

Spectral Overlap in Songs and Temporal Avoidance in a Peruvian Bird Assemblage

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Abstract

Acoustic signals are very important in communication among conspecifics for many animals, especially in relatively dark, densely foliated habitat such as tropical rainforest. However, as many species all have to use the same acoustic space, this may lead to interference and masking. Songs will function efficiently in attracting mates or defending territories depending on the level of spectral and temporal overlap with songs of other species in the local community. As signal efficiency has direct fitness consequences, organisms may have evolved a strategy to avoid competition for acoustic space. We hypothesize that, as a consequence, species in a complex rainforest community may show spectral segregation or temporal avoidance: singing at a different frequency or at a different time. As doing both is superfluous and acoustic space is limited, we expect a negative correlation between spectral and temporal overlap. We tested this hypothesis in recordings of 20 vocally dominant bird species from 14 families in a Peruvian rainforest. Using pair-wise comparisons between bird species, we found one significant correlation between spectral overlap and temporal overlap. All others were non-significant. However, we did find that, at frequencies more often used by multiple bird species, there was significantly less overlap than expected if all species were just singing randomly ignorant of each other's songs. Our analyses indicate that short-term auditory feedback mechanisms may also operate in the biodiverse environments of the tropics and may explain part of the community dynamics of acoustic signalling in the rainforest.

Introduction

Sound is the preferred mode of communication for many animals. Insects, frogs, birds and mammals are all well known for their acoustic signals through which they attract mates or repel rivals (Rogers & Kaplan 2000; Gerhardt & Huber 2002; Marler & Slabbekoorn 2004). The prevalence of vocalizations in this context of sexual selection is understandable: signal efficiency is closely linked to individual fitness and transfer of information through sound works well in many habitats, including those with low visibility. However, interference among signals may become a major drawback as many different species have evolved this same acoustic strategy. The ulti-

mate competition for acoustic space is undoubtedly found in the tropical rainforests around the world, characterized on the one hand by dense vegetation and low-light intensities and on the other hand by extreme biodiversity across taxa, among which there are many vocal species (e.g. Ryan & Brenowitz 1985; Narins 1995; Sueur 2002; Slabbekoorn 2004a, b).

Ambient noise produced by the local animal community will negatively affect detection and recognition of acoustic signals, in addition to the impact of abiotic noise sources (Klump 1996). Masking of critically important messages has led to the evolution of an array of counterstrategies by varying the make-up of sound structures, the timing of signaling and the potential to extract signals from a noisy

background (Brumm & Slabbekoorn 2005). Signaling at a time and frequency not used by others is a particularly successful way of avoiding the problem of interference, as masking impact depends heavily on the spectral and temporal overlap of signal and noise. However, acoustic environments such as tropical rainforests are very complex and little is known about whether animals are able to use signaling strategies that allow them to avoid masking under such extreme noise conditions.

Several case studies on restricted sets of species do suggest that at least some species do take the temporal activity of noisy community members into account. Some crickets shift between nocturnal and diurnal signaling depending on the presence of acoustic competitor species (Greenfield 1988). Periodicity in song activity of two neighboring bird species from the Californian chaparral was found to be correlated in a way that times of peak activity were not overlapping (Cody & Brown 1969; Fleischer et al. 1985). Other bird studies have revealed that some species limit signal interference by avoiding song onset when close neighbors are singing (Wasserman 1977) or by sliding in songs right after the outburst of other individuals from their own or other species (Ficken et al. 1974; Schroeder & Wiley 1983; Knapp 1987). Playback experiments have shown that frogs are even able to insert their calls in very short and unpredictable silent gaps in the chorus noise of surrounding frogs (Zelick & Narins 1985). The occurrence of such fine-tuned call alternation among individuals of the same species is a common phenomenon in insects and anurans (Greenfield 1994) and also occurs at least in some bird species under specific circumstances (e.g. Gaioni & Evans 1986).

There are also some examples in which the spectral design of signals seems to be shaped by common acoustic competitors in the natural environment. Frog and cicada communities have been put forward as examples of possible acoustic partitioning of the habitat, with each species using a unique frequency range or 'private communication channel' (Narins 1995; Sueur 2002). Again a cricket species provides a convincing example of a downward shift in call pitch to avoid spectral overlap with acoustic competitors, including a special perceptual adjustment which also makes the peak sensitivity of the auditory system shift toward that lower frequency (Römer & Bailey 1998). Furthermore, intraspecific differences in frequency use between populations of birds and primates have been attributed to habitat-specific shifts in response to variation in acoustic

competition by the local sound-producing community (Slabbekoorn & Smith 2002; de la Torre & Snowdon 2002). Recently, songs of a common urban bird species, the great tit (*Parus major*), were shown to be shifted upward in response to intense low-frequency traffic noise levels (Slabbekoorn & Peet 2003; Slabbekoorn & den Boer-Visser 2006).

