Song sharing and singing strategies in the winter wren *Troglogytes troglodytes*

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**Abstract**

The winter wren is a common forest bird living in groups of few adjacent neighbours during the breeding season. Inside each group, males vocally interact in the context of both territorial holding and sexual competition, forming a complex communication network. To study this network, we first analysed song type and syllable repertoires within and between distinct groups. We found a limited number of song types highly stereotyped in length, syntax and syllable composition, frequently shared among neighbours. Between groups, song type and syllable repertoires sharing decreased with increasing distance at a higher rate for song types than for syllables. Then, with continuous recordings, we focused on the dynamics of acoustic interactions between neighbours. We showed that male winter wrens can differentially use their song type repertoire (non-matching strategy), overlap their neighbours and modulate their singing rhythm producing longer inter-song intervals with no change in song length during acoustic interactions.

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1. Introduction

In most Oscine species, male birds sing territorial songs to attract females and defend a territory against other males. In regard to these functions, birdsong is thought to have evolved mainly through sexual selection (Byers and Kroodsma, 2009; Collins, 2004; Martens, 1996). Depending on the species, a great variety in repertoire size and singing behaviours can be found: from short and discrete song types to long and continuous ones, from one syllable produced repeatedly to hundreds of syllables produced with huge variety (Catchpole and Slater, 2008; Kroodsma, 1982, 2004; Todt and Hultsch, 1996).

Territorial songs are learned by imitation from template songs of at least one adult tutor bird and are thus culturally transmitted (Beecher and Brenowitz, 2005). As a consequence, bird songs of a species are susceptible to regionally and locally derive between distinct populations, leading to dialects and microdialecs respectively (reviewed in Baptista, 1996). Thus, closer birds (such as neighbouring males) share more song elements, and even entire songs, than more distant ones (Briefet et al., 2010; Kroodsma, 1982; Mundinger, 1982). Moreover, there is evidence that shared sequences of syllables can convey a group signature allowing birds to discriminate between neighbours and non-neighbours (Briefet et al., 2008a; Gentner and Hulse, 2000).

While singing, male birds can convey their species, group and individual identities as well as other individual information such as age, breeding status, territory settlement, motivation, physical or emotional state (Collins, 2004; Podos and Nowicki, 2004). The encoding of these different levels of information can be assigned to fine variations in the song structure itself (frequency modulation, energy repartition, rhythm and tempo of syllable emission,) and/or to the differential use of song type or syllable type repertoires.

In this context, shared songs, as a common part of the repertoire between neighbours, can be selectively used during counter-singing sessions (Brown and Farabaugh, 1997; Nelson, 1992; Payne and Payne, 1997). For example, a bird can selectively reply either with a shared song of the exact same type as the preceding song sung by a neighbour (song matching) or, on the contrary, reply with a non-matching song. Depending on the species, matching/non-matching strategies have been shown to be aggressively directed signals towards an opponent neighbour (Mennill and Ratcliffe, 2004; Searcy and Beecher, 2009; Stoddard et al., 1992; Vehrencamp, 2001) but also a way of strengthening spatial and social relationships between males of a neighbourhood against non-resident males seeking territories (Baker et al., 1981; Naguib, 2005).

Temporal organization of song production is also known to be a highly important feature in territorial encounters (Hultsch and Todt, 1982; Otter and Ratcliffe, 1993; Weary et al., 1988). While counter-singing, neighbours can carefully alternate their songs or start to sing before the end of its neighbour’s song, a strategy known as overlapping, which mask part of an opponent’s signal and impair mutual listening. Overlap, alternate, changes in cadences or song rate, drifts within songs were shown to have different aggressive/submissive values in escalating or deescalating territorial contests therefore influencing mate choice by...
females and territorial behaviour of males (Dabelsteen et al., 1996, 1997; Lambrechts, 1996; McGregor and Peake, 2000; Mennill and Ratcliffe, 2004; Naguib, 1999; Todt and Naguib, 2000). However, there exist different views on how to interpret song overlapping and further studies are needed to better understand the dynamics of vocal interactions between territory holders (Naguib and Mennill, 2010; Seeley and Beecher, 2009).

