SOME PARAMETERS OF SONG IMPORTANT IN CONSPECIFIC RECOGNITION BY GRAY CATBIRDS

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ABSTRACT.—Some parameters of Gray Catbird song important in species recognition were identified by playback of altered song to territorial individuals. Playback types included normal song, song played backwards, song in which the order of syllables was randomized and song in which the normal frequency excursion of sound energy versus time was altered. In addition, three parameters were measured from spectrographs of songs from five individuals. Statistical analysis of the responses from 67 individuals indicated that catbirds responded to song composed of sound energy traversing an approximately 4-kHz bandwidth at a characteristic rate. *Received 20 July 1976, accepted 7 April 1977.*

THIS paper identifies some parameters of song important in species recognition by the Gray Catbird (*Dumetella carolinensis*). Catbirds are mimics and their songs are composed of imitations of other species' songs. Because of this imitative ability songs of individual catbirds are variable, and the question arises of what parameters of the song code species specificity. Previously, Thompson and Jane (1969) measured several parameters of catbird songs and Harcus (1973) examined catbird song for species distinct parameters by using playback techniques. More recently Boughey and Thompson (1976) have shown by a series of playback experiments that catbirds can discriminate their song from those of Mockingbirds (*Mimus polyglottus*) and Brown Thrashers (*Toxostoma rufum*). However, these workers were not able to identify the parameters critical for this discrimination and concluded that perhaps an average value of several parameters was important. Thompson and Jane (1969), in an investigation of the song repertoires of five individual catbirds, found that songs were composed of approximately 180 different sounds or groups of sounds. They concluded that catbirds within the same geographic region shared many of the same syllables (see Fig. 1 for a definition of terms). Harcus (1973) found random syllable sequencing and minimal syllable repetition to be important in eliciting an aggressive response from catbirds. Since Harcus' findings indicated that species information is not coded in a fixed sequence of syllable patterns of the song, some other parameters of the vocalization are suspect. The quality of catbird song syllables and syllable patterns is distinctive to the listener in the field. It thus seemed possible that catbirds might use some aspect of syllable quality as a species identification cue.

Our main investigations focused more on individual syllables and syllable patterns than on sequence analysis. We emphasized playbacks of normal and edited tapes of naturally occurring catbird syllables and syllable patterns in addition to a statistical investigation of some parameters of catbird song. We present evidence to support our conclusions that some structural aspects of syllables and syllable patterns are important in species recognition by catbirds.

METHODS

The Gray Catbird is an abundant songbird common in the forests and forest edge habitats of the northern United States and Canada. Its natural history has been described by Saunders (1935), Bent

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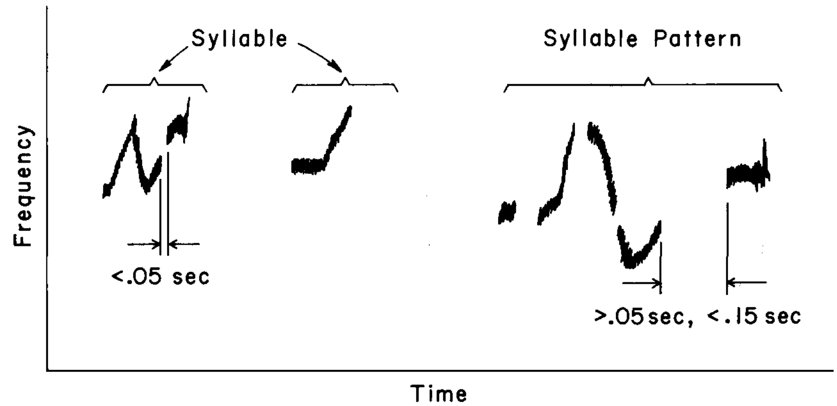

Fig. 1. Definitions of terms used in this paper. Syllables and syllable patterns are considered operationally the same. Syllables are traces on the spectrogram separated by 0.05 s or less. Syllable patterns are recurring groups of syllables separated by 0.15 s or more.