Studies in which spectral and temporal avoidance are investigated in concert with explicit attention to the degree of overlap in both do, to the best of our knowledge, not exist. Nevertheless, we suggest that such an approach may yield significant insight into the evolution of signal design in the context of acoustic competition. We expect that species will vary in their ways to avoid overlap as spectral and temporal avoidance are both efficient strategies. One can make the other superfluous, but some species may also benefit from a combination of both if avoidance is incomplete. As a consequence we expect a negative correlation between the two strategies: with no spectral overlap the need to avoid temporal overlap disappears and vice versa. If species benefit from a combination, then it is unlikely that either of them is complete. Spectral overlap will depend on the bandwidth of the acoustic signal and its position relative to other bandwidths within the community, while the potential for temporal overlap will depend on signal duration and repetition rate.

We investigated the relationship between spectral and temporal overlap in 20 identified bird species from a Peruvian rainforest. The selection was made for practical reasons from a much larger set of vocally active species, including many birds as well as frogs and insects of known and unknown identity. We selected vocally dominant species and aimed at variety in frequency use (high-low, broad-narrow) and phylogenetic background.

Methods

Recordings

Recordings from the Tambopata Candamo Reserve, Madre de Dios, Peru (12°51'S, 69°22'W) were collected during a 3-wk period in September and October 2003. On 15 d, a 3-min continuous recording was made at the start of each quarter hour period between 5:00 and 8:00 am from a fixed position using a Sony ECM-PB1C parabolic microphone and a Sharp MD-MT80 minidisc player. We recorded all vocalizing species at the fixed position throughout this period. This led to a total of 561 min of

Table 1: Overview of the 20 bird species used in this study. We provide the Latin, English and family names and we report frequency ranges with standard deviations for both minimum and maximum frequencies (in Hz). The last two columns indicate the number of recorded songs, and the mean song duration in seconds. Spectrograms for each of these species are given in Fig. 1

Nr	Scientific name (Family)	$f_{\min} \pm SD_{\min}$	$f_{\max} \pm SD_{\max}$	# songs	Duration (s)
1	<i>Crypturellus bartletti</i> (Tinamidae) Bartlett's Tinamou	1633 ± 143	1970 ± 120	265	0.90
2	<i>Crypturellus undulatus</i> (Tinamidae) Undulated Tinamou	1047 ± 7	1503 ± 50	295	1.80
3	<i>Columba plumbea</i> (Columbidae) Plumbeous Pigeon	490 ± 37	916 ± 41	621	0.787
4	<i>Amazona farinosa</i> (Psittacidae) Mealy Parrot	662 ± 86	5620 ± 1598	448	3.92
5	<i>Trogon melanurus</i> (Trogonidae) Black-tailed Trogon	787 ± 39	1266 ± 33	158	7.30
6	<i>Momotus momota</i> (Momotidae) Blue-crowned Motmot	317 ± 21	580 ± 11	724	0.312
7	<i>Electron platyrhynchum</i> (Momotidae) Broad-billed Motmot	698 ± 72	1238 ± 48	151	0.467
8	<i>Ramphastos tucanus</i> (Ramphastidae) White-throated Toucan	980 ± 75	2235 ± 677	725	3.16
9	<i>Automolus ochrolaemus</i> (Furnariidae) Chestnut-crowned Foliage-gleaner	1037 ± 57	3658 ± 524	219	1.13
10	<i>Xiphorhynchus guttatus</i> (Dendrocolaptidae) Buff-throated Woodcreeper	1391 ± 43	2107 ± 38	523	3.42
11	<i>Drymophila devillei</i> (Thamnophilidae) Striated Antbird	2501 ± 247	4166 ± 121	209	2.48
12	<i>Hypocnemis cantator</i> (Thamnophilidae) Warbling Antbird	2343 ± 201	3558 ± 154	275	2.10
13	<i>Myrmoborus leucophrys</i> (Thamnophilidae) White-browed Antbird	2137 ± 47	3037 ± 63	163	4.44
14	<i>Myrmeciza hemimelaena</i> (Thamnophilidae) Chestnut-tailed Antbird	2727 ± 196	4051 ± 188	221	1.31
15	<i>Formicarius analis</i> (Formicariidae) Black-faced Antthrush	1633 ± 24	2210 ± 48	319	2.07
16	<i>Attila bolivianus</i> (Tyrannidae) Dull-capped Attila	1576 ± 196	3239 ± 796	145	5.00
17	<i>Ramphotrigon megacephala</i> (Tyrannidae) Large-headed Flatbill	1051 ± 29	1426 ± 48	423	0.695
18	<i>Campy iorhynchus turdinus</i> (Troglodytidae) Thrush-like Wren	737 ± 28	3287 ± 15	85	3.63
19	<i>Turdus lawrencii</i> (Turdidae) Lawrence's Thrush	1895 ± 240	2904 ± 335	224	1.29
20	<i>Gymnostinops bifasciatus</i> (Icteridae) Amazonian Oropendola	372 ± 23	3187 ± 1594	302	0.960