Most studies on singing strategies focus on acoustic interactions between two individuals (either between two natural neighbours or in playback experiments), leaving the dynamics of behavioural interactions within a group of several birds largely unexplored. Indeed, during the breeding season, most Oscine species live in groups of adjacent neighbours forming spatially fixed communication networks composed by several signallers and receivers (Becher and Brenowitz, 2005; McGregor, 2005). Interestingly, in such acoustic networks, each member is able to extract information not only from interactions in which it is actively involved but also from interactions between other members of the group (eavesdropping) (Peake, 2005). Such networks involve adult males and females, as well as juveniles whose song learning may be influenced by acoustic interactions between adult males (Templeton et al., 2010).

In order to better understand how the structure of songs, the timing and the selective use of song types can be modulated at both inter- and intra-group levels, we have studied groups of winter wrens, Troglodytes troglodytes. This small, sedentary and common forest bird has the advantage of living in stable groups with a relatively small number (2–7) of adjacent neighbours (Armstrong, 1955). Although one can hear sporadically wrens singing all year long, male winter wrens sing mostly during the breeding season (from February to July). It is a songbird with a discrete repertoire, each individual having a moderately complex repertoire of 4–7 distinct song types. Song sharing and microgeographic variations in singing behaviour have been documented for both European and North American populations of winter wrens (Catchpole and Rowell, 1993; Kreutzer, 1974a, b; Kroodsma, 1980) but the role of song types repertoires remains unclear. Moreover, their singing behaviour, especially the timing of vocal interactions between males inside groups, is unknown.

In the present study, we analysed the composition of individual song type and syllable repertoires in 3 small groups of adjacent neighbours. We examined repertoire sharing between and within groups of neighbours. Finally, using continuous recordings, we investigated singing strategies between neighbours of one representative group, focusing on temporal organisation of acoustic interactions and selective use of song types in natural countersinging situations.

2. Materials and methods

2.1. Study area, subjects and recordings

This study was conducted from February to June, during the 2008 and 2009 breeding seasons. Three groups (3–4 territory holder males) of neighbours were followed in 3 distinct forest areas surrounding the University of Paris 11, Orsay, France. Two groups (A and C) were 1 km far from each other while the third group (Group B) was more than 2 km away. Individual territories of about 50–100 m of diameter were assessed by careful observations of movements and vocal activity (song posts) of the resident males. GPS coordinates were taken to map and locate the individual territory boundaries in each group.

Song recordings were made in the morning (from 30 min before sunrise to 10 am). Recordings of focal male songs were made with a Marantz PMD 690 digital recorder (sampling rate 44.1 kHz) connected to a Sehnhieper ME67 directional shotgun microphone.

Continuous 3 h recordings (beginning 30 min before sunrise) of all individuals in the group simultaneously, were conducted for one of the 3 groups (Group B), on May 15, 16 and 19 and June 25, 26 and 29 2009. We used Roland Edirol R09 digital recorders (sampling rate 44,1 kHz) connected to CS-15 Roland Edirol unidirectional microphones. The identity of each singing male was dictated by the experimenter immediately after the end of each song and was, thus directly included in the recordings.

2.2. Song analysis

The Avisoft SASLab Pro (Specht, 2004) software was used for acoustic analyses. Song measurements were realised on spectrograms (FFT-Length: 1024, Hamming window, overlap: 87%) and the different song types and syllables were visually identified then labelled. To ensure the reliability of labelling, two experimenters established independently the syllable and song type repertoires and confronted the two versions. The labelling of all recorded songs was then done according to the consensus repertoires.

A syllable was defined as a continuous trace or a group of 2–3 continuous traces never found either separately or in another configuration (Fig. 1). A song type was defined as a fixed specific syntactic organisation of distinct syllables (Fig. 1). This definition did not take into account syllable repetition, which means that two signals belonging to the same song type could have a different number of repeated syllables. Song types were identified and labelled according to an alphanumeric code indicating group (capital letters A, B, C), individual (number) and song type (lower-case letters a–j).

In continuous recordings, all songs from all males were identified in spectrograms and tagged. The songs were categorised in two distinct singing situations: (a) one individual in the group was singing and all the others remained silent (solo situation); (b) two or more males were singing together, either alternating or overlapping their songs (interaction situation). The absolute time of beginning and end of each song was noted to calculate song duration and inter-song interval (ISI), i.e. the period of time between the end of one song and the beginning of the next one. Group ISI was calculated using all consecutive songs exchanged by the 3 individuals during the periods of continuous recording. Individual ISI values were calculated using only songs produced by the same individual: (1) when singing in solo situation (soloISI), and (2) when engaged in singing interaction with another male (interactionISI).

