SHORT-TERM TEMPORAL AVOIDANCE OF INTERSPECIFIC ACOUSTIC INTERFERENCE AMONG FOREST BIRDS

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ABSTRACT.—We investigated whether birds of deciduous forests avoid temporal overlap in their songs. Singing patterns of four common species were analyzed. All species showed a strong tendency to avoid singing during the song of another species. One tactic used to avoid song overlap was to sing immediately after another species had stopped. Individuals sang more often and more regularly (less variance in the interval between songs) when they sang alone than when they sang with other species. The hypothesis that short-term adjustments in temporal patterning of songs minimize interspecific acoustic interference is supported. *Received 26 November 1984, accepted 11 April 1985.*

BIRDS giving long-range vocalizations face several sources of noise. Sound is both degraded and attenuated as part of the natural transmission process (Wiley and Richards 1976, Marten and Marler 1977). A source of noise given little attention in the literature is interference between vocalizations given simultaneously. Interference may mask the signal carried in vocalizations. Acoustic overlap should be avoided, so as not to waste time or energy in vocalizations whose message will be lost. Several studies suggest that birds actively avoid both intraspecific and interspecific acoustic overlap through short-term changes in the temporal patterning of song delivery (Ficken et al. 1974, Wasserman 1977).

While a single pair of species has been shown to adjust the temporal pattern of song delivery to avoid acoustic overlap (Ficken et al. 1974), this mechanism has not been investigated in an assemblage of birds, nor is there any supporting experimental evidence. This study investigates (1) whether interspecific avoidance of acoustic overlap occurs through shifts in the temporal patterning of songs in assemblages of chorusing forest birds; (2) if such avoidance occurs, how overlap is avoided; and (3) how the presence of singing individuals of another species affects the timing of singing. In addition, playbacks were used to experimentally test for avoidance of acoustic interference.

METHODS

Chorusing passerines were recorded in deciduous forest at the University of Wisconsin-Milwaukee Field Station, Saukville, Ozaukee County, Wisconsin and at Harrington Beach State Park, Lake Church, Ozaukee County, Wisconsin. The Field Station site was in an upland beech-maple forest; the dominant tree species were sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), beech (*Fagus grandifolia*), and basswood (*Tilia americana*) (Dunnum 1972). The state park site was a second-growth forest characterized by white ash, basswood, northern white-cedar (*Thuja occidentalis*), and paper birch (*Betula papyrifera*).

The date, time, location, and species for each recording period are given in Table 1. A Sennheiser MKH 104 omnidirectional condenser microphone connected to a Nagra 4.2L tape recorder was used about 1.5 m off the ground. Portions of tapes containing high levels of background noise (e.g. planes, trains) were not analyzed. Three thousand seventy-three songs were obtained from the remaining 173 min of recording. To determine relative timing of vocalizations, the tapes were analyzed using a Brüel and Kjaer 2305 Graphic Level Recorder with a 2,000-Hz high-pass filter. The length of each song and interval between songs were then measured.

Predicted number of song overlaps was determined using the method of Ficken et al. (1974). The predicted number of species A songs begun during species B songs is:

$$F_A = p(B)f,$$

where f is the total number of species A's songs and

TABLE 1. Date, time, length, location, and species of each recording period.

Date	Time	Length (min)	Used in analysis (min)	Location	Species recorded[a]
2 July 1975	1930	45	17.4	Field Station	3, 8, 10, 15
13 June 1979	0730	90	30.4	State Park	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 15, 17
16 June 1979	0530	135	66.0	State Park	1, 2, 3, 4, 5, 6, 7, 8, 11, 16
6 June 1982	0600	90	29.9	Field Station	1, 2, 6, 8, 10, 13, 14, 15, 18, 19
22 June 1982	0600	135	24.2	Field Station	1, 3, 6, 8, 10, 15, 18
24 June 1982	0600	45	5.1	Field Station	10, 15

