Production and perception of communicatory signals in a noisy environment

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Many animals communicate in situations that make it difficult to discriminate a species' signals from those of others. Consequently, coexisting species usually have signals that differ by more than the minimum required to prevent overlap in acoustic features. These gaps between signals might facilitate detection and discrimination of degraded signals in noisy natural conditions. If so, perception of signals should have broader scope than production. We investigated this possibility by studying song production and perception of two species of birds in an especially noisy environment, the Amazonian dawn chorus. With software developed for this study, we digitally synthesized songs of two species, as well as intermediate versions of their songs. Experimental playbacks of these synthesized songs to individuals of both species confirmed that perception (as indicated by responses) was broader than production of songs. We propose that broader perception than production of song promotes communication in noisy situations and limits the similarity between signals of coexisting species.

Keywords: animal communication; acoustic partitioning; bird song; neotropical birds; signal detection

1. INTRODUCTION

Many animals rely on long-range communication for species recognition, mate selection and territorial defence, but degradation of signals during transmission and irrelevant noise in the background often limit the ability of receivers to detect a signal or to discriminate between signals (Ryan & Brenowitz 1985; Klump 1996; Bradbury & Vehrencamp 1998; Wollerman & Wiley 2002). Multi-species choruses make it especially difficult for animals to detect or to discriminate signals (Wiley 1994; Gerhardt & Huber 2002; Wollerman & Wiley 2002; Brumm & Slabbekoorn 2005).

Features of signals that differ distinctly from those of other species would promote accurate recognition of conspecific signals (Marler 1960; Miller 1982; Nelson 1988; Nelson & Marler 1990). For instance, coexisting species using acoustic signals should partition multidimensional acoustic space, as defined by the acoustic features of their signals. The difference between species' signals, however, is usually

more than the minimum required to avoid overlap. Instead, signals occupy regions of acoustic space that are disjunct (separated by gaps; Nelson & Marler 1990), so acoustic space is not continuously occupied by the production of signals. These gaps might serve to reduce errors in detection and discrimination of conspecific signals degraded during propagation through the environment.

It remains unclear whether the regions of acoustic space in which different species respond to signals are also disjunct (Richards & Wiley 1980; Wiley & Richards 1982; Naguib & Wiley 2001). Characteristic responses indicate the processing, or perception, of sensations. Although in many cases it is clear that the sense organs of different species respond to each other's vocalizations, individuals only perceive signals with certain features as conspecific and thus respond to them. Does this perception of signals by coexisting species leave gaps in acoustic space as does the production of signals or does perception fully occupy acoustic space? Greater scope for perception of signals than for their production would accommodate variation in signals introduced by degradation during transmission. Previous reports have indicated that birds respond to signals at least one standard deviation from the population mean (e.g. Nelson & Marler 1990), but none has investigated the entire acoustic space between two species' songs.

Avian dawn choruses in tropical forests provide an example of communication in high levels of background noise from other species. The combination of many species and a brief time in which most of them broadcast their signals limits possibilities for signal divergence. Although it is clear that each species has a distinct species-specific song, it is not clear how the production and perception of these signals are distributed in acoustic space.

To examine this issue, we focused on two species that are distantly related but acoustically similar. Both are suboscines (Passeriformes: Tyranni), a group that includes most of the species of birds in the understorey of Amazonian forests. In comparison with oscines (Passerini), this group has relatively little variation among individuals' songs (Wiley 2005). To test their recognition of songs, we measured the responses of each species to playbacks of its own song, the other species' song and three intermediates. The intermediate versions, spaced along a continuum between the two species' songs, allowed us to determine whether these species partition acoustic space for perception of conspecific songs either disjunctly, as they do for production of songs, or continuously.