A repertoire similarity coefficient (RS) was calculated to compare song type repertoires as well as syllable type repertoires between pairs of individuals. This coefficient was defined as the proportion of elements (song types or syllables) of the entire repertoire of a pair of individuals that was shared by the pair (Hultsch and Todt, 1989):

\[ RS = \frac{2(R_1 \cap R_2)}{R_1 \cup R_2} \]

where \( R_1 \) and \( R_2 \) = repertoire of individuals 1, 2 respectively. RS values range from 0 for entirely different repertoires, to 1 for identical repertoires.

For acoustic analyses we used a sample set of 368 songs. Ten songs of each shared song type for each individual were chosen when possible. We used only songs of good signal to noise ratio. Songs were filtered to eliminate background noise and songs of other species (FFT Band-pass filter 2.70–9.00 kHz) and acoustical measures were extracted from the mean spectrum of the entire signal: peak frequency, and 25%, 50% and 75% energy quartiles (quart 25, quart 50, quart 75). Two measures of internal temporal organisation of songs, tempo (number of syllables per unit of time) and rhythm (sound to silence ratio) were calculated from duration of syllables and inter-syllable silences inside songs. Only song types shared by all group members were analysed here for each group.
The Coefficient of Variation of each spectral and temporal parameter was calculated for songs produced by a same individual (\(CV_w\)) and songs from different individuals (\(CV_b\)) using the equation (Scherrer, 1984; Sokal and Rohlf, 1995):

\[
CV = 100 \left(1 + \frac{1}{4n}\right) \left(\frac{SD}{X_{\text{mean}}}\right)
\]

where \(n\) = sample size, \(SD\) = standard deviation of the sample and \(X_{\text{mean}}\) = mean of the sample.

Potential for Individual Coding (PIC) of each parameter was calculated as the ratio (Scherrer, 1984; Sokal and Rohlf, 1995):

\[
\text{PIC} = \frac{CV_b}{\text{MeanCV}_w}
\]

where \(\text{MeanCV}_w\) = mean of CVw values of all the individuals considered.

For a given parameter, a PIC value superior to 2 means that this parameter may potentially be used for individual discrimination since its intra-individual variation is twice less important than inter-individual variability (Robisson et al., 1993).

In order to evaluate matching/non-matching strategies during interactions (\(ISI < 2\ s\)) in group B, we quantified which song type was sung in response to each particular song type. It was either the exact same one (match) or any of the 4 possible remaining ones (non-match).

### 2.3. Statistical analysis

As data were not normally distributed we used non-parametric statistics. All statistical analyses except permutation tests were carried out using Statistica v.6 (StatSoft, 2001).

Permutation test was carried out using StatXact v.3.1 (Cytel Software Corp, 1997) and was used to compare RS values for song types and syllable types between neighbours (intra-group similarity) and non-neighbours (inter-group similarity).

Kruskal–Wallis ANOVA was used to compare song output between males and between different days on continuous recordings. Kolmogorov–Smirnov test was used to compare distributions of song and ISI duration in solo- vs. counter-singing situations. \(\chi^2\) test was used to compare the occurrence of different song types between singing situations or between individuals.

### 3. Results

#### 3.1. What do wrens sing? Repertoires at the individual level

**3.1.1. Song type and syllable repertoires**

5397 songs were recorded from 10 individuals in 3 distinct groups (Table 1). 17 different song types were identified on the basis of syllable composition (types of syllables used and their order in the sequence, Fig. 1) and a total of 62 different syllable types were found. Song types were composed of series of 17–27 different syllables (Mean ± SD: 23.08 ± 5.34, N = 368) with alternated sequences of repeated and non-repeated syllables (Fig. 1).

Cumulative curves showed that the individual’s song type and syllable repertoire size was reached with 300 songs analysed (data not shown). For only one individual, 2 rare song types were found after 600 and 800 recorded songs and only once. Individual song type repertoires ranged from 5 to 9 song types with a mean song type repertoire size of 6 ± 1.5 (Mean ± SD, N = 10) song types per individual. Individual syllable repertoire size ranged from 33 to 41 syllable types with a mean of 36.4 ± 2.5 syllables (Mean ± SD, N = 10). Each song type contained 45.46 ± 4.94% (Mean ± SD, N = 10) of the entire syllable repertoire of each male.