(1948), Zimmerman (1963), Darley et al. (1971) and Harcus (1973). Utilizing the fact that catbirds respond aggressively to the songs of conspecifics, playback of normal and edited tapes was used to determine some parameters of song used in conspecific discrimination. Recordings of naturally occurring song were made from individual catbirds in Old Field, New York and Nissequogue State Park in Smithtown, New York. The recordings were made at 7½″ per second on a Nagra IV-L tape recorder through a Sennheiser MD 211U microphone mounted on an 47.8-cm aluminum parabola.

Playback experiments were conducted during the 1974 catbird breeding season (May through July). Six different types of recordings composed of edited and otherwise modified portions of normal catbird song were played to 31 territorial catbirds. Individual birds were used no more than three times for playbacks. The same individual was never used twice for a playback of the same "Type." These playbacks used in 1974 are listed below and will be referred to by "Type" in the remainder of the paper (see Fig. 2).

Type 1—"Normal" is a portion of naturally occurring song recorded from a vigorously singing male in Old Field, New York. This acted as a "control" song. The response to the "control" song was used as comparison to responses to the other playback types.

Type 2—"Backwards" is the normal tape (Type 1) played backwards. This playback was designed to determine whether the syllable or syllable pattern conveyed species information even if played backwards. We predicted that "symmetrical" syllables or syllable patterns would elicit similar responses regardless of the direction in which they were played.

Type 3—"Randomized order of syllables or syllable patterns" is a tape made up of the syllable patterns from the normal tape (Type 1) but the syllable patterns along with the time intervals following them were spliced together in a randomized order according to a random number table. This playback was designed to test whether a specific sequencing of syllable or syllable pattern types was essential to elicit aggressive behavior.

Type 4—"Added randomized time" is made from the original sequence of syllables from the normal tape but time intervals of .25, .50, .75, and 1.00 s were added between the syllables or syllable patterns according to a random number table. This resulted in a playback with less sound energy per playback. This playback was designed to determine if characteristic time intervals after specific syllables or syllable patterns are important in species recognition.

Type 5—"Narrow bandwidth" is made by playing the normal tapes through a General Radio Universal Filter (Model #1932). This resulted in a tape with attenuated sound energy above 4 kHz and below 2 kHz but leaving sound energy between 2 and 4 kHz unaltered. Time intervals between syllables were affected slightly by this treatment (see discussion). Spectrographic analysis of naturally occurring catbird song indicated that the majority of syllables and syllable patterns contain energy in this 2-kHz bandwidth. We wanted to test whether energy in this 2-kHz bandwidth was sufficient to elicit aggressive responses.

Type 6—"Narrow bandwidth with added randomized time" is made from the narrow bandwidth tape (Type 5) with randomized time added in the same way and with the same time intervals as "added randomized time" (Type 4) playback.