recordings available for analyses ($13 \times 15 \times 3$ min; minus eight recordings of 3 min that failed). A different location was picked for each day using GPS-coordinates taken from a Magellan 315 GPS. Different locations were chosen at least 500 m apart to ensure that recordings for each day contained a different set of individuals. For the analyses, we focused on a selection of 20 vocally dominant bird species from the 185 species observed at least once on our recordings (see Fig. 1, Table 1).

Spectral Overlap

For a species A, minimum and maximum frequencies (f_{\min}^A and f_{\max}^A , respectively) were determined as follows. First, the 10 clearest songs were selected, each one from a different location (and thus from a different individual). Using Fourier transforms (sampling frequency 44.1 kHz; time window length 0.00195 s; frequency precision 43.1 Hz or 1024 grid points), f_{\min} and f_{\max} were measured for each song using cursor placement in the software package wavesurfer (Sjölander & Beskow 2000; see Fig. 2). The mean minimum and maximum frequencies, f_{\min}^A and f_{\max}^A now defined the frequency range for a species A, R_A (Table 1). The spectral overlap between any pair of distinct bird species A and B was then defined as the intersection between R_A and R_B .

Temporal Overlap at Two Scales

We scored all occurrences of songs on the recordings for each of the 20 species in Table 1. We determined presence or absence for each species in all 3-min periods and we determined the start and end times for each song using cursor placement. An example of overall activity for all 20 species during a selected interval of 3 min is presented in Fig. 3.

We analyzed temporal overlap at two scales: the crude realized temporal overlap and the fine realized temporal overlap. The *crude realized temporal overlap* between species A and B was defined as the fraction of 3-min time intervals both species were recorded. The *crude expected temporal overlap* between species A and B was defined as $q_A q_B$, where q_A is the fraction of time intervals in which species A was singing. The *fine realized temporal overlap* between species A and B was defined as the intersection between T_A and T_B , where T_A is the set of time intervals corresponding with all songs given by A over the entire recording period, normalized by the total recording time. The *fine expected temporal overlap* between species A and B was defined as $p_A p_B$, where p_A is the fraction of time species A was singing over the entire recording period. For two bird species that do not behaviorally respond to one another, we expect these realized and expected overlap measures not to differ significantly. For those species pair that do, we

