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Neighbours' talk: interspecific choruses among songbirds

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Neighbours' talk: interspecific choruses among songbirds

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In territorial songbirds, duets between mates represent one of the best-known examples of communal display, with the main function being the defence of joint resources. In this study, we found evidence of a coordinated choral display performed by neighbouring heterospecific songbirds. In such choruses, most of the participating species perform a deliberate temporal overlap of songs, thus suggesting agonistic behaviour. However, they then utilize a complex form of behaviour to avoid signal jamming, making the aggressive purpose unlikely. We define these displays as "coordinated interspecific choruses". We recorded dusk choruses of songbirds living in a mixed turkey oak wood in central Italy, and then carried out a niche overlap analysis using null models that were intended for investigations of concurrent emissions of songs, finding that species tend to sing concurrently instead of using the refractory period of another species. Among the species singing concurrently, about half used the same frequency range, but instead of finding considerable spectral overlap between their vocalizations, the number of real spectral overlaps was lower than would be expected by chance. We propose a tentative explanation for this, where such choruses are the expression of the existence of a neighbourhood of different species that has evolved a communal signal that is similar to that used by mates in a pair, i.e. coordinated vocalizations. As coordination requires experience of each other's songs, we propose that evolution has selected individuals that are more skilled at learning heterospecific songs.

Keywords: bird choruses; jamming avoidance; concurrent emissions; heterospecific communication

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Introduction

The function of communal displays in the animal kingdom is a matter of debate, and two hypotheses have been proposed to explain their structure: they can arise as the result of agonistic interactions (Rogers et al. 2007), or as an honest signal of coalition and/or individual quality (Marshall-Ball et al. 2006). In hostile interactions, the consequences are coordinated events, or differentiating an individual's signal from the coordinated signals of others (e.g. frog choruses, Greenfield et al. 1997; crab waves, Burford et al. 1998) or covering the competitor's signal (in birds, Vehrencamp et al. 2007). In cooperative interactions, the meaning of communal displays is provided by the ability to produce a new signal that emerges from the coordination of individuals, rather than by the ability to jam each other's signals (Brumm and Slater 2007). One well-known cooperative example is that of bird duets (see Hall 2004, 2006, 2009). In territorial songbirds, duets between mates are known to have a cooperative function in terms of defending joint resources (Seibt and Wickler 1977; Logue 2005), signalling individual quality (Smith 1994; Marshall Ball et al.

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2006) and probably maintaining the bond between mates (Thorpe 1967; Wickler 1980). Studies support the hypothesis that coordinated vocalizations require time and energy to be expended on practising (Wickler 1980), and that performance quality reflects the fitness and commitment of the mates (Marshall-Ball et al. 2006) and the amount of time they spend together (Hall and Magrath 2007).

To date, the most complex emission patterns of coordinated vocalizations in songbirds ever recorded were obtained by Mann et al. (2006) and Seddon (2002), who captured highly synchronized conspecific choruses emitted by three (Seddon 2002) or four or five (Mann et al. 2006) tropical songbirds. As duets, choruses among conspecifics have a common mechanism in terms of the concurrent emission of sounds, which is in turn what defines the dawn and dusk choruses among heterospecifics. With some structural differences, several syllables of one song are alternately and synchronously sung by the two sexes during conspecific choruses. Both Mann et al. and Seddon take the view that these choruses contribute to group cohesion, or mutual territorial defence, by signalling the quality and commitment of individuals.

This type of coordination, where individuals sing elements of the same song, can only be achieved by conspecifics. Nevertheless, coordinated choruses among heterospecifics are theoretically possible. In coordinated interspecific choruses, the temporal overlap of songs is deliberate and not due to the lack of free airspace to sing alone. In the case of deliberate temporal overlap, individuals of different species that use the same frequency range for their emissions should encounter a high frequency of signal masking, resulting from the spectral overlap of their songs. Signal masking often mediates agonistic interactions among hetero- or conspecifics, whereby an individual begins singing before the end of another's song and obscures its frequency range (see Naguib and Mennill 2010 for a review of the signal value of song overlapping; Hultsch and Todt 1982; Dabelsteen et al. 1996, 1997). However, if an aggressive intent is lacking, individuals that deliberately overlap their songs in time may encounter enormous difficulties in sending a clear, un-masked message.

According to the dear enemy model (defined by Fisher 1954), established neighbours benefit from monopolizing an area (a neighbourhood) encompassing various territories, and whose inhabitants have a mutual interest in preventing the introduction of newcomers (Axelrod and Hamilton 1981; Hultsch and Todt 1982; Getty 1987). A dear enemy relationship comes at a cost of lengthy and strenuous negotiation (Krebs 1982). The establishment of a new neighbour means that some of the holders of adjacent territories must re-negotiate their territorial boundaries, which entails the risk of losing part of their own territory. Even without spatial loss, the amount of energy required to negotiate makes the establishment of new neighbours a losing strategy. Accordingly, one of the main advantages of maintaining the same territory for a long period of time is the maintenance of a network of known neighbours (the relative threat hypothesis, Temeles 1994; e.g. Booksmythe et al. 2010).

