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Animal behaviour

Signaller: receiver coordination and the timing of communication in Amazonian birds

David A. Luther*

Curriculum in Ecology, University of North Carolina-Chapel Hill,
Chapel Hill, NC 27599-3275, USA
**dluther@unc.edu*

The efficacy of communication relies on the detection of signals against background noise. Some species are known to alter the timing of vocalizations to avoid acoustic interference from similar signals of other species, but nothing is known about the possibility of coordinated adjustments in the timing of receivers' attention. I examined the possibility that co-occurring species might respond as well as vocalize at different times in a diverse tropical avifauna by presenting playbacks of recordings to territorial birds at typical and atypical times for singing during the dawn chorus. The results show that co-occurring species of birds in a diverse avifauna partition the timing of both production and response in a way that would reduce acoustic interference between species.

Keywords: acoustic communication; dawn chorus; neotropical birds; background noise; acoustic interference

1. INTRODUCTION

Many animals rely on long-range communication for species recognition, mate selection and territorial defence, but background noise often constrains interactions between signallers and targeted receivers. A receiver must often detect a signal or discriminate between signals in the presence of many irrelevant but similar signals from other species (Ryan & Brenowitz 1985; Klump 1996; Bradbury & Vehrencamp 1998; Wollerman 1999; Wollerman & Wiley 2002*a*). To increase the detectability and discriminability of a signal and to reduce interference from irrelevant signals, signallers could increase the contrast between their signals and the background noise (Endler 1993; Wiley 1994, 2006). Because background noise in natural environments is rarely continuous (Klump 1996), adjusting the timing of signals to take advantage of gaps in noise can also reduce acoustic interference (Cody & Brown 1969; Greenfield 1988; Narins 1992). For instance, some birds avoid acoustic interference by means of short-term changes in the timing of their songs in the presence of other species' songs (see Brumm & Slabbekoorn 2005). However, adjusting the timing of signal transmission to avoid acoustic interference can only be effective if receivers pay attention and respond at the appropriate time (Wiley 1994). If adjustments of signals are not matched by adjustments by receivers, communication will fail.

An avian dawn chorus provides an example of communication in the presence of high levels of heterospecific and conspecific background noise. During the dawn chorus, species differ in the timing of their singing (Thomas *et al.* 2002; Berg *et al.* 2006). Acoustic censuses of the dawn chorus at Rio Cristalino, Mato Grosso, Brazil, revealed a large turnover in vocal activity of species during the morning (Luther 2008). Here I show that co-occurring species of birds in a diverse avifauna partition the timing of both song production and response in a way that reduces acoustic interference from other species' songs. By coordinating the time at which signallers sing and receivers respond during the dawn chorus, species minimize acoustic interference, reduce incorrect responses to other species' signals and increase the efficiency of intraspecific communication.

2. MATERIAL AND METHODS

Research took place at the Rio Cristalino Private Natural Heritage Preserve (RPPN), 40 km northeast of Alta Floresta, Mato Grosso, Brazil (9°41′ S, 55°54′ W). In 2004 I collected, standardized and replicated recordings between 05.30 and 08.30 in mature tropical moist (terra firma) forest. From these censuses, I determined that many species sang primarily at distinct times in the dawn chorus. Of the 106 species regularly detected during the acoustic censuses, 34 species sang primarily in one 30 min or one hour block of time (Luther 2008). Four of the latter species were chosen for experiments with playbacks of recordings. Two of these species sang primarily within 30 min of sunrise (white-browed antbird *Myrmoborus leucophrys* and warbling antbird *Hypocnemis cantator striata*) and two sang primarily from one to two hours after sunrise (chestnut-backed antshrike *Thamnophilus palliatus palliatus* and black-faced antthrush *Formicarius analis*) (figure 1). All four are suboscines in the families Thamnophilidae and Formicaridae. Each also had populations in the study area that were large enough for me to attempt to test at least six different individuals. A one-way analysis of variance (ANOVA) confirmed that the two early species differed significantly from the two late species in their times of singing. All four species defended year-round territories and used one species-specific long-distance vocalization throughout the year. Their behaviour at Rio Cristalino suggested that all the four species had protracted breeding seasons throughout most of the year. During both the wet and the dry seasons of 2006, I successfully presented playbacks to 23 individuals of these four species, including six to eight individuals of three of the species. Each subject received two treatments, one early and one late in the morning. Playback trials began when the subjects had been silent for at least 5 min. Early playbacks were conducted during the first hour after sunrise, and late playbacks were conducted during the second hour after sunrise.

After each playback, I recorded 10 categories of behaviour to assess each bird's strength of response to the playback treatments. Since many of the behavioural categories were correlated, I used principal components (PC) analysis to reduce the measures of response to a smaller number of independent variables. This analysis extracted four PC with eigenvalues greater than 1. Together they explained 75 per cent of the variations in responses (electronic supplementary material, table S1).