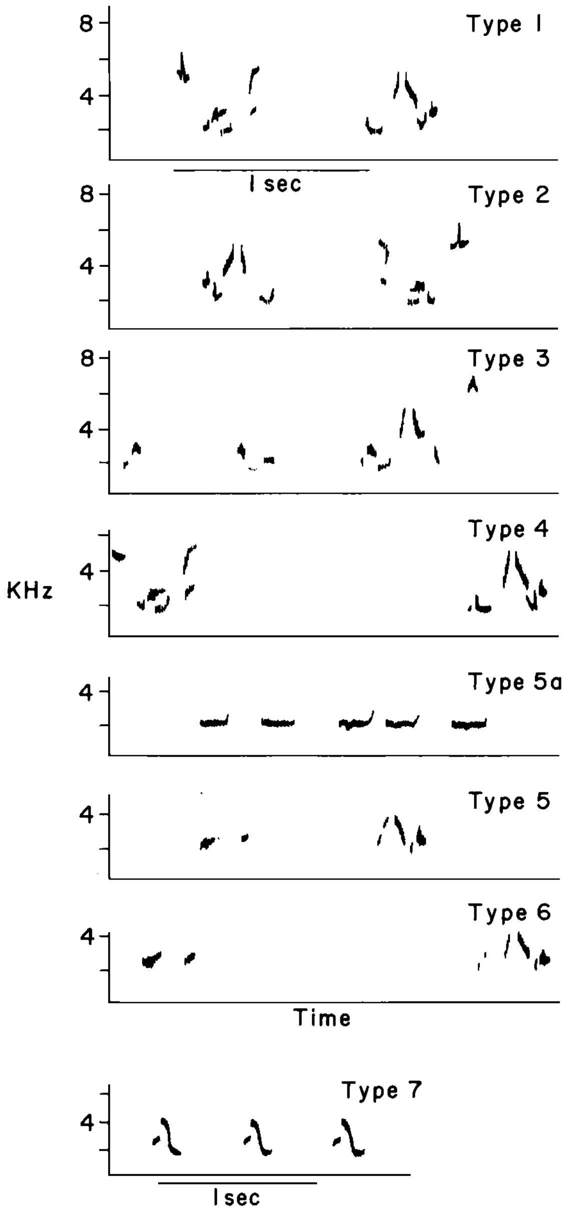

Fig. 2. Some of the syllables and syllable patterns that make up the playback loops used in these experiments. See text.

Type 7—"Wide bandwidth" excursion playback was composed of a single syllable taken from Type 1 playback. Each syllable was separated by the same time intervals as the Type 5a syllable.

During the 1975 breeding season three "Types" of recordings were used in playback experiments to 36 individuals (see Fig. 2). Each bird was used for only one playback experiment. The playback Types were:

Type 1—"Normal" which was the same playback used in 1974.

Type 5a—"Narrow bandwidth" excursion playback was composed of a single syllable taken from the Type 1 playback. This syllable subtended a narrow bandwidth and was repeated with a random order of time intervals of .12, .25, .37, .50, and .62 s. We wanted to determine whether the catbirds' response

TABLE 1. The playback type, year conducted, song length, time intervals between song, and total length of playbacks used in these experiments

	Playback type	Year conducted	Song length used (s)	Silent intervals used (s)	Total length (min)
1	Normal	1974, 1975	22, 60	22, 30	3.5, 5.5
2	Backward	1974	22	22	3.5
3	Added random time	1974	40	22	3.7
4	Random order of syllable patterns	1974	22	22	3.5
5	2–4-kHz bandwidth	1974		22	3.5
5a	Narrow frequency excursion	1975	60	30	5.5
6	2–4 kHz bandwidth with added randomized time	1974	40	22	3.7
7	Wide frequency excursion	1975	60	30	5.5

to a single narrow bandwidth syllable was stronger or weaker than their response to a single wide bandwidth syllable (Type 7).

These timings were arbitrarily selected but fall well within the normal vocalization times and intervals of silence between songs of normal catbird singing. The number of syllables composing the various playback Types were not equal. Table 1 summarizes the composition of the playback Types. In an attempt to compensate for the response differences imposed by seasonal changes, all playback types were played at least once during the beginning, middle, and late portions of the breeding season.