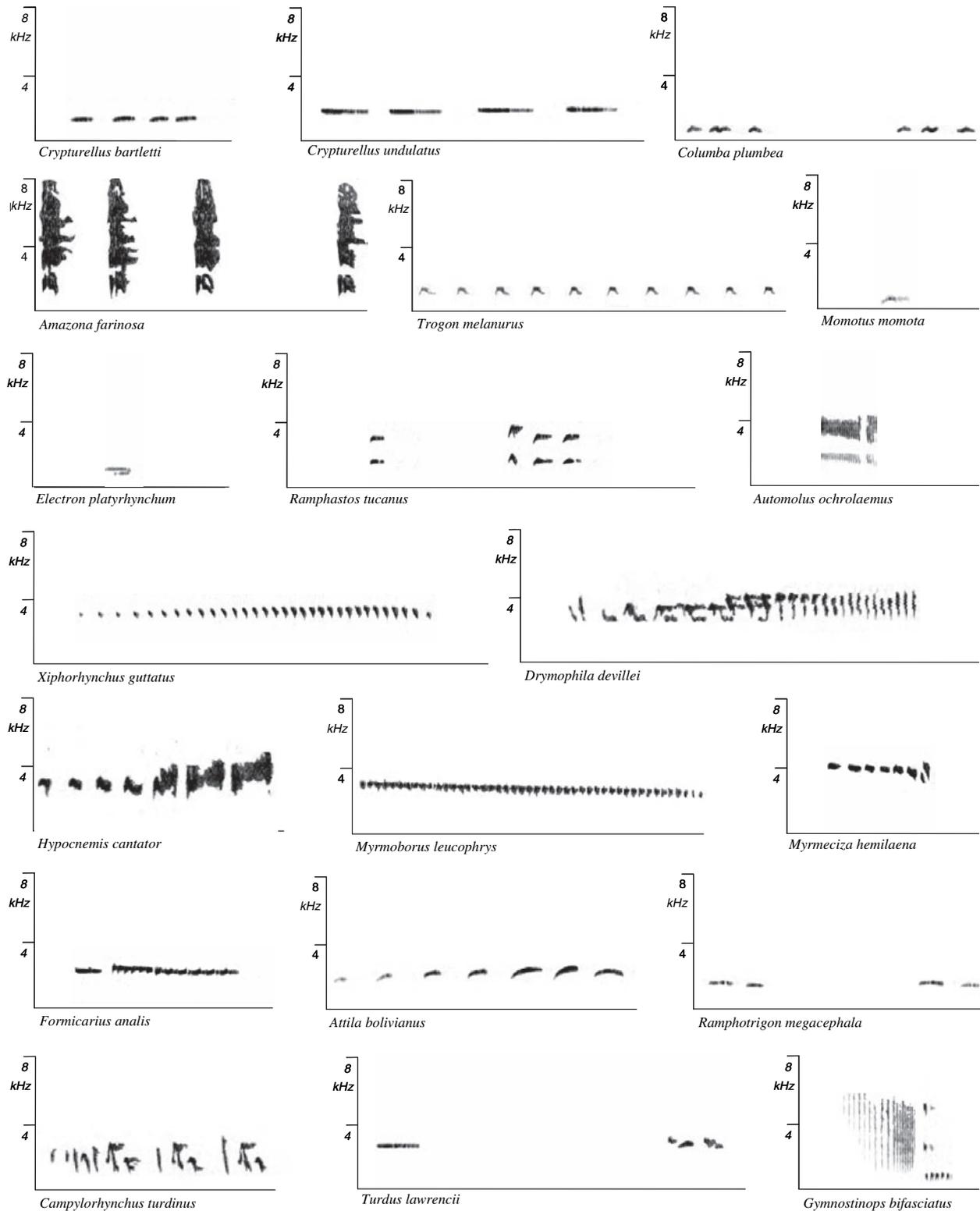


Fig. 1: Overview of the acoustic characteristics of the 20 bird species used for the analyses. Each species is represented by a spectrogram of a typical song recording. The common name in English and the family name are given in Table 1 together with details on mean spectral and temporal measures.

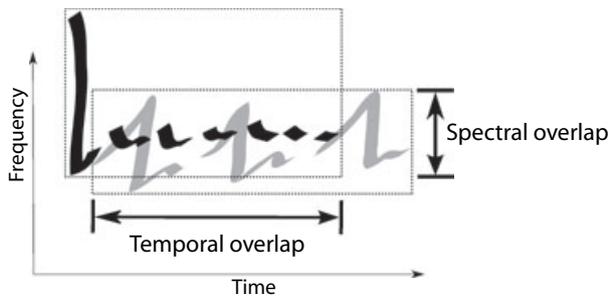


Fig. 2: Schematic representation of the measurements of spectral and temporal overlap in two songs of two virtual species, one in black, the other in grey.

expect that realized values are significantly lower than expected. Thus, for each species pair, we tested the hypothesis that the crude or fine realized temporal overlap was significantly lower than its corresponding expected temporal overlap using a one-tailed pair-wise t-test.