**3.1.2. Individual temporal and frequency characteristics of song**

To examine individuality in the structure of songs inside groups, the potential for individual coding (PIC) of the spectral and temporal measurements from a set of 368 songs was estimated (Table 2).

<table>
<thead>
<tr>
<th>Male code</th>
<th>N songs</th>
<th>N song types</th>
<th>N syllable types</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1</td>
<td>344</td>
<td>6</td>
<td>38</td>
</tr>
<tr>
<td>A2</td>
<td>248</td>
<td>5</td>
<td>33</td>
</tr>
<tr>
<td>A3</td>
<td>152</td>
<td>5</td>
<td>34</td>
</tr>
<tr>
<td>Group A</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B21</td>
<td>188</td>
<td>5</td>
<td>35</td>
</tr>
<tr>
<td>B25</td>
<td>897</td>
<td>5</td>
<td>36</td>
</tr>
<tr>
<td>B27</td>
<td>955</td>
<td>5</td>
<td>34</td>
</tr>
<tr>
<td>B29</td>
<td>787</td>
<td>5</td>
<td>36</td>
</tr>
<tr>
<td>Group B</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C11</td>
<td>392</td>
<td>7</td>
<td>37</td>
</tr>
<tr>
<td>C12</td>
<td>978</td>
<td>9</td>
<td>41</td>
</tr>
<tr>
<td>C13</td>
<td>456</td>
<td>8</td>
<td>40</td>
</tr>
<tr>
<td>Group C</td>
<td>1826</td>
<td>9</td>
<td>41</td>
</tr>
</tbody>
</table>

Fig. 1. Example of two different winter wren song types sung by the bird B29. Bold lines show sequences of repeated syllables. Two sequences shared between song types are marked by rectangles.
Table 2
Potential for individual coding (PIC) values for frequency (peak frequency and quartiles 25, 50, 75) and temporal (song duration, tempo and rhythm) parameters. Only song types shared by all males of one group are taken into account. PIC values > 2 are in bold and indicate that the corresponding parameter could potentially represent an individual acoustic marker.

<table>
<thead>
<tr>
<th>Song type</th>
<th>PIC</th>
<th>Peak freq.</th>
<th>Quart 25</th>
<th>Quart 50</th>
<th>Quart 75</th>
<th>Song duration</th>
<th>Tempo</th>
<th>Rhythm</th>
<th>Analysed songs (n)</th>
<th>Males (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aa</td>
<td>1.037</td>
<td>1.567</td>
<td>1.504</td>
<td>2.357</td>
<td>0.746</td>
<td>1.561</td>
<td>0.463</td>
<td>30</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Ac</td>
<td>0.079</td>
<td>0.757</td>
<td>1.013</td>
<td>1.808</td>
<td>0.782</td>
<td>0.783</td>
<td>1.644</td>
<td>30</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Ad</td>
<td>1.467</td>
<td>1.522</td>
<td>0.961</td>
<td>1.506</td>
<td>0.579</td>
<td>1.814</td>
<td>0.817</td>
<td>30</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Ba</td>
<td>0.372</td>
<td>0.907</td>
<td>1.009</td>
<td>0.572</td>
<td>0.895</td>
<td>0.418</td>
<td>0.723</td>
<td>40</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Bb</td>
<td>0.361</td>
<td>1.259</td>
<td>1.44</td>
<td>0.676</td>
<td>0.82</td>
<td>1.111</td>
<td>0.544</td>
<td>40</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Bc</td>
<td>0.653</td>
<td>1.333</td>
<td>1.558</td>
<td>1.153</td>
<td>0.997</td>
<td>1.477</td>
<td>0.955</td>
<td>40</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Bd</td>
<td>1.456</td>
<td>0.985</td>
<td>2.256</td>
<td>1.51</td>
<td>1.232</td>
<td>0.871</td>
<td>0.305</td>
<td>40</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>0.179</td>
<td>0.596</td>
<td>0.334</td>
<td>0.505</td>
<td>0.556</td>
<td>1.105</td>
<td>0.187</td>
<td>30</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Cb</td>
<td>2.623</td>
<td>1.474</td>
<td>1.505</td>
<td>0.819</td>
<td>0.475</td>
<td>0.547</td>
<td>1.147</td>
<td>29</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Cc</td>
<td>0.558</td>
<td>2.088</td>
<td>2.164</td>
<td>0.765</td>
<td>1.204</td>
<td>0.297</td>
<td>0.586</td>
<td>30</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Cd</td>
<td>0.715</td>
<td>1.492</td>
<td>0.425</td>
<td>0.926</td>
<td>0.34</td>
<td>0.542</td>
<td>0.734</td>
<td>29</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.864</td>
<td>1.271</td>
<td>1.288</td>
<td>1.145</td>
<td>0.847</td>
<td>0.847</td>
<td>0.847</td>
<td>30</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>SD</td>
<td>0.747</td>
<td>0.43</td>
<td>0.617</td>
<td>0.585</td>
<td>0.433</td>
<td>0.433</td>
<td>0.433</td>
<td>30</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