2. MATERIAL AND METHODS

Table 1. Parameters of synthesized songs (frequencies in Hz and times in ms).

| song type	no. of notes	length of note			low frequency of note			high frequency of note			distance between notes				no. of elements per note		
		first	average	last	first	average	last	first	average	last	first and second	average	last P. chloris	last T. schistaceus	first	average	last
Thamnophilus schistaceus 100%	9.0	180.0	125.9	121.0	1808.0	1550.0	947.0	1808.0	1722.0	1550.0	287.0	188.4	128.0	37.0	1.0	1.0	2.0
T. schistaceus 67%, *P. chloris* 33%	8.7	159.7	112.8	109.7	1664.7	1521.3	1119.3	1693.3	1664.7	1550.0	236.7	189.5	120.0	n.a.	1.0	1.3	2.0
T. schistaceus 50%, *P. chloris* 50%	8.5	149.5	106.2	104.0	1593.0	1507.0	1205.5	1636.0	1636.0	1550.0	211.5	190.1	116.0	n.a.	1.0	1.3	2.0
T. schistaceus 33%, *P. chloris* 67%	8.3	139.3	99.7	98.3	1521.3	1492.7	1291.7	1578.7	1607.3	1550.0	186.3	190.7	112.0	n.a.	1.0	1.7	2.0
P. chloris 100%	8.0	119.0	86.6	87.0	1378.0	1464.0	1464.0	1464.0	1550.0	1550.0	136.0	191.8	104.0	n.a.	1.0	2.6	1.0
difference between *P. chloris* and *T. schistaceus*	1.0	61.0	53.6	34.0	430.0	86.0	517.0	344.0	172.0	0.0	151.0	100.2	24.0	37.0	1.0	1.0	2.0
confidence intervals, *P. chloris* (n=7)	1	19.3	33.7	21.7	48.2	50.3	44.0	68.1	58.9	96.3	44.6	63.7	39.0	n.a.	0.0	0.4	0.0
confidence intervals, *P. schistaceus* (n=7)	0	36.8	29.8	20.6	79.9	82.7	71.2	70.9	73.5	68.1	15.8	15.2	n.a.	15.5	0.0	0.0	0.0
overlap between species (n=7)	2	12	77	64	86	86	345	86	115	258	−12	112	371	n.a.	0	2	−1
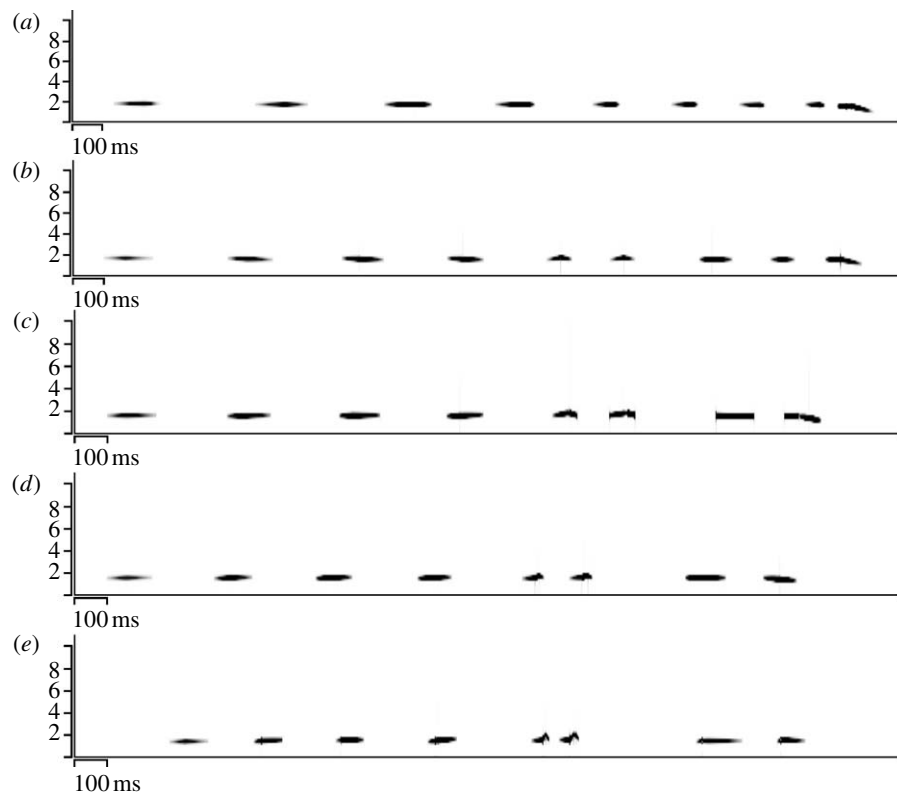
Figure 1. Sonograms of synthesized songs (see text for explanations of the different morphs). (*a*) 100% *T. schistaceus* and 0% *P. chloris*, (*b*) 67% *T. schistaceus* and 33% *P. chloris*, (*c*) 50% *T. schistaceus* and 50% *P. chloris*, (*d*) 33% *T. schistaceus* and 67% *P. chloris* and (*e*) 0% *T. schistaceus* and 100% *P. chloris*.