To test for differences in responses at typical and atypical times for each species, I used a nested ANOVA of the first PC of the behavioural responses, with species nested within their typical times for singing, early or late, and typical times for singing crossed with times of playback, early or late. In an assessment of the residuals, one point was an outlier (greater than 2 standard deviations from the mean). This point was removed before the final analysis, although this step did not affect the statistical significance of the results. All statistical tests were calculated with JMP v. 5.1.

3. RESULTS

The species defined in the present study as early and late-singing differed significantly in the mean times at which they sang (figure 1) ($F_{1,313} = 681.1$, $p < 0.001$).

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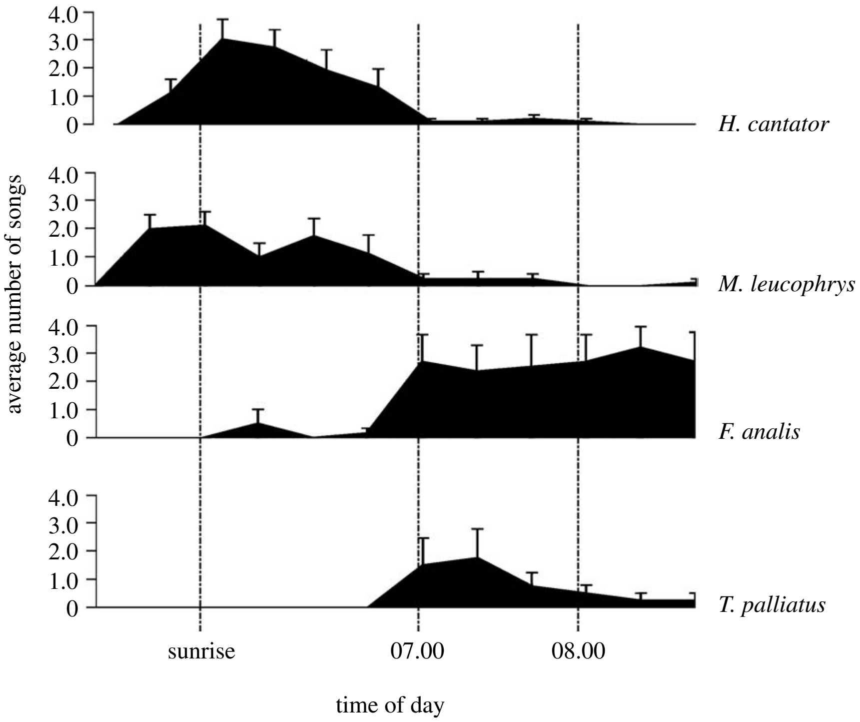

Figure 1. Rates of singing throughout the morning for each study species. The numbers of songs in successive 10-min periods are averaged (±s.e.) across multiple days ($n=12$) and census locations ($n=6$) for each species in both rainy and dry seasons at the study site.

Table 1. Responses of the four species to early and late playback treatments (mean values of principal component 1 and the respective standard errors).

singer category	species	number of individuals	response to early treatments	response to late treatments
early	*H. cantator*	7	1.97 (±0.58)	−0.28 (±0.57)
early	*M. leucophrys*	8	1.28 (±0.45)	−0.86 (±0.64)
late	*T. palliatus*	6	−1.55 (±0.48)	1.01 (±0.56)
late	*F. analis*	2	−2.94 (±0.19)	0.79 (±0.85)

All four species were heard singing during both experimental periods. Nevertheless, each species had stronger responses to songs played during its typical times for singing than to songs played during atypical times (table 1). The strong responses included shorter approach latency, shorter song latency and closer approaches, as well as a greater number of songs, calls, duets, number of minutes singing, number of flights past the speaker, time spent closer to the speaker and higher perch heights (electronic supplementary material, figure S1). While each species showed the majority of these responses, the magnitudes of responses differed among species. For example, *H. cantator* responded with a greater number of duets to the playback at the typical time of singing, *M. leucophrys* responded with shorter song latency and *F. analis* responded with shorter latency for approach. In general, individuals from each species responded to both typical and atypical timing of playback treatments, but responses at the atypical time of singing were less intense and less immediate.

ANOVA of the first PC scores revealed that both early and late-singing species had stronger responses to songs played during their typical times of singing (figure 2, table 2) ($F_{1,39}=17.67$, $p<0.001$). Individual species in each of the singing categories, early and late, showed no statistical differences in their responses to playbacks ($F_{2,39}=1.196$, $p=0.31$). Therefore, no one species in either the early singing or the late-singing category was responsible for the differences in responses to early and late playbacks.

4. DISCUSSION

A strong preference for singing during specific blocks of time during the dawn chorus coincided with an equally strong preference for responding during those same blocks of time. In other words, these species provide an example of temporal acoustic partitioning in response as well as production of signals. This temporal partitioning might serve to reduce acoustic interference between species in the same area.