Measuring Competition for Frequencies

Each bird species sings songs of a specific frequency range, a specific duration, at a specific repetition rate. If we consider the 20 species in this study, we see that some frequencies are used by more species than

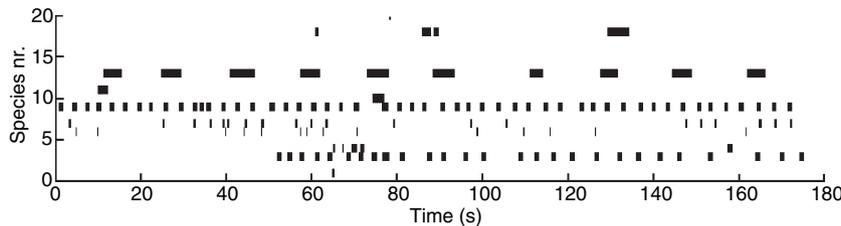


Fig. 3: Vocal activity of all 20 study species during an example 3-min interval with especially heavy competition for acoustic space. Species numbers on the y-axis correspond to those in Table 1. Note that 10 out of the 20 species were active to a variable extent.

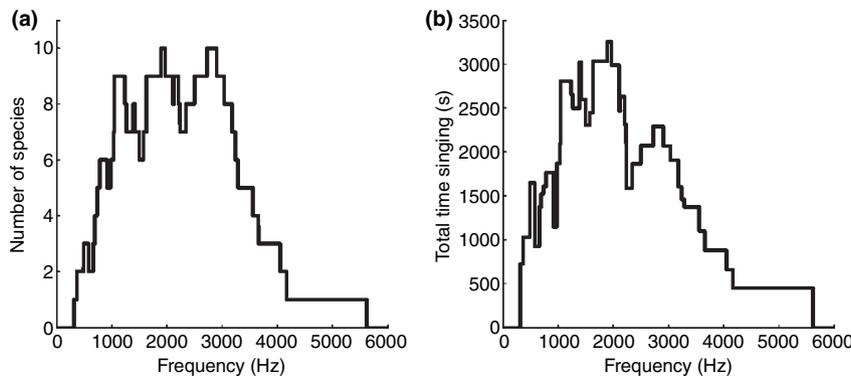


Fig. 4: Accumulated frequency use by the 20 species in this study (a), and the total time that songs were present in our recordings at each frequency (b). The accumulation of frequency ranges is based on the mean minimum and maximum frequencies per species (see Table 1). Note that the 8–10 species singing around 3 kHz sing markedly less than a similar number of species singing around 1 and 2 kHz.

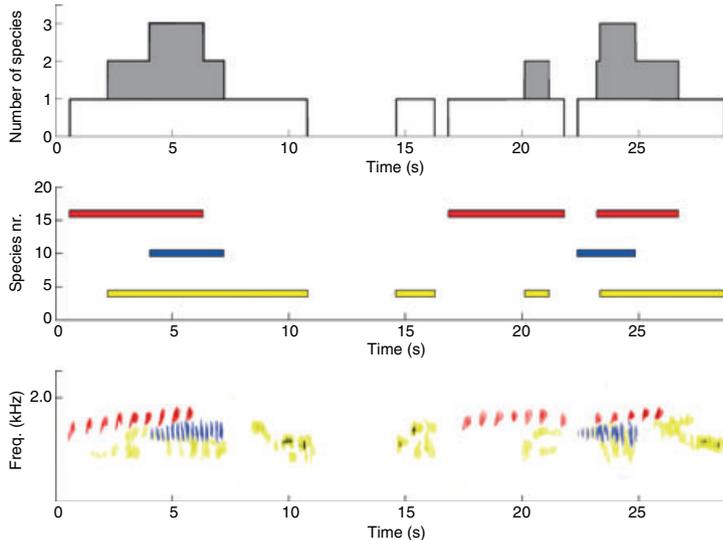


Fig. 5: An example of temporal overlap at one frequency during a selected 30-s interval: the number of bird species using $f = 1800$ Hz over time on day 3 (a) and the individual songs for the species whose frequency range includes $f = 1800$ Hz over time (b). The realized competition for frequency f is defined as the area of the graph in (a) that lies above 1 (light-gray). The three species using this frequency are highlighted in the corresponding spectrogram at the bottom (c): *Automolus ochrolaemus* in red, *Xiphorhynchus guttatus* in blue, and *Amazona farinosa* in yellow.

others, both in species numbers, and in amount of time (see Fig. 4a, b). Assuming that the spectral bias in our sample of selected species reflects a skewed selection pressure for the assemblage, we explored the hypothesis that such unevenness has induced a competition-dependent divergence between the *expected competition* and the *realized competition*, through temporal avoidance especially at heavily used frequencies. The expected and realized competitions were defined as follows. Fix a frequency f . Let $S(f)$ be the set of species whose frequency range includes f . Now we first calculate over time the number of species from $S(f)$ that simultaneously use f (time gaps between recordings were deleted). This creates a graph such as in Fig. 5a which gives an example of three vocally active species (see also Fig. 5b, c). The realized competition for frequency f is now defined as the area of the graph that lies above 1 (note that when one species is singing there is no competition), normalized by the total recording time.