[a] 1 = Wood Thrush (*Hylocichla mustelina*), 2 = Eastern Wood-Pewee (*Contopus virens*), 3 = Great Crested Flycatcher (*Myiarchus crinitus*), 4 = Northern Oriole (*Icterus galbula*), 5 = Red-winged Blackbird (*Agelaius phoeniceus*), 6 = Veery (*Catharus fuscescens*), 7 = Common Grackle (*Quiscalus quiscula*), 8 = Blue Jay (*Cyanocitta cristata*), 9 = Brown-headed Cowbird (*Molothrus ater*), 10 = Red-eyed Vireo (*Vireo olivaceus*), 11 = American Robin (*Turdus migratorius*), 12 = Rose-breasted Grosbeak (*Pheucticus ludovicianus*), 13 = Scarlet Tanager (*Piranga olivacea*), 14 = House Wren (*Troglodytes aedon*), 15 = Ovenbird (*Seiurus aurocapillus*), 16 = Black-capped Chickadee (*Parus atricapillus*), 17 = American Redstart (*Setophaga ruticilla*), 18 = American Crow (*Corvus brachyrhynchos*), 19 = White-breasted Nuthatch (*Sitta carolinensis*).

$p(B)$ is the proportion of total time spent singing by species B. Predicted values were calculated for each tape and then combined. As not all species sang on each tape, the predicted values for a species depend on which species it is paired with. The *G*-test (Sokal and Rohlf 1981), a one-tailed log-likelihood ratio test, was used to compare observed and expected values.

To experimentally test for interspecific avoidance, recordings of Chestnut-sided Warbler (*Dendroica pensylvanica*) songs were played to Ovenbirds (*Seiurus aurocapillus*). The Chestnut-sided Warbler was used as the stimulus because this species was not present at the Field Station study site and there could be no interference from them. Warbler songs were played through a Nagra DH amplifier and speaker. The amplitude was 94 dB at 1 m from the speaker using the slow setting on a Brüel and Kjaer 2204 sound-level meter. The stimulus song, an accented type 2 song (Lein 1978), was played 50 times at randomly determined intervals (minimum 6, maximum 48 s) over a 12-min period, during which song was recorded. The range of intervals was chosen to simulate the natural song rate (see Lein 1978). Recordings were made with a Sennheiser MKH 104 omnidirectional condenser microphone connected to a Nagra 4.2L tape recorder placed 20 m from the speaker and 1.5 m off the ground. Recordings were made on 5 days (1 experiment/day) between 20 June and 1 July 1984. Observed and expected overlaps were calculated as described above.

RESULTS

The 19 species recorded had a total song rate of 17.8 songs/min and sang for a total of 61.5 min. Together the species used 35.6% of the air

TABLE 2. Timing of songs relative to singing and silent periods.

Species overlapped	Species overlapping	Number of songs: Overlapping Exp.	Overlapping Obs.	Not overlapping Exp.	Not overlapping Obs.	*G*	*P*
Wood Thrush	Eastern Wood-Pewee	22.6	2	537.4	558	20.619	<0.001
	Great Crested Flycatcher	13.9	0	299.1	313	19.600	<0.001
	Ovenbird	22.5	2	314.5	335	18.231	<0.001
Eastern Wood-Pewee	Wood Thrush	20.3	0	443.7	464	28.596	<0.001
	Great Crested Flycatcher	12.3	1	287.7	299	10.284	<0.005
	Ovenbird	16.3	4	266.7	279	8.250	<0.005
Great Crested Flycatcher	Wood Thrush	19.8	2	507.2	525	17.164	<0.001
	Eastern Wood-Pewee	23.0	1	485.0	507	25.391	<0.001
	Ovenbird	9.9	3	259.1	266	4.017	<0.05
Ovenbird	Wood Thrush	46.7	1	298.3	343	58.192	<0.001
	Eastern Wood-Pewee	51.7	2	195.3	245	30.787	<0.001
	Great Crested Flycatcher	20.7	0	237.3	258	30.567	<0.001

TABLE 3. Songs begun during first quarter vs. last three quarters of the silent periods of another species.