All 11 distinct song types analysed for each group were shared by all the males in the group.

A PIC value of 2 means that the intra-individual variation is twice less important than inter-individual variability (Robison et al., 1993). In this study, overall mean PIC values ranged from 0.847 to 1.288, showing no strong potential for individual coding in the measured frequency and temporal parameters in any group. However, in each group, there were 1–2 song types with PIC values greater than 2 for some spectral parameters (in bold in Table 2), suggesting a possible PIC only for these specific song types.

3.2. What do wrens share? Repertoires at the group level

Neighbours shared 90% of their song type repertoires (RS = 0.901 ± 0.117, N = 12). We examined song type repertoire similarity in relation to distance between individuals (neighbours: <500 m; close non-neighbours: 1 km; far non-neighbours >2 km) and found significant differences between the 3 categories of distances (Fig. 2a) (Permutation tests, p < 0.01). Song type repertoire similarity decreased with the inverse of distance between individuals, with close non-neighbours 1 km apart sharing only 50% of their song type repertoires (RS = 0.504 ± 0.093, N = 9) and far non-neighbours separated by more than 2 km sharing no song types at all (RS = 0.000 ± 0.000, N = 24).

When looking at the level of syllables (Fig. 2b), similar results were obtained, although higher coefficients of similarity were found at this level. Neighbours shared 93% of their syllable repertoires (RS = 0.934 ± 0.039, N = 12) and there was again a significant decrease in repertoire similarity (Permutation tests, p < 0.05) when the distance between individuals increases: close non-neighbours 1 km apart shared 70% of syllables in their repertoires (RS = 0.796 ± 0.042, N = 9) and far non-neighbours at 2 km from each other shared 50% of their syllable repertoires (RS = 0.595 ± 0.021, N = 24).

3.3. How do wrens sing? Dynamics of acoustic interactions

3.3.1. Song output

During the 6 continuous recording periods, a total of 9036 songs from the 3 males of Group B were analysed (Fig. 3). More than 90% of songs were found in counter-singing situation while only 10% of total songs took place in solo situation. No significant differences were found in total song production between males (Kruskal–Wallis test, df = 2, N = 18, p > 0.2) or between days (Kruskal–Wallis test, df = 5, N = 18, p > 0.05). Analysis per singing situation (songs in solo or in interaction situation) showed again no significant differences either between individuals (Kruskal–Wallis test, df = 2, N = 18, p > 0.2) nor between days (Kruskal–Wallis test, df = 5, N = 18, p > 0.05). Thus, there was no male producing more songs than its neighbours or singing more in solo or interaction situation in the group.

3.3.2. Temporal organisation of songs

The distribution of all inter-song intervals ISI values obtained for the group followed a bimodal curve (group ISI in Fig. 4) with a main peak between 0 s and 1 s (corresponding to ISI between songs of different males in interaction) and a secondary peak between 4 and 6 s (corresponding to ISI between consecutive songs of a given male in solo situation). The negative part of the curve (dashed area in

![Fig. 2. Repertoire similarity index (RS) between pairs of individuals related to inter-individual distance for (a) song type repertoires and (b) syllable repertoires.](image-url)
Fig. 3. Percentage of songs per situation (solo situation in black bars and interaction situation in white bars) for each continuous 3 h recording period, per male (B25, B27, B29); n = total number of songs for each day.

Fig. 4) corresponded to overlapping events in interaction situation, which occurred in 38.58% of song exchanges.