In birds, several studies have successfully applied the dear enemy model to conspecific flocks (reviewed by Stoddard 1996; e.g. Hyman 2005, Hardouin et al. 2006, Briefer et al. 2008), with only a few exceptions, where the model did not seem to apply (e.g. Brunton et al. 2008). However, as far as we know, the model has never been applied to heterospecific songbirds living in the same community, where the conditions for establishing a dear enemy relationship can be met.

In birds, seasonal communities have long been considered to be composed of anonymous individuals (Curio 1978), thus precluding the possibility of opting for cooperative behaviours. Nevertheless, recent studies demonstrate that birds living in breeding communities are not anonymous and that their social behaviour is based on the

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temporal stability of the community (Naguib et al. 1999; Krams and Krama 2002; Krams et al. 2008). Indeed, migratory birds even recognize individual neighbours a year after returning from migration (Godard 1991).

In this study, we investigated whether songbirds living in the same area organize their vocal displays in coordinated interspecific choruses for at least part of the day. Such choruses are defined as acoustic phenomena, where most of the participating species avoid signal jamming while, at the same time, performing a deliberate temporal overlap of songs. Our hypothesis is that species use this acoustic pattern as the expression of a neighbourhood of different species, which evolved a communal signal similar to that used by mates in a pair, i.e. coordinated vocalizations, with similar functions.

We addressed this issue by conducting acoustic analyses of field recordings made at dusk in a mixed turkey oak wood in Central Italy. Little is known about the function of dusk choruses (Kacelnik 1979; Hutchinson 2002; Erne and Amrhein 2008). We carried out a niche overlap analysis using null models that were intended for investigations of concurrent emissions of heterospecific songs. The search for new methods based on null models that allow for temporal-pattern identification is an issue of great importance for future research (Fitzsimmons et al. 2008). After carrying out the temporal niche analysis, we conducted a spectral overlap analysis to verify the occurrence of signal jamming. If a coordinated interspecific chorus existed, we expected to find that individuals singing concurrently would not spectrally overlap with each other, even if they used the same frequency range. Jamming avoidance can be achieved by adjusting vocal production on a very short temporal scale.

Materials and methods

Field recordings were obtained from a protected area of the Latium region, Italy, namely the "Macchia Grande di Manziana" wood (express authorization for the research was not required). The area is a mixed turkey oak wood (Habitat code 9280, EU categorization), 810 ha in size and surrounded by cultivated land. The woody portion, where the field recorder was placed, had an average tree age of 93 years and has not been subjected to cutting or wood removal for almost 60 years. The recorders (ZOOM Manufacturer, Tokyo, Japan; H4 model; *X*/*Y* configuration for microphones, omnidirectional) were placed about 20 in off the ground and at least 0.3 miles from the protected area's boundaries (coordinates: 42.1116°N, 12.098°E). Recordings in WAV format were obtained between 18:30 and 19:30 during the breeding season on 4, 8 and 11 May 2009 (known as S_1, S_2 and S_3 – sessions 1, 2 and 3). The samples were taken under favourable environmental conditions, avoiding extreme rain and strong winds.

The study was conducted in an environment with a low fragmentation level, with the aim of collecting data from a relatively stable community (a community is defined as stable if its internal structure is maintained over the years; Järvinen 1979). Communities from habitats with a low degree of fragmentation display low internal species turnover and have a relatively stable structure (Odum 1971). The social behaviour of known individuals is based on the temporal stability of breeding communities, and, consequently, stable environments are more suitable when it comes to establishing stable neighbourhoods.

We obtained our recordings some time after the start of the breeding season, when mates and individual territories have already been established; at this time, dear enemy relationships should have been established and neighbours should no longer be demonstrating reciprocal competitive behaviours, whereas agonistic behaviour towards intruders is a feature all season long (Briefer et al. 2008). We chose the hours of dusk because

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we expected this pattern to be more likely to emerge at this time than at dawn, when birds have more individual reasons for singing (for the functions of dawn and dusk choruses, see Staicer et al. 1996; Dabelsteen and Mathevon 2002; Hutchinson 2002; Burt and Vehrencamp 2005).

Data analysis

Spectrograms were visualized with the software Song Scope version 2.4 b (Wildlife Acoustics Inc. MA, USA) and then generated with a fast Fourier transformation length of 1024 points and a spectral overlap of 87.5% (Kaiser window). We adopted a sampling rate of 44.100 kHz and an accuracy of 16 bits.

The richest eight consecutive minutes in the songs were selected for each recording, because we anticipated that interspecific choruses would occur when most of the species were singing. We therefore analysed 24 min of recording. We did not consider alarm calls.