Sometimes during this study the various playback Types were paired with "normal" (Type 1) song. When this was done there was a 5-min silent period between playback Types. The "Normal" playback (Type 1) always followed the altered song playback. Thus Type 1 song acted as a control and was done to determine the "level of arousal" or "motivation" of the catbird at approximately the same time an altered playback Type was played. In no case was a playback of Type 1 song completely ignored. All playbacks were done using an Uher 4400 stereo recorder connected to a Nagra DH amplifier and speaker. The measured frequency response of the Uher and Nagra amplifier was adjusted to vary less than 4.0 db over the range of frequencies encountered in catbird song. The Nagra speaker was always placed 9.2 m from the Uher. We attempted to keep the volume of the playbacks consistent although physical measurements were not made. The volume of all playbacks was in the apparent range of naturally occurring catbird song. The speaker was always positioned so that a responding catbird had room to perform display flights. Catbirds live in habitats characterized by trees and bushes although there is variation in their distribution. In an effort to standardize the placement of the speaker in the habitat, it was always placed within at least 3.1 m of branches strong enough to support a catbird. Beyond this distance the branches formed a mostly continuous layer. As nearly as we could determine the speaker placement represented the behavioral center of the catbird's territory. This estimation was based on numerous observations over 2 days preceding a playback.

In 1974, 4 days were allowed between playbacks to the same bird because they apparently habituated rapidly to the playbacks. Because of this an individual bird was used only once for a playback in 1975.

A catbird's response to a playback was scored according to the scale shown in Table 2. This scale was derived from observations of natural encounters between catbirds and supported by the observations of Harcus (1973). The use of scaling assumes a number of untested judgments and the results discussed in this paper hold insofar as those judgments are correct. As the playbacks were conducted only on territories where a catbird was heard singing just prior to a playback experiment, we could be sure that the catbird was present at the beginning of the playback. The category "Response Latency" is defined as the time from the onset of the playback until the catbird comes into view and orients towards the speaker. This is the most subjective parameter of those we used. The category "Nearest Distance to the Speaker" recorded the closest approach of a bird. The category "Number and Types of Flights over the Speaker" records the two types of flights over the speaker. The swoop flight is the same as undulating flight described by Harcus (1973) and appears to represent a higher level of arousal than non-swoop flight. The "Body Postures" category records the four levels of arousal as evidenced by posture. A quivering posture with fluffed plumage and the tail down and spread is considered to indicate a high level of arousal. A bird with normal plumage contour and the tail held only slightly down but flicking is considered to be less aroused (Harcus 1973). The "Vocalization" category is divided into three levels of arousal: the soft song that appears to be the most submissive response of a highly aroused bird, the normal song that is indistinguishable from the normal maintenance song delivered by catbirds, and single syllables such as "meow" and

TABLE 2. Point scale for the responses to the playbacks

	Points
1. *Latency of response*	
a. 0–30 s	5
b. 31–60 s	4
c. 61–90 s	3
d. 91–120 s	2
e. >120 s	1
2. *Nearest distance to the speaker*	
a. 0–1.5 m	4
b. 1.51–3.1 m	3
c. 3.11–4.65 m	2
d. >4.65 m	1
3. *Number and types of flights over the speaker amplifier*	
a. each swoop flight	2
b. each non-swoop flight	1
4. *Body postures*	
a. quivering, plumage fluffed, tail down and spread	4
b. plumage fluffed, tail down and spread	3
c. plumage normal, tail down and spread	2
d. plumage normal, tail down but not spread, tail twitching	1
5. *Vocalizations*	
a. soft song	3
b. normal song	2
c. meow, grr, syllables	1

"grr" sounds that are apparently indicative of low arousal. The scores for responses to the various playback Types were compared using non-parametric multiple comparisons by Simultaneous Test Procedure (STP) or the Mann-Whitney U Test (Sokal and Rohlf 1969).

Although the main thrust if this study is the analysis of response to the playback taped in the field, the recorded songs of five different catbirds were also analyzed to determine the relatively stereotyped parameters of song common to all individuals. It seemed reasonable to assume that this might provide clues to potential species-identifying parameters. Two of these songs were recorded at the Nissequogue River State Park and three were recorded in Old Field, New York. The number of syllables and syllable patterns analyzed for each individual ranged between 294 and 332, and represented approximately 3 min of continuous song per individual. Recordings of the songs were transcribed onto a pieced-together "continuous spectrograph" made with a Kay Vibralyzer Model #7030A. A frequency range of 80–8,000 Hz with a fixed bandwidth 150-Hz filter and a 10-db dynamic range was used throughout the study. Measurements were made from the spectrographs of the duration of syllables, the interval between syllables, and the frequency limits of the syllables.