Let us assume that $S(f)$ contains n species. We define the expected competition for frequency f , $EC(f)$, by

$$EC(f) = 1 - \prod_{k=1}^n (1 - p_k) - \sum_{k=1}^n \left(p_k \prod_{\substack{j=1, \\ j \neq k}}^n (1 - p_j) \right).$$

In other words, we calculate the probability that at any given moment fewer than two species are singing in $S(f)$, and take its complement. The left product is the expected fraction of time that no species is singing (we simply multiply the fractions of time each species is silent). The sum of products on the right is the expected fraction of time that exactly one species is singing, summed over all possible species in $S(f)$.

Statistical Tests

The spectral and temporal overlap data were analyzed as follows. Using paired t-tests, for each pair we calculated whether the realized temporal overlap was significantly lower than the expected temporal overlap. Then we binned all species pairs into those with spectral overlap less than 1 kHz and the rest, and considered the fraction of bird pairs whose realized temporal overlap was significantly lower than expected. We tested whether this fraction was significantly greater for birds that overlap more than 1 kHz in frequency than for those that do not, using chi-square tests. This hypothesis was tested both using crude temporal overlap measures and fine temporal overlap measures. In addition, we also per-

formed Mantel tests on the spectral and temporal overlap values to investigate possible correlations between the two. We performed Mantel tests with 10 000 randomizations in R with the *ade4* package (Chessel et al. 2004) and reported one-tailed p-values. We used the actual overlap values between each pair of species in Mantel tests comparing the matrix of spectral overlap with matrices of both measures of temporal overlap. To be more precise, we computed the matrix of relative differences between expected and realized temporal overlaps: for any pair of species A and B, we computed $(E_{AB} - R_{AB})/E_{AB}$, where E_{AB} and R_{AB} denote the expected and realized (fine or crude) overlap for A and B. Finally, we analyzed the differences between expected and realized temporal overlap at different frequencies using a linear regression to investigate competition-dependent divergence, and a t-test to examine whether its slope is significantly less than 1.

Results

Our selection of 20 vocally dominant bird species revealed considerable overlap in frequency use, especially in low- and mid-frequencies. Up to 10 different species may potentially interfere with each other because of spectral overlap between 1.0 and 3.0 kHz (Fig. 4a). We recorded song activity by at least 1 of the 20 focal species in all 187 3-min intervals. In 92.0% of these intervals, two or more species were recorded, in 39.6% five species or more, and in 4.3% ten species or more. In total, we recorded 6495 songs with a cumulative duration of 13 460 s (in 33 600 s of recordings). With respect to fine temporal overlap: during 36% of all recording time at least one of the 20 species in our sample was singing. Two or more species were singing at the same time for 5.7% of the time, and in 0.7% of the time three or more species were singing synchronously.

We found no significant correlation between spectral overlap and our measure of crude temporal overlap (chi-square test, $p = 0.58$). The number of species pairs that passed the normality test was 172. Five out of 148 species pairs (3.4%) with ≤ 1.0 kHz spectral overlap had a significantly lower crude realized temporal overlap compared with the expected overlap. This was 2 out of 24 (8.3%) for species pairs with > 1.0 kHz spectral overlap. This indicates that pairs of species are active in the same 3-min period, independent of their spectral overlap. Considering the fine measure of temporal overlap gave a similar picture: species pairs with large spectral overlap did