ISI between songs of an individual were significantly longer in interaction situation (interactionISI in Fig. 4, Mean ± SD = 9.21 ± 5.65, N = 5466) than in solo situation (soloISI in Fig. 4, Mean ± SD = 6.77 ± 3.84, N = 1924) (Kolmogorov–Smirnov test, p < 0.001). On the contrary, song duration values were not significantly different between the two singing situations: interaction with another male (Mean ± SD = 4.56 ± 1.59, N = 5466) and solo singing (Mean ± SD = 4.34 ± 1.50, N = 1924) (Kolmogorov–Smirnov test, p > 0.05).

3.3.3. Use of song type repertoires

In Group B, neighbours shared their entire song type repertoire composed of 5 song types. We found (Table 3) that all song types were used in similar proportions by all neighbours in the group (Chi-square df = 14, p < 1) and that the proportion of each song type emitted by each individual was similar in solo and counter singing situations (Chi-Square df = 9, p < 0.99). However, when we looked in more details to matching/non-matching strategies, we found that male wrens replied less often with the same song type as previously sung by the neighbour than expected by chance (14% vs. 20%, N = 4694; Chi-square (df = 1) = 11.25, p = 0.0008).

4. Discussion

4.1. What do wrens sing?

At the individual level, each male possessed a moderately complex syllable repertoire with a mean of 36 distinct syllables organised in an average of 6 different song types. These results are in agreement with other studies on winter wrens in Europe (Kreutzer, 1974a), Japan (Kroodsma and Momose, 1991) and Eastern North America (Kroodsma, 1980). From more than 5000 songs analysed for the 10 male wrens we found a limited set of 62 distinct syllables. Although these syllables could potentially be used as construction bricks to generate a high number of sequences with different combinations varying in length, we found them combined in a very limited set of 17 distinct song types, i.e. discrete sequences highly stereotyped in syntax and length. Thus, song types are the product of a construction following fixed structural and syntactic rules probably dictated by neural and/or motor constraints of the vocal apparatus of the species and by specific learning and perceptual processes. On the other hand, the repetition of particular syllables inside song types and the existence of some syllables included in all the wren song types found in this study could be related to a strategy for enhancing transmission of the signal in the forest habitat of the species, since habitat constraints are thought to be determinant in the shaping of acoustic signals in birds (Handford and Lougheed, 1991; Mathevon and Aubin, 1997; Wiley and Richards, 1982).

In conclusion, the syllable content in addition with the syntactic organisation of songs showed to be crucial for repertoire definition and song variability assessment in winter wren as it is also the case in other species with discrete song type repertoires (Lehongre et al., 2008; Searcy et al., 1999).

4.2. What do wrens share?

Inside each group, adjacent neighbours shared more than 90% of their song type and syllable repertoires. Our results also showed that repertoire sharing decreased when distance between groups increased, confirming the existence of micro-dialectal variations in Eurasian winter wren songs as previously suggested by Catchpole and Rowell (1993).

High levels of repertoire sharing between neighbours inside a group can be useful to discriminate between familiar group mem-
Table 3
Number of song types (and % of occurrence) sung by each individual belonging to group B and by the whole group in solo and counter-singing situations. Observations are based on 6 continuous recording periods of 3 h. There is no significant difference in the percentage of occurrence between individuals, days and singing situations (Chi-squared tests, p > 0.05 in all cases).

<table>
<thead>
<tr>
<th>Male</th>
<th>Song type</th>
<th>Solo N</th>
<th>% Occurrence</th>
<th>Interaction N</th>
<th>% Occurrence</th>
<th>Any situation N</th>
<th>% Occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>B25</td>
<td>a</td>
<td>91</td>
<td>0.1348</td>
<td>282</td>
<td>0.1334</td>
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bers and unfamiliar individuals potentially searching for a new territory or a mate. Such discrimination would allow the receiving wren to assess the relative threat and respond adequately to it. In skylarks, group signature used by birds for neighbour–stranger discrimination is encoded by the shared sequences found in the songs of neighbouring birds (Briefer et al., 2008a,b).

Interestingly, repertoire similarity values (RS) decreased with distance at a higher rate for song type repertoires than for syllable type repertoires, meaning that syllables tend to be conserved over distances but are re-arranged differently between groups, leading to different song types. In winter wren, as in most songbird species, songs have both territorial and sexual functions. It can be proposed that the syntax of song types would serve for group cohesion between territory owners, whereas sexual selection was made mostly on the basis of the structure of some syllables or trills as honest signals of male quality (De Kort et al., 2009; Griessmann and Naguib, 2002; Vallet et al., 1998).