The songs were manually identified for each analysed portion of a recording: a rectangle was drawn around each song, with the lower, left-hand corner representing the beginning of the song and the minimum frequency, and the higher, right-hand corner representing the end of the song and the maximum frequency. Each rectangle was attributed to the proper species name. Successively, to obtain data that were as precise as possible with respect to the frequencies occupied over time for each song, the rectangles were split up into sub-rectangles. Each sub-rectangle was therefore drawn around consecutive elements of the song occupying the same frequency range (Figure 1). Songs belonging to the same species were essentially split up in the same way, but when necessary preference was given to following the individual shape of the song. This different form of sub-division had no consequence for the analysis, because it did not affect the global length of the songs, nor the faculty for detecting spectral overlaps. Each song was therefore composed of a number of sub-rectangles which together carefully described the progress of its spectral parameters over time. The sub-rectangles had x and y coordinates (respectively, time and frequency), making it possible to track their exact position in the plane. These data meant that for each species we were able to calculate the number of songs emitted, the fraction of time occupied with respect to the emission time of all of the species, the average frequency range occupied, the average duration of emissions and how many songs overlapped in time and for how long. Above all, thanks to this form of treatment of the acoustic data, we were able to identify precisely how many songs overlapped both in time and frequency, meaning that we could exclude the false positives derived from only having data that are relative to the start and end time of each song, or to the minimum and maximum frequency (Figure 1).

Statistical analyses and simulation procedures

All of the analyses were carried out using the EcoSim 7.72 software. EcoSim creates “pseudo-communities” (Pianka 1986) using Monte Carlo randomizations and then statistically compares the patterns in these randomized communities with those in the real data matrix (Gotelli and Entsminger 2010). Results have a different meaning if observations are significantly higher or lower than their expected values. ANOVA are based on 5000 permutations (Manly 2007), and niche overlap analyses are based on 30,000 permutations (Lehsten and Harmand 2006).

To eliminate the impact of sporadic visitors, we only considered species which were present in all of the three recordings and whose duration of songs was higher than the 1% of the fraction of the songs emitted in the recording, as suggested by Luther (2008).

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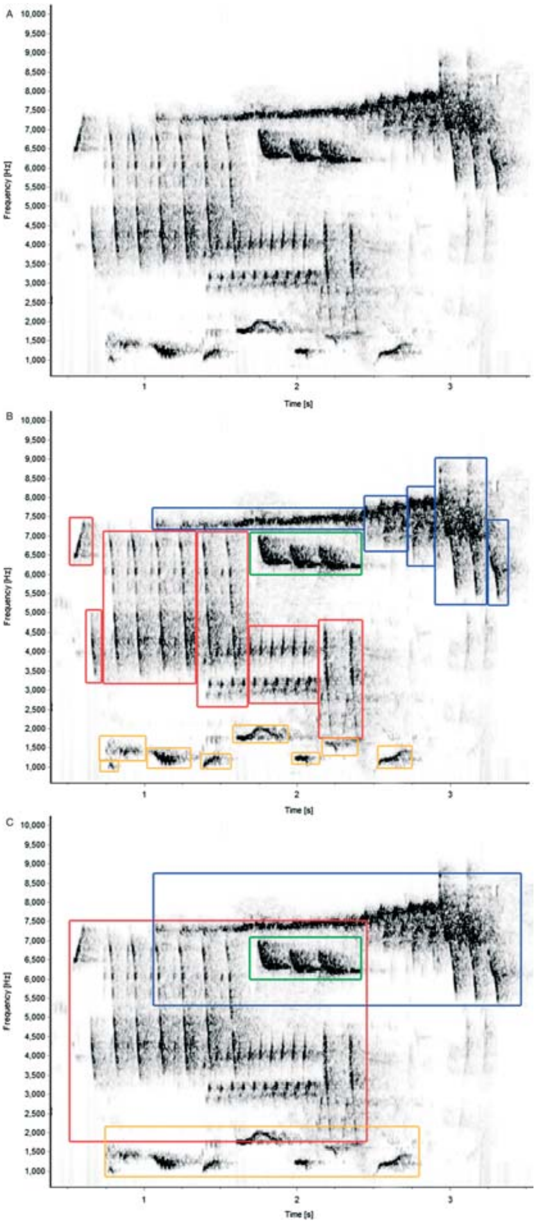

Figure 1. Scheme of the method adopted for the analysis. (A) Sample spectrogram of about 3 s of recording. (B) Songs were split up into between one and several sub-rectangles to obtain data that are as precise as possible in terms of the frequencies occupied over time. Sub-rectangles belonging to the same song or species are indicated with the same colour. We could use a parallel to the Tetris puzzle videogame, where differently shaped blocks (here, the bird songs) are manipulated by the emitter to fit within a given space (here, temporal slots). Blocks are composed of fixed elements; likewise bird songs have fixed spectral parameters. (C) If we had not performed a distinction in sub-rectangles, we would have only obtained the start and end time of each song and the minimum and maximum frequency. In this example, we would have obtained several false positive overlaps.

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In order to avoid an overestimation of time overlaps, songs that overlapped in time for $< 10\%$ of their duration were considered to be unaccompanied. We also excluded from the analyses temporal overlap within individuals of the same species, because intraspecific relationships were not part of our assessment and could have influenced our results.