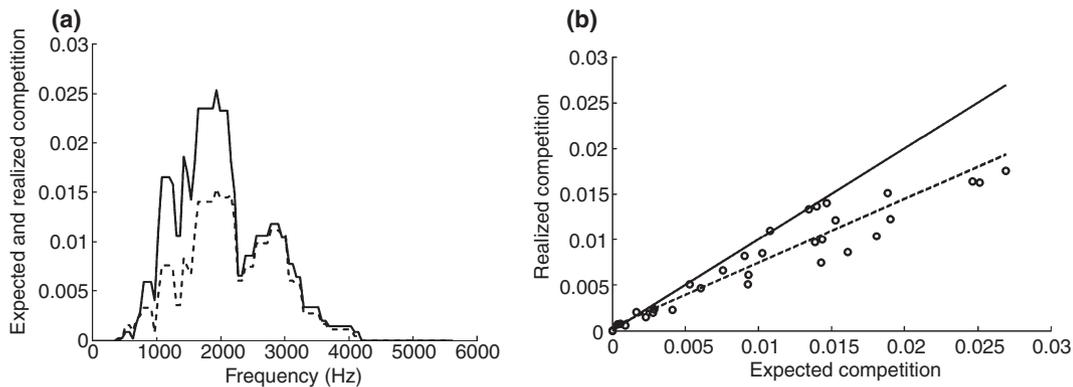


Fig. 6: Realized competition (dashed line) and expected competition (solid line) for all frequencies among the set of 20 bird species (a). Note that for frequencies roughly in the range 800–2200 Hz, the realized competition is consistently lower than the expected competition. Expected and realized competition are directly compared (b): the solid line denotes the equal-values line and the dashed line is the regression line ($Y = 0.7047X + 0.0004$; $R^2 = 0.936$, $p < 0.0001$).

not avoid overlap more than those with little spectral overlap (chi-square test, $p = 0.58$). Now, 78 species pairs passed the normality test. Of these, 3 out of 66 species pairs (4.6%) with ≤ 1.0 kHz overlap had a significantly lower realized temporal overlap, while this was 1 out of 12 (8.3%) for species pairs with > 1.0 kHz spectral overlap. This is a non-significant difference.

In the Mantel tests, for the crude measures of temporal overlap, we again found a non-significant correlation with spectral overlap ($p = 0.50$), but the fine measures of temporal overlap did correlate significantly with spectral overlap ($p = 0.049$). This implies that there are enough species pairs to make the overall pattern deviate from random with respect to spectral overlap relative to the amount of synchronized vocal activity, but these pairs do not lead to a simple negative linear relationship.

In addition, we explored the competition-dependent divergence between the expected competition and the realized competition by performing a linear regression (Fig. 6a, b). The realized competition was lower than expected, the higher the expected competition: the slope of the regression line ($Y = 0.604X + 0.0004$, $p < 0.0001$, $df = 98$) was significantly lower than 1 ($t = -18.97$, $df = 98$, $p < 0.0001$).

Discussion

Twenty vocally dominant species of a Peruvian bird assemblage revealed considerable potential for spectral and temporal overlap. Up to 10 different species potentially interfered with each other because of spectral overlap between 1.0 and 3.0 kHz. Many species sang at similar periods over the morning, often

with two or more species vocally active synchronously. We found spectral overlap-dependent temporal avoidance within our selection of bird species: first, fine temporal overlap measures between species pairs were non-randomly distributed with respect to spectral overlap, as shown by the Mantel tests. Second, the realized competition among species was significantly lower than expected for frequencies with high expected competition. However, neither co-occurrence of species in the same sample periods nor being synchronously active within those periods was negatively correlated to spectral overlap. These results show that some species pairs may actively avoid overlap with each other, but that such pairs are not necessarily those with the largest spectral overlap. The data suggest instead, at a more general level, that such behavior may be more common among species within the range of most heavily used frequencies.

Active Overlap Avoidance

Animals that use acoustic signals have evolved a wide variety of strategies to overcome detrimental signal-to-noise ratios, one of which concerns active overlap avoidance by timing relative to others (Brumm & Slabbekoorn 2005). Wrentits (*Chamaea fasciata*), e.g. were shown to avoid overlapping with loud hetero-specific songs by neighboring Bewick's wrens (*Thryomanes bewickii*) (Cody & Brown 1969). In another study, least flycatchers (*Empidonax minimus*) actively avoided masking by red-eyed vireos (*Vireo olivaceus*) (Ficken et al. 1974). In an experimental study, ovenbirds (*Seiurus aurocapillus*) were shown to avoid overlapping with songs of other species by inserting their song not long after the

playback stimulus song (Popp et al. 1985). The same behavioral mechanism was experimentally confirmed recently for nightingales (*Luscinia megarhynchos*) (Brumm 2006). Adaptive timing seems a widely distributed ability and also a likely explanation for the assemblage-wide pattern of our current study.