		Number of songs					
		First quarter		Last three quarters			
Species	Following songs of	Exp.	Obs.	Exp.	Obs.	G	P
Wood Thrush	Eastern Wood-Pewee	14	15	42	41	0.046	NS[a]
	Great Crested Flycatcher	5	4	15	16	0.144	NS
Eastern Wood-Pewee	Wood Thrush	16.75	30	50.25	37	5.827	<0.025
	Great Crested Flycatcher	8	10	24	22	0.364	NS
Great Crested Flycatcher	Wood Thrush	6.5	15	19.5	11	5.855	<0.025
	Eastern Wood-Pewee	11	18	33	26	2.539	NS
Ovenbird	Wood Thrush	11.75	26	35.25	21	9.164	<0.005
	Eastern Wood-Pewee	12	29	36	19	12.608	<0.001
	Great Crested Flycatcher	5	14	15	6	8.425	<0.005

[a] NS = $P > 0.05$.

time available for singing. Only a few recordings of song were obtained for many of the species. The small sample prevented a G-test analysis of observed and expected values for some species. Because of this, data are presented on only the four species singing the most: the Ovenbird, Great Crested Flycatcher (*Myiarchus crinitus*), Wood Thrush (*Hylocichla mustelina*), and Eastern Wood-Pewee (*Contopus virens*). These four species accounted for over 75% of the songs recorded. The common species overlapped the rare species only four times, indicating interference was low between the common and rare species.

All four species avoided singing during the song of another species (Table 2). In all cases overlap was rare or absent. There was no evidence that any species avoided song overlap with certain heterospecifics more than others.

Individuals do not sing immediately after themselves. Each song is followed by a period of silence known as a refractory period. Thus, overlap could be avoided by singing immediately after another species. If this mechanism of overlap avoidance was being used, more songs than would be predicted by chance alone would be given during the first quarter of the other species' refractory period. This was determined only at times when two species were alternating their songs. Because of the long interval between Ovenbird songs (see Table 4), there was rarely only one heterospecific song between Ovenbird songs. This prevented testing whether species sang immediately after Ovenbird song. The results of this analysis were mixed (Table 3). The Ovenbird had a strong tendency to sing immediately after another species' song. The Wood Thrush showed no tendency to sing immediately after any of the other species. The wood-pewee and flycatcher sang immediately after only the Wood Thrush's song.

If birds actively avoid song overlap, they must remain silent while heterospecifics sing. This pattern should affect the individual's song delivery. The mean and variance of the interval

TABLE 4. Mean and variance of the silent period between songs (in seconds) when singing alone and when singing with other species. For the Wood Thrush, Eastern Wood-Pewee, and Great Crested Flycatcher the t-test performed does not assume equal variances (Sokal and Rohlf 1981).

	Mean				Variance			
Species	Alone	Not alone	t	P	Alone	Not alone	F	P
Wood Thrush	3.55	7.03	1.64	NS	2.26	52.38	23.21	<0.001
Eastern Wood-Pewee	3.35	5.37	3.06	<0.01	2.16	7.70	3.58	<0.01
Great Crested Flycatcher	3.62	8.76	4.21	<0.001	4.22	27.34	6.48	<0.005
Ovenbird	7.31	14.63	5.35	<0.001	26.69	35.14	1.32	NS

between songs were compared for each species when singing alone and when singing with other species (Table 4). Data were taken from a single tape, picked at random, to avoid variation due to time of day or weather condition. Singing occurred more often (shorter silent period between songs) and more regularly (lower variance in the interval between songs) when species sang alone than when species sang with other species.

The results of the playback experiment strongly support the descriptive results. During 170 songs, Ovenbirds overlapped the stimulus song only once, significantly less than the predicted 17 times ($G = 18.02$, $P < 0.001$). Ovenbirds also tended to sing immediately after Chestnut-sided Warbler stimulus songs. A greater percentage of Ovenbird songs occurred during the first quarter of the silent interval between stimulus songs than would be predicted by chance (55.6% vs. 25.0%; $G = 17.81$, $P < 0.001$).

DISCUSSION

The most obvious advantage of avoiding song overlap is an increase in the probability of being heard by conspecifics. Two songs given simultaneously may mask each other. Having all of a song heard would be particularly important if different parts of the song coded for different information (Wasserman 1977). Avoidance of song overlap also could be important if individuals use song to judge distances between individuals (Richards 1981). Avoiding song overlap may involve costs, however, by causing birds to sing at other than optimal song rates.