The tendency for species of the same community to sing at the same time, and to thus associate in a non-random pattern, was verified by using a temporal niche overlap analysis (Pianka index, Pianka 1973). Association patterns between individual social animals can be tested using the Monte Carlo methods, which are a straightforward way of testing non-random associations and social structures, including in interspecific groups (Whitehead 1999; Stensland et al. 2003). For this form of analysis, each row of the data matrix represented a species and each column a temporal slot of 3 s, with the exact duration of a song emission for each species being placed in that slot, unprocessed. The 3-s interval was chosen because it represents the closest approximation to the highest average value of the song durations plus the standard deviation (e.g. for *Sylvia atricapilla*: $1.86 + 0.67 = 2.52$ s), thus reducing the probability of placing a song in different slots.

The temporal niche overlap analysis was based on the RA3 algorithm (Winemiller and Pianka 1990), according to which the entries in each row of the utilization matrix were randomly reshuffled. As reviewed by Searcy and Beecher (2009), several methods have been used to establish the chance levels of overlapping, but Naguib and Mennill (2010) still suggest the use of null models calculated on the basis of no overlapping whatsoever. As they consider signal timing to be non-random (since species tend to avoid overlapping), these authors argue that any calculations based on random song timing may yield misleading conclusions. The algorithm used for the present analysis did not randomize the entire numerical matrix, but instead retained the observed niche breadth of the species (in this case, a song's length), while allowing for the use of any of the possible resource states (temporal slots). If the actual number of observations significantly exceeds what is expected, events are considered to be aggregated, whereas if they are significantly below expectations they are regarded as segregated.

This analysis was carried out for each recording, with all of the selected species initially being considered at the same time and then paired in order to detect eventual significant associations in the pairs. If a species displayed only segregated patterns, it was removed and the analysis was repeated to reduce the possibility of the general result being affected by the habits of a single species. This type of species removal does not influence the results, but instead considers the existence of sub-groups within the community.

During temporal niche overlap simulation, the real refractory period of each species was not considered, i.e. during the simulation, songs of the same species could be shuffled into consecutive intervals. Our aim was to determine whether an aggregate timing pattern existed among species during a single temporal slot, meaning that findings should not be affected by the pattern found in adjacent temporal slots.

Species could adopt time-overlapping behaviour simply because their frequency ranges do not structurally overlap, meaning that time overlaps do not determine signal jamming. To evaluate the entity of this phenomenon, we only selected songs that overlapped in time and, among these, we evaluated if the number of spectrally distinct songs was significantly different from that of songs with a potential spectral overlap (one-way ANOVA, number of spectrally distinct × potentially interfering songs). We then selected only the potentially interfering songs, and evaluated the amount of signal jamming by comparing real and potential spectral overlaps (one-way ANOVA). To evaluate potential interference, we calculated the mean frequency range of emission for each species, paired all of them to see whether their ranges overlapped, and then counted

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how many times the matching pairs sang at the same time. Real interference was calculated as the actual number of frequency overlaps during concurrent emissions among matching pairs. Pairs which overlapped for $<10\%$ of the surface of the involved rectangles were regarded as non-overlapping in frequencies.

Results

The rarefaction curves of the species plateaued in all of the three recordings, suggesting that our 8-min sampling period was adequate for sampling all of the species singing in the community. In total, 1125 songs were identified, belonging to 12 species, with a cumulative duration of 1349 s (Table 1). Rarefaction procedures revealed that species diversity did not differ among the three recordings, thus permitting comparisons among the samples to be made. Seven of the 12 species sang in all of the three recordings (Table 1).

From this point on, all of the results referred to will relate only to the selected species, or rather those species singing in all of the three recordings for $>1\%$ of the total singing time. In each recording, these species were responsible for $>90\%$ of the total duration of the songs detected in that single recording, amounting to 94.1% of the total duration of the songs detected in the community (1264 s). Song emissions per species per minute were not statistically different between sessions (ANOVA: $F_{2,5} = 0.243$, $P = 0.83$), nor were the song durations per species (ANOVA: $F_{2,5} = 0.898$, $P = 0.429$).

At least one species was singing for 88% of all of the recording time; during the singing time, the species were singing unaccompanied for 18% of the time, two species were singing at the same time for 31% of the time and three or more species were singing for 51% of the time. In all of the three recordings, species spent more time singing concurrently than alone (ANOVA: S1: F1, 5 = 11.582, P = 0.007; S2: F1, 4 = 6.311, P = 0.037; S3: F1,5 = 10.966, P = 0.001; Figure 2).

The temporal niche overlap analysis, which included all of the selected species, revealed a random temporal pattern in two of the three recordings (niche overlap analysis, Pianka index, 30,000 simulations: S_1: $P = 0.007$; S_2: $P = 0.455$; S_3: $P = 0.450$; Table 2). The European Robin (*Erithacus rubecula*) was the only species with a segregated temporal pattern with respect to other species in all of the three sessions (Table 3), singing for 11.0% of the total singing time in S_1, 15.6% in S_2 and 8.2% in S_3. After removing the vocalizations of this bird, an aggregated pattern emerged in all of the three recordings, demonstrating that the majority of the species tended to sing at the same time (niche overlap analysis, Pianka index, 30,000 simulations: S_1: $P = 0.003$; S_2: $P = 0.052$; S_3: $P = 0.006$; Table 2).