RESULTS

We attempted to determine species identifying parameters by focusing our attention on alterations of song that affected structural aspects of individual syllables and syllable patterns and the time intervals between these patterns. The responses to playbacks of these song alterations are shown in Fig. 3.

1974 playbacks.—We compared 1974 responses to various playbacks using non-parametric multiple comparisons by STP. The critical value of "U" was calculated several times for the same measurements because we were comparing unequal sample sizes. Sample sizes must be equal for this test so the number of samples of responses to playback Type 5 was reduced to 9 by random elimination of sampled responses. This reduction allows the comparison of the responses to playback Types 1, 5, and 6. Playbacks of Types 5 and 6 were sometimes followed by playback of "normal" song (Type 1) in an attempt to determine if a lack of response was due to motivational factors. Comparison of responses to Type 1 song played after Type 5

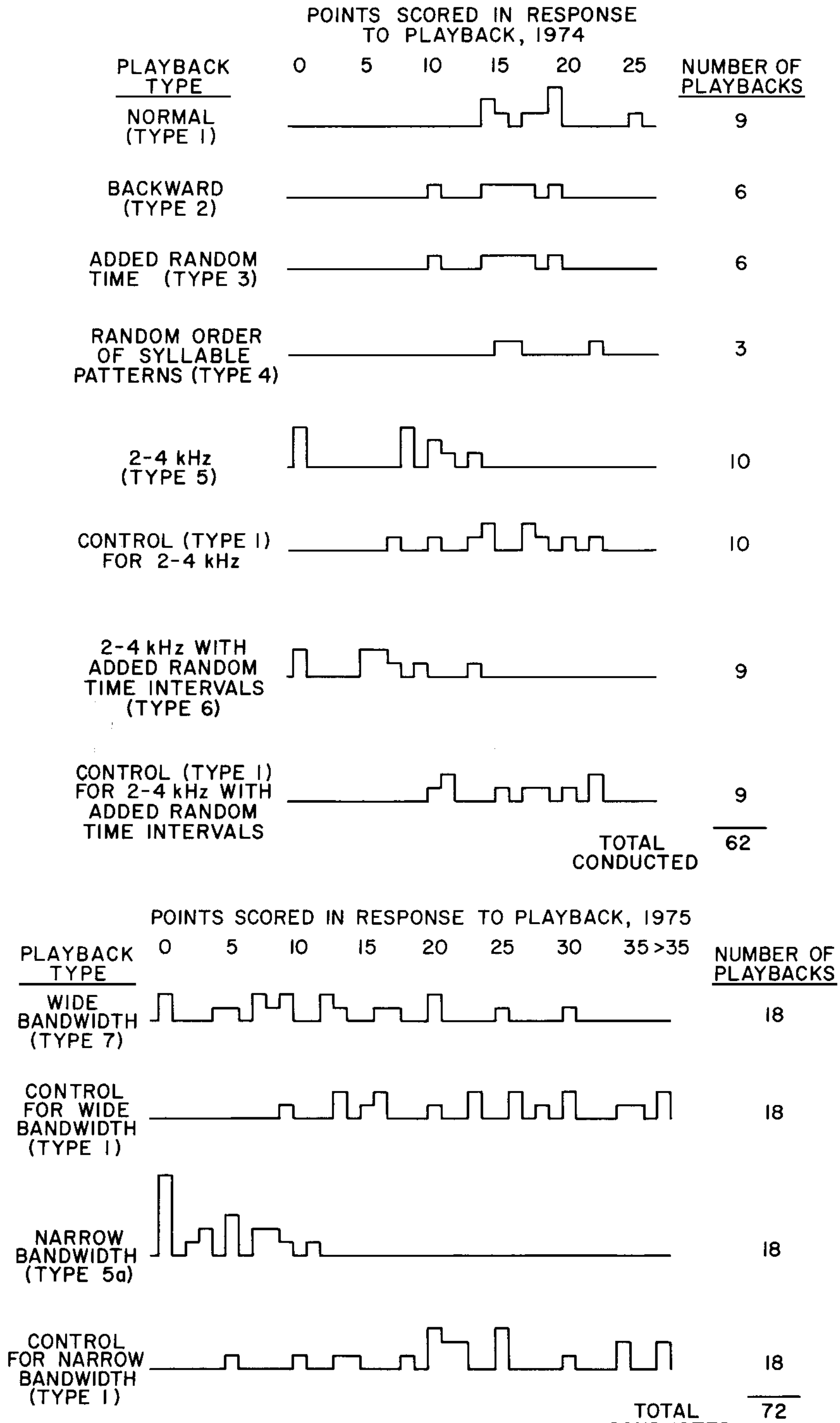

Fig. 3. The response of individuals to the playbacks for 1974 and 1975. The strength of response is plotted as histograms of the number of individuals against response score, according to the point scale shown in Table 2.

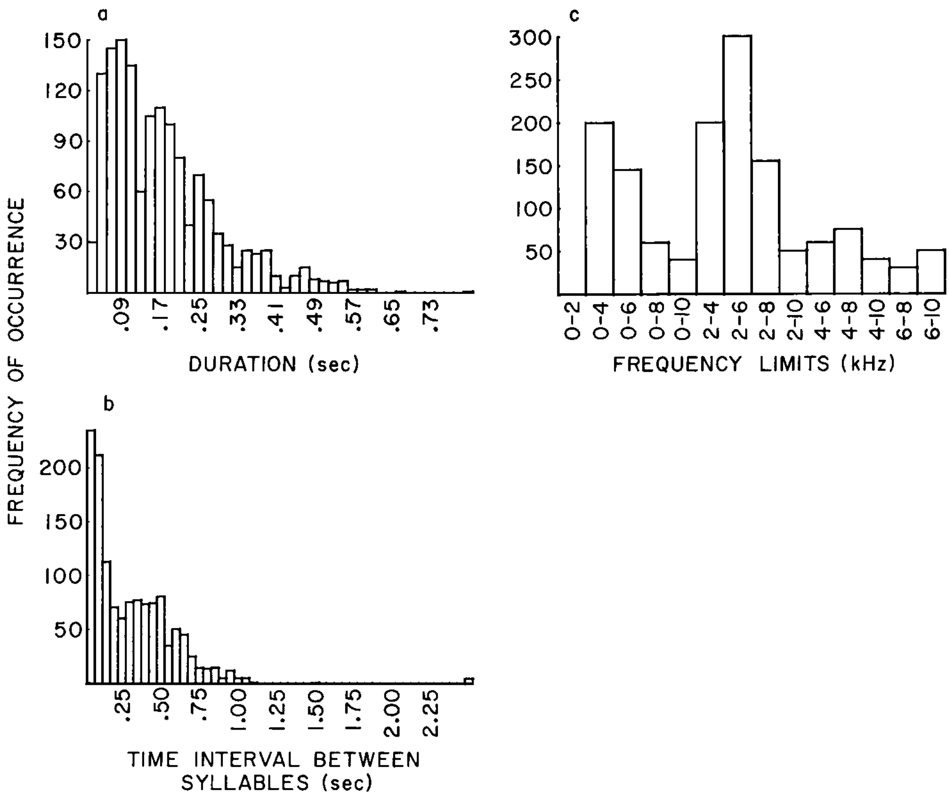

Fig. 4. Syllable patterns from combined measurements of five catbird songs: a) histogram of syllable pattern duration; b) histogram of time intervals between syllables; c) histogram of the frequency limits of five syllable patterns.