Our study provides strong evidence that birds actively avoid interspecific acoustical interference through short-term temporal changes in song delivery. Birds almost always avoided singing while an individual of another species was singing. The Ovenbird also avoided overlapping the experimental playback song. Avoidance of acoustic interference among forest passerines appears to be a general phenomenon, as demonstrated by the most common species at both study sites.

Wasserman (1977) found that White-throated Sparrows (*Zonotrichia albicollis*) avoided intraspecific acoustical interference, and the response was strongest for conspecifics in close proximity, perhaps due to the greater possibility for interference when individuals are closer to each other. The methods used in this study recorded only those individuals in close proximity, or those that would be predicted to benefit the most by avoiding song overlap.

One way for an individual to avoid song overlap would be to sing during the refractory period of the other individual. This form of overlap avoidance was used by all the species studied, except for the Wood Thrush. It was also experimentally demonstrated for the Ovenbird. The wood-pewee and flycatcher showed their strongest responses following the song of the Wood Thrush. This may indicate that the Wood Thrush is not as active in avoiding song overlap as the other species. To compensate for this, the other species may be paying particular attention to the Wood Thrush to prevent it from overlapping them. The Wood Thrush also could be avoiding overlap through some mechanism not investigated. Occasionally two Wood Thrushes were recorded, and it is possible that the thrushes were paying more attention to conspecifics than heterospecifics. In most cases only one Wood Thrush was recorded, so this probably was not an important influence.

In avoiding song overlap, birds alter the timing of their singing. As the number of singing individuals of other species increases, there is increasing noise to be avoided and individuals sing less often. An individual's song rate may fall below optimal. Species have strong effects on each others' song patterns. McGeorge (1979) has suggested that this interaction between species is competition for noiseless time. As only a small part of the available air time in this study was used for singing, competition would not seem to be important. The high song rate, however, makes the available air time very unpredictable. Shifts in temporal patterning of song may not be caused by competition, but rather by the attempts of an individual to maximize the probability that its song will be heard.

Other ways of avoiding acoustic interference have been suggested. Individuals could sing with different daily rhythms (Cody and Brown 1969, McGeorge 1979) or at different frequency bands (Littlejohn and Martin 1969, McGeorge 1979). The species analyzed in this study had extensive overlap in song frequencies. Short-term adjustment of the temporal patterning of songs is the only immediate and flexible means of avoiding song overlap. When short-term temporal adjustments are used, other means of avoiding overlap may be unnecessary.

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LITERATURE CITED

CODY, M. L., & J. H. BROWN. 1969. Song asynchrony in neighboring bird species. Nature 222: 778-780.

DUNNUM, J. 1972. The upland hardwood forest of the Cedar-Sauk Field Station. Univ. Wisconsin-Milwaukee Field Sta. Bull. 5(1): 17-23.

FICKEN, R. W., M. S. FICKEN, & J. P. HAILMAN. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. Science 183: 762-763.

LEIN, M. R. 1978. Song variation in a population of Chestnut-sided Warblers (*Dendroica pensylvanica*): its nature and suggested significance. Can. J. Zool. 56: 1266-1283.

LITTLEJOHN, M. J., & A. A. MARTIN. 1969. Acoustic interaction between two species of Leptodactylid frogs. Anim. Behav. 17: 785-791.

MARTEN, K., & P. MARLER. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behav. Ecol. Sociobol. 2: 271-290.

MCGEORGE, L. W. 1979. Circumvention of noise in the communication channel by the structure and timing of the calls of forest animals. Unpublished Ph.D. dissertation, Durham, North Carolina, Duke Univ.

RICHARDS, D. G. 1981. Estimation of distance of singing conspecifics by the Carolina Wren. Auk 98: 127-133.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry, 2nd ed. San Francisco, W. H. Freeman.

WASSERMAN, F. E. 1977. Intraspecific acoustical interference in the White-throated Sparrow (*Zonotrichia albicollis*). Anim. Behav. 25: 949-952.

WILEY, R. H., & D. G. RICHARDS. 1976. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalization. Behav. Ecol. Sociobiol. 3: 69-94.