We found no evidence that species overlapping in time had different frequency ranges (ANOVA: S_1: $F_{1,5} = 2.534$, $P = 0.147$; S_2: $F_{1,4} = 1.944$, $P = 0.204$; S_3: $F_{1,5} = 2.131$, $P = 0.188$). Accordingly, among the species singing concurrently, about half use the same frequency range, and we therefore expected to find considerable spectral overlap between their vocalizations. Instead, the number of real spectral overlaps was lower than expected by chance (ANOVA: S_1: $F_{1,5} = 4.446$, $P = 0.019$; S_2: $F_{1,4} = 5.165$, $P = 0.021$; S_3: $F_{1,5} = 42.610$, $P = 0.000$; Figure 3).

Discussion

Our results show that, at least for the example of dusk choruses in this Italian forest over the timeframe of our recordings, neighbouring songbirds can perform a deliberate temporal overlap of their songs instead of singing during the refractory period of other species. This may in turn be indicative of the absence of interspecific temporal acoustic competition

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Table 1. Composition of species and acoustic parameters.

	Species	N	CumT	FrT	$F_{\mathrm{Min}} \pm$ SE	$F_{\mathrm{Max}} \pm$ SE	$D_{\mathrm{mean}} \pm$ SE	Pres
1	*P. caeruleus* – Blue Tit	390	5:00.02	0.22	5035 ± 847	7613 ± 885	0.766 ± 0.316	+
2	Fam. Turdidae[a]	234	4:59.47	0.22	1707 ± 407	3108 ± 616	1.284 ± 0.754	+
3	*F. coelebs* – Eurasian Chaffinch	94	2:45.40	0.12	2188 ± 338	5515 ± 910	1.771 ± 0.582	+
4	*Regulus ignicapilla* – Firecrest	91	2:38.66	0.12	6726 ± 493	8850 ± 463	1.744 ± 0.582	+
5	*E. rubecula* – European Robin	92	2:31.56	0.11	3002 ± 520	6722 ± 1443	1.647 ± 0.843	+
6	*S. atricapilla* – Blackcap	55	1:42.38	0.08	2207 ± 310	4562 ± 892	1.862 ± 0.664	+
7	*Certhia brachydactyla* – Short-toed Treecreeper	104	1:31.64	0.07	4608 ± 521	6739 ± 630	1.002 ± 0.406	+
8	*Troglodytes troglodytes* – Winter Wren	17	0:40.14	0.03	3040 ± 593	6222 ± 1129	2.361 ± 1.239	−
9	*Parus major* – Great Tit	11	0:16.31	0.01	3837 ± 190	5700 ± 897	1.483 ± 0.545	−
10	*Dendrocopos* sp. – Woodpecker	16	0:10.13	0.01	2033 ± 904	5392 ± 1583	0.331 ± 0.498	−
11	*Oriolus oriolus* – Eurasian Golden Oriole	14	0:08.30	0.01	1624 ± 476	3371 ± 539	0.593 ± 0.236	−
12	*Phylloscopus bonelli* – Bonelli's Warbler	7	0:04.77	0.00	2929 ± 703	4590 ± 725	0.681 ± 0.136	−

Notes: N, number of songs detected; CumT, cumulative time singing in minutes:seconds.cms (species are sorted according to this parameter); FrT, fraction of T in respect of the total singing time; F_{Min} and F_{Max}, maximum and minimum mean frequency with standard deviation; D_{Mean}, mean song duration in seconds with standard deviation; Pres, constant presence in all of the three recordings.

[a] *Turdus merula* (Eurasian Blackbird) and *Turdus philomelos* (Song Thrush) have been merged under their family name due to the difficulty in distinguishing their vocalizations.

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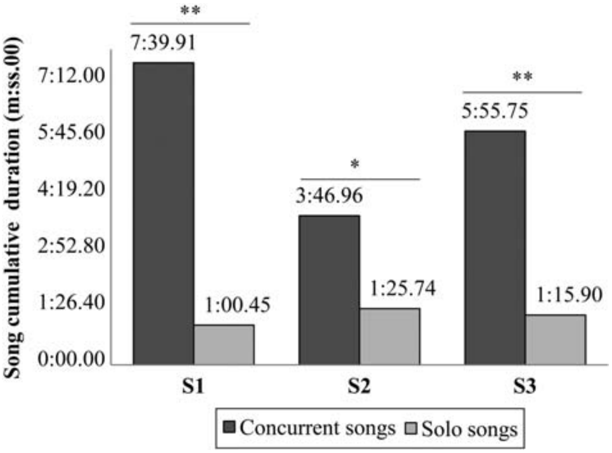

Figure 2. Cumulative duration of solo songs versus concurrent songs. For a preliminary analysis of temporal niche overlap, the cumulative duration of solo songs has been compared with that of concurrent songs (more than one species singing at the same time). The duration of solo songs is significantly lower with respect to the concurrent versions for all of the recordings. The total time singing is given in minute:seconds.cms. **Significance at 0.01 level. *Significance at 0.05 level (one-way ANOVA).

during dusk choruses, suggesting that the competitive function assumed for dawn choruses may not be applied at dusk. As about half of the species singing concurrently used the same frequency range, we expected to find considerable spectral overlap. Deliberate temporal overlap with signal jamming would suggest agonistic behaviour among species. Instead, spectral overlap occurred less frequently than expected, suggesting that any temporal overlap did not have an aggressive intent, and that species adopted a different strategy to avoid signal masking.

