playback experiments to evaluate in indigenous species the degree of direct or indirect competition caused by the acoustic performance of the Red-billed Leiothrix have already been done in a follow-up to this study, and the first results indicate temporal shifts of the song performance, at least in the Blackcap (Farina, per. com.).

The fact that the Red-billed Leiothrix is acoustically active more than the indigenous species could be an example of temporary maladaptation (*sensu* Dias and Blondel 1996) for a trait like song activity. However, there is currently no way to predict if this species will synchronize its acoustic activity, whether in the medium- or long-term, and adapt to the indigenous community.

If we assume that the song repertoire of a species is strongly influenced by the environmental context and the density of individuals, this means that an abundant population should have a more diverse acoustic repertoire, as argued by Laiolo et al. (2008). The process of spreading by the Red-billed Leiothrix can be regarded as an inverse process of demographic fragmentation. From an isolated original nucleus of cage-escaped birds, after a period of recruitment we are witnessing a phenomenon of area filling (saturation). Moreover, in the future, when the population of this species has expanded and stabilized even more, we should expect a more acoustically differentiated repertoire of the Red-billed Leiothrix population.

Conclusions

The Red-billed Leiothrix is an important invasive species in the Mediterranean shrubland. With its loud vocalizations uttered over the course of the majority of the year, this species can be seen as a new acoustically dominant species that broadly overlaps with the acoustic performances of the indigenous species, at least during the breeding season. Consequently, it is a potential modifier of the soundscape patterns of the local bird community. In conclusion, the Red-billed Leiothrix seems to be a favoured candidate when it comes to discussing the role of the song repertoire as a proxy to shape a community soundscape.

The ACI_t metric has been demonstrated to be useful when it comes to characterizing the abiotic soundscape and better evaluating the acoustic patterns of an entire community. It thus represents a new efficient descriptor of the soundscape structure (geophonies, anthrophonies and biophonies), particularly when coupled with aural analysis. When compared to long-term studies, the results obtained by applying the ACI_t metric could reveal new acoustic patterns that are culturally driven according to different levels of alien intrusion in communities.

Supplementary information

The following Supplementary Information is available for this article online:

Table 1s – Meteorological records for Deiva Marina in 2011 (from Sarzana Luni, the archive of the closest fix climatic station).

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