In neighbourhoods as communication networks, the evaluation of acoustic interactions between all neighbours – by direct interaction or eavesdropping – is thought to be an essential cue for the establishment of stable relationships inside the group (McGregor and Peake, 2000; McGregor, 2005). In order to achieve this process efficiently, some cognitive abilities (to discriminate between distinct group members and memorize previous events), as well as detectable individual variations in acoustic signals are required. In this study, adjacent neighbours shared almost all their song types regarding syllable shape and syntax, which excludes the possibility of individual differentiation by means of a unique non-shared song type typical of each male. Continuous recordings revealed that song types are equally sung by all birds, thus excluding the possibility of individual recognition by means of a distinct “preferred” song type sung more frequently by each male in the group. Nevertheless, pheno-typic inter-individual differences in the sensory–motor system of song production can lead to individual differentiation in voice characteristics even when singing the same songs (Lambrecht, 1996). Although this had been demonstrated in great tits (Blumenrath et al., 2007; Weary and Krebs, 1992) and song sparrow (Nordby et al., 2007), the low values of potential for individual coding (PIC) of shared song types in this study suggest that there is no such individual identity encoded in songs of the winter wren. However, it does not rule out the possibility of individual discrimination between adjacent neighbours. First, we cannot exclude a role of fine differences at the level of some individual syllables not detected in our analysis. Second, since territories are well-defined and stable, the resulting communication network is fixed in space and the relative position of interacting individuals could constitute a major indication for group members to identify the emitter (Briefer et al., 2009).

4.3. How do wrens sing in a group?

Adjacent male winter wren neighbours shared several song types which they sing without detectable individual characteristics and in equal proportion in the two different situations (solo vs. interaction situation), suggesting equivalence in the intrinsic function of all song types in the repertoire. However, the different song types are not randomly sung since we showed that neighbours tend to avoid singing the same song type as the one previously sung by its neighbours (non-matching), as previously shown in the song sparrow (Beecher et al., 2000).

Concerning the temporal organisation of the songs exchanged inside a group, we showed that inter-song intervals of a male’s consecutive songs were significantly longer in counter-singing situation than in solo situation, without changing its song length. When engaged in acoustic interactions, neighbours showed a high tendency to alternate songs with each other, each individual starting a song almost immediately (0–1 s) after its neighbour has finished its own song. It seems thus possible that singing shortly or immediately after a neighbour can be used to address one particular neighbour and/or to maintain the singing interaction. Signal overlapping can be used by individuals to limit the information transmitted by a rival. Overlap is found to have an aggressive value denoting readiness to escalate the contest in some species (reviewed in Naguib and Mennill, 2010). In our study, weak overlapping events (in which only 1–2 s of the song type sequence is masked) occurred in a high proportion (around 40%) and has been observed especially in close distance encounters (personal observation).
Thus, male winter wrens can use both temporal and repertoire-based strategies to interact and further studies involving interactive playbacks are required to determine the potential aggressive value of the non-matching and overlapping strategies as well as their potentially combined use in this species.

Hierarchical interactions between neighbours have been shown to be important in networks (Foote et al., 2010). From our analysis of the continuous recordings, there was no male singing systematically more. Moreover, there was no preferential interactions between one particular pair of neighbours at least in the amount of songs exchanged. These symmetric relationships between neighbours may be in part explained by the symmetrical triangular disposition of territories of the 3 adjacent neighbours studied, with each territory sharing a frontier with the other 2 territories. In the winter wren, more detailed behavioural analyses are needed, including geographical positions, individual singing strategies (overlapping, matching, initiating/terminating song bouts . . .) and different time scales as interactions between neighbours could vary along season, being potentially affected by the timing of arrival of the different group members at the beginning of the reproductive season, by the reproductive stage of the birds and by the degree of familiarity between neighbours (Briefer et al., 2008b), as well as by long-term memory of past interaction events (Amhrin and Erne, 2006).

Recent technological development like effective acoustic localisation systems enabling continuous and simultaneous automatic recordings of several interacting individuals (including information about the respective position of group members) may allow exploring more precisely the roles of song types, timing and space in the complex regulation of acoustic interactions between neighbouring birds (Foote et al., 2010).

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References