species had nearest neighbours that were reciprocal. Of these species, we selected the plain-winged antshrike, *Thamnophilus schistaceus* (PWA), and wing-barred piprites, *Piprites chloris* (WBP), which had one of the smallest nearest-neighbour distances and populations sufficient for playback experiments. Both are year-round territorial residents. Territories were mapped by following the movements of singing birds and by marking the locations of singing across mutual boundaries.

To synthesize songs with intermediate features, we used SOUNDSYNTHESIS2 (v. 060906, www.unc.edu/~rwhiley), a program developed for this study, which uses a spreadsheet of frequencies and amplitudes to specify successive smoothed segments of notes with a resolution of 1 ms. We synthesized a mean song for each species as well as songs with features 2/3, 1/2 and 1/3, the distance between the two species' means (figure 1; table 1). We call the synthesized songs the 100, 67, 50, 33 and 0% morphs of a species' song. A 0 per cent morph of one species' song is the same as a 100 per cent morph of the other species' song.

Experiments were conducted on eight PWA and eight WBP in September and October 2006. All morphs (100–0%) were presented in randomized order to all individuals of each species. Preliminary trials with both species compared responses to natural and synthetic versions of their own songs in randomized order.

During and after each playback, we recorded nine measures of behavioural response (see the electronic supplementary material). PCA extracted three PCs with eigenvalues >1, which together explained 77 per cent of the variation (see table S1 in the electronic supplementary material). PC1 (51% of the variation) was used as the response variable in all tests. An initial examination showed that the relationship of this variable to the predictor approximated a logistic S-shaped curve (figure 2). Consequently, we treated PC1 as a logistic function of song morph.

To compare song production by the two species, we measured the same 15 features mentioned above (table 1) in randomly selected songs of seven individuals of each species. PCA extracted four PCs with eigenvalues >1 that together explained 81 per cent of the variation. PC1 and PC2 (61% of the variation) were used to plot 2 standard deviations around the mean signals for each species in two-dimensional signal space. To compare song perception, we analysed individuals' responses to each of the synthesized morphs. PC1 and PC2 (65% of the response variation; see table S1 in the electronic supplementary material) were used to plot 2 standard deviations around the mean responses to each morph in two-dimensional response space.

3. RESULTS

Both species responded similarly to natural and synthetic versions of their own songs. Responses to synthetic songs were slightly stronger, perhaps because the recordings were so clean. For both species, responses were strong to 100 per cent and 67 per cent morphs, moderate to low to 50 per cent morphs and low to absent to 33 per cent and 0 per cent morphs (figure 2). The diminishing responses across the series of morphs indicated continuity in perception along the continuum between the two species' songs. Each species responded to the 50 per cent morph about half as strongly as to the appropriate 100 per cent morph. For these species, there were no gaps in the perception of their songs. By contrast, production of their songs was disjunct. Although most of the features of their natural songs overlapped (table 1), the PCs of all measured features revealed that the two species' songs were separated by a gap in multidimensional acoustic space (see figure S3 in the electronic supplementary material).