A special case of active avoidance concerns avoiding temporal overlap with conspecifics, which obviously sing songs of large spectral overlap. White-throated sparrows (*Zonotrichia albicollis*), e.g. avoid singing during song of conspecifics, especially if their neighbors are closer (Wasserman 1977). We have excluded temporal overlap within species from the analyses as information about intraspecific overlapping strategies (see Todt & Naguib 2000; Collins 2004) is largely lacking for our current species set and it is also hard to distinguish different individuals in dense vegetation.

Studies at Bird Assemblage Level

There are a few studies that analyze competition for acoustic space among more than two species within a bird assemblage. For example, a pattern of interspecific avoidance was found among four vocally dominant species in deciduous forest in Wisconsin, United States (Popp et al. 1985). The ovenbirds inserted songs immediately following songs of all three of the other species. The great-crested flycatcher (*Myiarchus crinitus*) and the eastern wood-peewee (*Contopus virens*) did so only after the fourth species, the wood thrush (*Hylocichla mustelina*), which did not show this behavior itself at all. The thrush uses a wide frequency range with large overlap in the lower part with the flycatcher and in the upper part with the ovenbird. The latter two have limited overlap in the mid-frequencies, while the relatively narrow-band wood-peewees show complete spectral overlap with all three others. In another study, only one out of ten individual eastern meadowlarks (*Sturnella magna*) displayed a pattern of temporal avoidance with only one of the nine bird species co-occurring in open habitat in Ontario, Canada (Knapton 1987). The broad frequency range of meadowlarks showed large spectral overlap with most species, but the single case for temporal avoidance concerned songs with considerably lower frequency limits from the bobolink (*Dolichonyx oryzivorus*).

These studies undeniably show that at least some species are capable of timing their songs in such a way that they reduce overlap with others. However,

not all species do so and the variation is not easily explained by spectral overlap between species. There are several potentially confounding factors, such as relative song amplitude, interspecific territoriality, or seasonal and diurnal fluctuations in motivational state. Species with more subtle voices and less persistent singing behavior may rely more on timing as a noise-coping strategy than loud and dominant singers. Also in our study, confounding factors may contribute to the fact that a negative correlation between spectral and temporal overlap was absent in our pair-wise analyses.

Acoustic Competition beyond Bird Taxa

Another factor not taken into account in any of the studies discussed is that species other than birds may also affect competition for acoustic space (Ryan & Brenowitz 1985; Slabbekoorn & Smith 2002). Especially cicadas are well-known to be noisy and able to leave their imprint in the mid-to-high frequencies of tropical and Mediterranean soundscapes (Sueur 2002; Slabbekoorn 2004a, b). Acoustic competition among birds and insects may drive birds to use lower frequencies, and this may account for the relative lack of more high frequency-users among our avian selection. Analyses including dominant noise sources across taxonomic groups might reveal whether birds and insects also affect each other's timing.

Besides insects, another well-studied and vocally active taxonomic group concerns frogs (e.g. Littlejohn 1959; Duellman & Pyles 1983; Narins 1995). Chek et al. (2003) combined spectral and temporal call features, and found evidence for acoustic resource partitioning in 3 out of 11 frog assemblages. Frog studies have also considered *spatial segregation* as a potential modifier of the relationship between spectral and temporal overlap (Hödl 1977; Drewry & Rand 1983). In our bird study, the crude measure of temporal overlap in fact to some extent incorporated both temporal avoidance and spatial segregation, as two species of a pair may not co-occur in our 3-min recordings because they do not sing during the same periods of the day, or because they do not co-occur at the same locations in the forest. However, neither of these two turned out to be correlated to spectral overlap in the Peruvian bird assemblage.

Conclusions

To our knowledge this study is the first in analyzing simultaneously both spectral overlap in songs and temporal avoidance among multiple species of a

tropical rainforest bird assemblage. We aimed at bridging the typical two-species studies and the more general ambient noise analyses in which specific species and interactions are ignored. Our data show that many species are active at the same locations and during the same time of the day. Several species may be actively avoiding the song of others in time, particularly if they sing at frequencies heavily used by many active species. However, there was no clear negative relationship between spectral and temporal overlap among species pairs. More studies are needed to understand which characteristics make species likely to show temporal avoidance and what species are likely to be avoided. This is especially true for the tropics: we have hardly begun to understand the community dynamics of acoustic signaling in the biodiverse and noisy rainforest.

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