Most of the literature on acoustic emissions in bird communities reveals a tendency for species to avoid temporal overlap (e.g. Brumm and Slabbekoorn 2005; Brumm 2006; Planqué and Slabbekoorn 2008; Luther 2008). One of the reasons for the opposite pattern we

Table 2. Temporal niche overlap analysis.

	S_1		S_2		S_3	
	All species	− *E. rubecula*	All species	− *E. rubecula*	All species	− *E. rubecula*
Mean_{obs}	0.297	0.307	0.234	0.268	0.254	0.313
Mean_{exp}	0.265	0.264	0.232	0.238	0.253	0.275
$N_{(\text{obs}<\text{exp})}$	204	93	13659	1565	13506	187
$N_{(\text{obs}>\text{exp})}$	29796	29907	16341	28435	16494	29813
$P_{(\text{obs}\leq\text{exp})}$	0.993	0.997	0.545	0.947	0.5498	0.993
$P_{(\text{obs}\geq\text{exp})}$	0.007**	0.003**	0.455	0.052*	0.450	0.006**

Notes: Pianka index, 30,000 permutations. Recordings have been split into 3-s intervals, each containing the precise duration of each species' song. A temporal niche overlap analysis was carried out for each recording, with all of the selected species initially being considered altogether ("All species" column) and then paired in order to detect eventual significant associations in the pairs (see Table 3). Species showing a segregated pattern only (and never showing an aggregated pattern) were removed, and the same analysis was repeated ("−*E. rubecula*" column). If the mean concurrent duration of songs is significantly higher than expected, the pattern is defined aggregated, while it is defined segregated in the opposite circumstances. Obs, observed; Exp, expected. **Significance at 0.01 level. *Significance at 0.05 level.

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Table 3. Temporal niche overlap analysis between pairs of species.

	S_1			S_2			S_3		
Positive interactions (aggregate pattern)									
Species	2 vs. 4	3 vs. 4	6 vs. 7	1 vs. 2	1 vs. 8	2 vs. 4	1 vs. 3	1 vs. 7	4 vs. 6
Mean$_{obs}$	0.547	0.460	0.507	0.497	0.167	0.243	0.454	0.457	0.385
Mean$_{exp}$	0.395	0.354	0.051	0.421	0.077	0.097	0.194	0.248	0.293
Var$_{exp}$	0.002	0.003	0.006	0.002	0.002	0.004	0.004	0.003	0.003
$P_{(obs \geq exp)}$	0.001**	0.022*	0.000**	0.038*	0.041*	0.026*	0.000**	0.000**	0.053
Negative interactions (segregate pattern)									
Species	3 vs. 5	5 vs. 8	2 vs. 5	3 vs. 5	5 vs. 7	1 vs. 5	1 vs. 4	3 vs. 5	5 vs. 7
Mean$_{obs}$	0.129	0.071	0.151	0.048	0.144	0.047	0.129	0.026	0.032
Mean$_{exp}$	0.304	0.175	0.244	0.188	0.256	0.213	0.288	0.129	0.167
Var$_{exp}$	0.003	0.004	0.003	0.004	0.003	0.004	0.003	0.005	0.004
$P_{(obs \leq exp)}$	0.000**	0.040*	0.052	0.004**	0.021*	0.001**	0.001**	0.037*	0.007**

Notes: Pianka index, 30,000 permutations. A temporal niche overlap analysis was carried out with all of the selected species paired in order to detect eventual significant associations in the pairs. If the mean concurrent duration of songs is significantly higher than expected, the pattern is defined aggregated, while it is defined segregated in the opposite circumstances. Only the species showing significant interactions are displayed. Obs, observed; Exp, expected; Var, variance. **Significance at 0.01 level. *Significance at 0.05 level. Species: (1) Blue Tit, (2) Fam. Turdidae, (3) Eurasian Chaffinch, (4) Firecrest, (5) European Robin, (6) Blackcap, (7) Short-toed Treecreeper and (8) Winter Wren.

found is the methodology we adopted, which uses very short temporal intervals (3 s; in other studies, the longest was 30 s, Planqué and Slabbekoorn 2008). However, our utilization of short intervals was an attempt to identify fine-scale patterns that other studies might have missed. A second reason for the unusual pattern we observed is that we chose to analyse only the richest intervals in terms of song presence. We made this decision because we anticipated that interspecific choruses would occur when most of the species were singing.