4. DISCUSSION

Receivers in natural situations must detect and discriminate conspecific signals in the presence of background noise. Noise in the form of signals from other individuals and species is especially likely to interfere (Gerhardt & Klump 1988; Wollerman & Wiley 2002). Although coexisting species usually evolve distinct signals, little is known about the evolution of perception in coexisting species (Gerhardt 1994; Amezquita *et al.* 2006). Perception of sounds as conspecific is indicated in our experiments by the
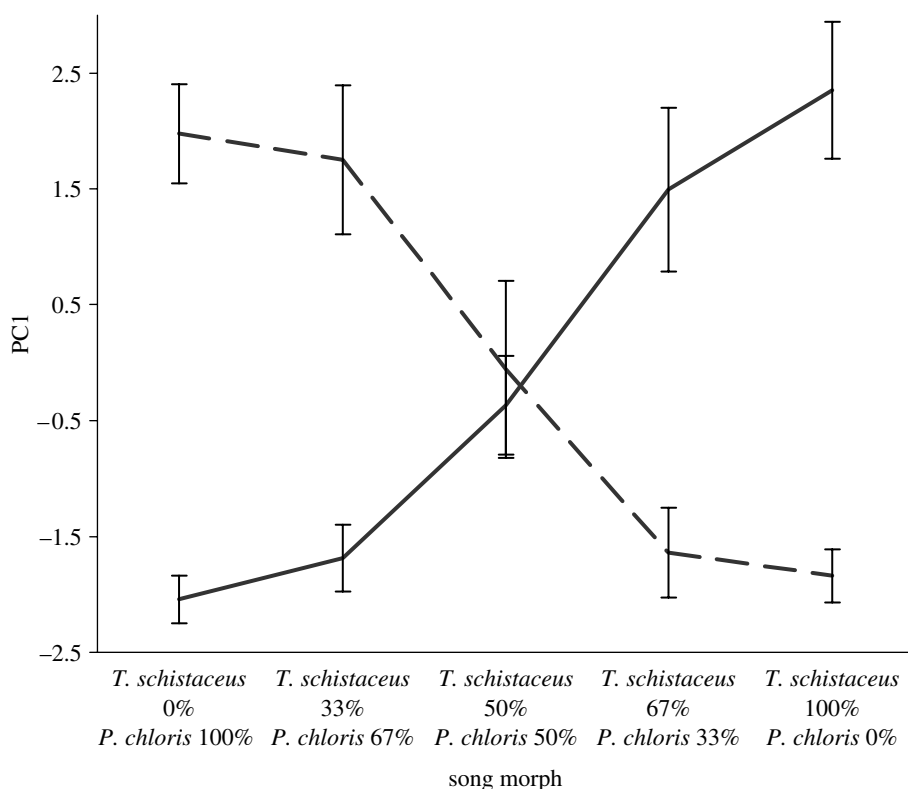
Figure 2. Mean responses ($\pm$s.e.) of each species to the different synthesized morphs (high values of PC1 indicate a strong response). Solid line, *T. schistaceus*; dashed line, *P. chloris*.

characteristic response of a territorial male towards a rival. Our results indicate that two species with similar songs in a noisy environment use signal space disjunctly, with a gap between their signals, but use perceptual space continuously, without a gap.

A greater scope for perception than for production of signals in acoustic space is a plausible adaptation for communication in a noisy environment. During transmission, a signal becomes degraded in complex ways and mixed with background noise (Wiley & Richards 1982; Naguib & Wiley 2001). As a result, signals when received are more variable than when broadcast. In these conditions, receivers cannot afford to be too narrowly focused on the features of a clean signal. Furthermore, signals should differ enough to allow receivers to discriminate between signals despite degradation during transmission. Noisy conditions thus constrain the similarity of coexisting species' signals as a result of the benefits of a broader scope for perception than for production of signals.

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