Signalling and responding during restricted times might also occur because a species focuses on foraging at other times. For instance, singing at dawn might occur when light levels are insufficient for foraging (Leopold & Eynon 1961; Kacelnik 1979). Evidence for the fact that singing and foraging might often be incompatible in neotropical birds comes from a recent report (Berg *et al.* 2006) that foraging height and eye-size are inversely correlated with the sequence of singing by neotropical passerines. Birds

Table 2. Results of the nested ANOVA of the first PC of the behavioural responses. (Species are nested within their typical times for singing, early or late (species (singer category)) and a species' typical times for singing are crossed with time of playback, early or late (time of playback×singer category).)

source	d.f.	sum of squares	mean square	*F*	*P*
ANOVA-whole model					
model	5	82.38107	16.4762	8.1078	<0.0001
error	39	79.25346	2.0321		
combined total	44	161.63453			
source	number of parameters	d.f.	sum of squares	*F*	*P*
effect tests					
time of playback	1	1	35.905567	17.6688	0.0001
singer category	1	1	12.067078	5.9381	0.0195
time of playback×singer category	1	1	63.379548	31.1886	<0.0001
species (singer category)	2	2	4.860869	1.196	0.3132

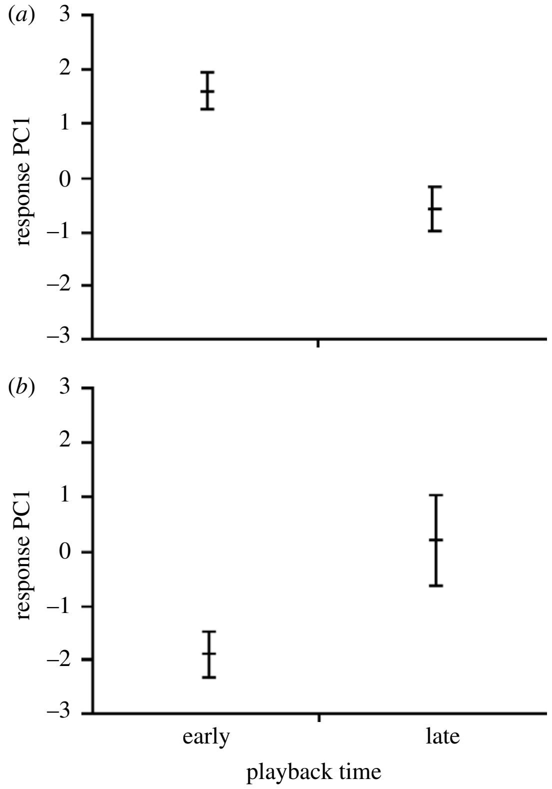

Figure 2. Means of the first principal component of responses (±s.e.) by (*a*) early-singing species and (*b*) late-singing species to early and late playbacks. Positive PC values indicate stronger responses than do negative PC values. See also table 1. For ANOVA of these data, see table 2.

in the understorey as a rule sing later in the day than birds that forage in the middle and upper layers of the forest, and birds with smaller eyes sing later than those with larger eyes. This general pattern, however, does not apply to all the four species in the present study. The late-singing *T. palliatus*, which generally forages in the middle and upper layers of the forest, sang later than *H. cantator* and *M. leucophrys*, which generally forage in the understorey. While hypotheses of constraints of foraging and acoustic interference on the time of singing are not mutually exclusive, foraging seems unlikely to explain the temporal restriction of dawn signalling and responding in these species. Avoidance of acoustic interference is a more plausible explanation in this case.

Previous studies have documented avoidance of short-term interspecific acoustic interference in birds (Cody & Brown 1969; Brumm 2006), frogs (Littlejohn 1959; Schwartz & Wells 1984) and insects (Greenfield 1988), but no previous study has documented acoustic partitioning of responses in birds. For acoustic partitioning to occur, both signallers and receivers must coordinate their behaviour. A shift in the timing of signal transmission would require a coordinated shift by the receiver to obtain a match in production and response. In the presence of high levels of background sound from other species, both signallers and receivers might realize immediate advantages by focusing the time of signalling to minimize overlap with other species (Wiley 1994). Communication that minimizes acoustic interference would be expected to increase correct detections of conspecific and rejections of heterospecific signals. It would also reduce erroneous responses to heterospecific signals and missed detections of conspecific signals (Wiley 1994; Wollerman & Wiley 2002*b*).

In summary, this study addressed the correspondence of song production and response in a complex tropical avifauna. The results are consistent with the hypothesis of temporal acoustic partitioning as a result of species-specific patterns of coordinated production of and response to signals to improve intraspecific communication.

All birds were treated in accordance with animal care guidelines of the host country and institution.

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