This behaviour which, to the best of our knowledge, occurs at dusk needs an explanation in evolutionary terms. Negative interactions are thought to prevail between coexisting species with overlapping resource use, meaning that traits that minimize temporal or spatial

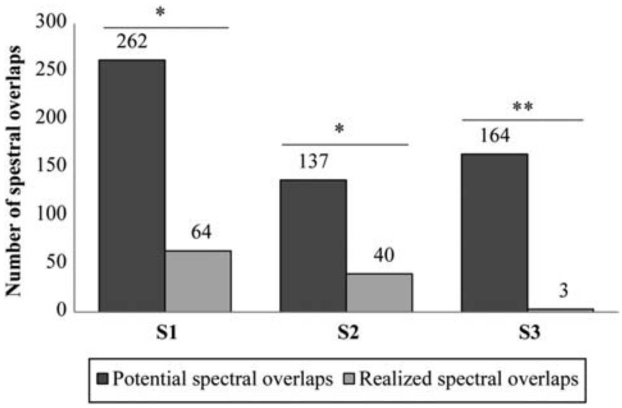

Figure 3. Potential versus realized spectral overlap of concurrent emissions. For all of the concurrent emissions, the number of songs with a potential spectral overlap has been compared with the number of songs with a realized spectral overlap. Spectral overlaps occur less often than expected for all of the recordings. **Significance at 0.01 level. *Significance at 0.05 level (one-way ANOVA).

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overlap should be selected (Forsman et al. 2002). But why do these species deliberately sing concurrently instead of occupying the refractory period of other species? If temporal overlap occurs for competitive reasons, then why avoid frequency overlap? Finally, if this pattern can be interpreted as a coordinated interspecific chorus, why is it adaptive to expend energy on performing this complex task? Due to the paucity of data, we can only attempt to give an explanation for this acoustic behaviour, proposing a hypothesis that nevertheless has a strong theoretical basis.

Singing in a neighbourhood

Following the path suggested by Brumm (2006), which is to interpret signalling interactions as a platform for competitive as well as cooperative behaviours, we interpret this acoustic pattern as the expression of a neighbourhood of different species, which evolved a communal signal that is similar to that used by mates in a pair, i.e. coordinated vocalizations, with similar functions. The meaning of this signal is given by the interplay between the single components produced by different individuals. According to Tobias and Seddon (2009), jamming and jamming avoidance can mediate competitive as well as cooperative interactions, and the adoption of this mechanism may explain the evolution of sophisticated communal signals.

In our view, in breeding communities, evolution may have favoured the selection of individuals that are more skilled in learning songs, thus enabling coordination within interspecific choruses (see Magrath et al. 2009). According to Todt and Naguib (2000), neighbours can signal a strong dyad by means of vocal coordination (in terms of song matching), which is possible only if individuals have had adequate experience of each other. To avoid signal jamming, individuals need to have experienced the songs of the other species, and thus need to learn their spectral structure. More skilled individuals may need less exposure to heterospecific songs, meaning that they can invest more time in gathering resources. Individuals joining the interspecific chorus may thus be perceived as healthier by competing individuals or eavesdroppers (potential mates; e.g. Wilson and Vehrencamp 2001). This is because their coordinated songs signal that they have available energy to be expended on practicing and because they have more time to gather resources.

Coordinated interspecific choruses may also emerge as a mere epiphenomenon induced by jamming avoidance, whereby individuals adjust their signals to minimize overlap (Brumm and Slater 2007). Yet our findings suggest that the concurrent emission of songs is deliberate, and not a consequence of the inability of species to partition the acoustic space. Signalling space is limited along the time axis, and temporal overlap could have been avoided by singing during the refractory period of another species, i.e. during the period of silence following song emissions (Popp et al. 1985). The only species to adopt this behaviour was the European Robin which, in each of the three recordings, showed a segregated acoustic pattern with respect to other species. Since this bird is a solitary species with highly territorial behaviour (Portmann 1947; Tellerıa et al. 2008), it was easily predictable that it would not have joined the chorus. As for the other species, tits are known to be the leader in interspecific flocks (e.g. Szekely et al. 1989), and Portmann (1947) defined the Blue Tit and the Blackbird as transactional species (species for which are described between-individual social interactions or socially transferable cognitive tasks), and the Chaffinch as covey (species commonly showing dominance structures such as pecking orders and leks). The vocal behaviour of the European Robin confirms the availability of singing space during the refractory period of other species. Therefore, the tendency of individuals to sing concurrently was not due to airspace unavailability.

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This finding makes it unlikely that temporal coordination is a mere epiphenomenon, but further analyses are required.

The answer to our second question (If temporal overlap occurs for competitive reasons, then why avoid frequency overlap?) has to be found in the interpretation of the observed pattern in non-competitive terms. Indeed, this chorus could be the product of diffuse competition, the process by which an individual faces competition from multiple species in various combinations and densities, and thus the volume of its niche is reduced in proportion to the usage of the same resources by other species (McArthur 1984). Reduction of the acoustic niche may therefore determine the temporal overlap of songs, whereas signal jamming would reduce the presence of competitors, thus enabling the restoration of the original niche volume. Nevertheless, temporal overlap between signals assumes an agonistic function inasmuch as vocalizations occupy the same frequency range, and thus one signal blocks the reception of the other. Interspecific choruses, as defined in this paper, result from concurrent vocalizations where spectral overlap is avoided. That said, temporal overlap loses its competitive function, and so in this particular case it seems that the diffuse competition explanation cannot be applied.

Multiple purposes of interspecific choruses

Like many other joint displays (Tobias and Seddon 2009), coordinated choruses are potentially multipurpose and context dependent (in duets, Mennill and Vehrencamp 2008). By signalling the presence of healthy individuals, they may also have a role in resource defence, mate selection and the maintenance of social bonds, thus justifying the expenditure of energy in vocal coordination (third question).

It is plausible to hypothesize that resource defence within a heterospecific neighbourhood is achieved with a mechanism that is similar to that used by pairs of mates or small groups of conspecifics (Seddon 2002; Mann et al. 2006), i.e. through coordinated vocalizations, which would in turn signal the internal stability of the neighbourhood: species belonging to the same neighbourhood do indeed have a mutual interest in limiting the presence of intruders. Moreover, cooperative resource defence is the basis for the evolution of duets (Seibt and Wickler 1977; Todt and Naguib 2000). Similarly, Todt and Naguib (2000) suggested that neighbouring songbirds could prevent strangers from settling too close to an area by signalling a strong dyad. With particular reference to song matching, these authors also suggest that high matching rates could signal a well-established relationship among known individuals that may, ultimately, have an aversive effect on outsiders.

Another possible explanation of interspecific choruses, which does not necessarily exclude what has been put forward above, is mate attraction. Dawn and dusk choruses are certainly a reliable indicator of individual fitness (Smith 1994) and, as we have suggested, coordinated interspecific choruses may have a role in signalling the fitness of individuals. Females are attracted by male displays that prove their fitness and/or the likelihood of a long tenure of territory, such as by matching among established neighbours (Todt and Naguib 2000; Amrhein et al. 2004; Marler and Slabbekoorn 2004) or being engaged in well-coordinated acoustic emissions (Maynard Smith 1978; Hutchinson et al. 1993). From these performances, females extrapolate the ability of a male to establish long-term cooperative behaviours and steadily keep hold of a territory over time (Trainer and McDonald 1995, Trainer et al. 2002), which are in turn also an essential prerequisite for establishing dear enemy relationships.

It is safe to assume that interspecific choruses may play a role in social bonding as well. One of the hypotheses proposed by Staicer et al. (1996) to explain dawn choruses is social

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dynamics, according to which individuals maintain social relationships within the community by establishing a network of interactions during choruses. The ability to maintain these relationships is nevertheless highly dependent on the number of individuals, which is limited to 10 for cases of reciprocal cooperation (Boyd and Richerson 1988), and 10–15 (Jullien and Thiollay 1998) or 10–30 (Greenberg 2000) for heterospecific flocks. Our findings reveal that at least seven species joined the chorus and, if we divide the number of songs detected by the number of species, we deduce an average of one or two individuals per species. Our choruses are composed of 7–14 individuals, a number adequate to maintain social relationships within the community.

Conclusions

This study provides evidence of a coordinated chorus among different species of songbirds in the same community, where most of the participating species avoid signal jamming while, at the same time, performing the deliberate temporal overlap of songs. Temporal overlaps occur regardless of the potential spectral overlaps of songs: when songs that occupy similar frequency ranges overlap in time, species adapt the timing of emissions at a fine temporal scale. We propose a tentative explanation whereby these choruses play a role in preserving a shared neighbourhood, thus providing greater resource-holding potential for each participant (Parker 1974).

Further analyses are needed to test the proposed hypothesis. We suggest similar, but longer, recordings, recordings in less stable communities (e.g. in fragmented areas) or playbacks with artificial coordinated choruses proposed to settling migrants (see, e.g. Krams and Krama 2002), where we expect individuals to choose a different area to settle.

The precise timing of songs during song overlapping in natural conditions is an issue that deserves to be explored in more detail (Naguib 2005), since it is focusing attention on community dynamics instead of on the acoustic emissions of a few selected species. To date, as far as we know, only a few studies have addressed this topic, and all of them have been conducted in tropical environments (Luther 2008; Planqué and Slabbekoorn 2008; Luther and Wiley 2009). Popp et al. (1985) did conduct a similar study in a bird community located in a temperate environment, but the interspecific temporal avoidance they found is probably related to the high fragmentation and/or degree of disturbance of the study areas.

Supplementary material

Supplementary material for this article is available via the supplementary tab of the article's online page at http://dx.doi.org/10.1080/09524622.2012.710395.

Audio file – 30-s extract from one recording session (4 May 2009): a number of concurrent vocalizations of different species are followed by relatively silent temporal slots. The sequence is repeated again and again.

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