and Type 6 with responses to Type 1 song played alone showed no significant differences ($P > 0.05$). This comparison of responses was necessary to demonstrate that there was no "enhancement" or "priming effect" of playbacks 5 or 6 upon Type 1 song. However, when responses to "normal" (Type 1) playback were compared with the responses to playback of Type 5 ("narrow bandwidth") a significant difference ($P < 0.05$) was found. The catbirds responded much more strongly to "normal" (Type 1) than to Type 5 song. When the responses to the normal (Type 1) playback were compared with the responses to Type 6 ("narrow bandwidth with added randomized time") a significant difference ($P < 0.05$) was found. No significant difference ($P > 0.05$) was found in a comparison of the responses to Type 5 and Type 6 song playbacks. This indicated that "narrow bandwidth" song with naturally occurring time intervals between syllables accounted for the difference in the intensity of response to Type 1 playback compared with Type 6 playback. Responses to Type 1, Type 2 ("backwards"), and Type 4 ("added randomized time") did not differ in intensity. There were only three sampled responses to "randomized order of syllables" (Type 3) so they were not treated statistically. These three samples, however, indicated strong responses and these probably do not differ significantly from responses to the "normal" (Type 1) tape.

1975 playbacks.—The "narrow" (Type 5a) and the "wide" (Type 7) playbacks were always followed by "normal" (Type 1) playbacks so that the sample sizes (N = 18)

TABLE 3. Statistics on parameters of the songs of five individual catbirds

Individual catbirds	Duration of syllables (millis)	Time interval between syllables (millis)
Bird 1	N = 294 $\bar{x}$ = 147.0 SD = 112.8 CV = 76.7	N = 293 $\bar{x}$ = 284.0 SD = 213.0 CV = 75.0
Bird 2	N = 267 $\bar{x}$ = 201.0 SD = 124.0 CV = 61.7	N = 266 $\bar{x}$ = 337.0 SD = 268.0 CV = 79.5
Bird 3	N = 241 $\bar{x}$ = 157.0 SD = 106.0 CV = 67.6	N = 239 $\bar{x}$ = 336.0 SD = 337.0 CV = 100.3
Bird 4	N = 332 $\bar{x}$ = 138.0 SD = 94.0 CV = 68.5	N = 326 $\bar{x}$ = 391.0 SD = 341.0 CV = 87.2
Bird 5	N = 258 $\bar{x}$ = 138.0 SD = 94.0 CV = 68.5	N = 251 $\bar{x}$ = 399.0 SD = 406.0 CV = 101.6

are equal. The intensity of responses by catbirds to the "narrow bandwidth excursion" (Type 5a) and "wide bandwidth excursion" (Type 7) playbacks were significantly weaker ($P < 0.05$) than the responses to "normal" (Type 1) playback. Furthermore, samples of responses to the "narrow bandwidth excursion" (Type 5a) playback differed significantly ($P < 0.05$) from "normal" playback even more than the responses to "wide bandwidth excursion" (Type 7) syllable pattern playback. Judging from the response strength, "wide" (Type 7) syllable playback is apparently more species characteristic than the "narrow" (Type 5a) syllable pattern playback, although both syllable types normally occur in catbird song.

Statistical analysis of naturally occurring song.—Sample population variability of three parameters of song for five individuals is shown in Fig. 4. The mean, standard deviation, and coefficient of variation were calculated for the duration of syllables and the interval between syllables for each of five catbirds (Table 3). Eleven intervals were extemely hard to measure accurately and were eliminated from analysis. The results showed that durations of syllables and syllable patterns and the intervals between syllables and syllable patterns did not differ between individuals. These findings suggested that there was no dependence of time interval occurring after or before a syllable (or syllable pattern) of a particular duration. An R $\times$ C Test of independence showed that there was no dependence of one parameter on the others. Only the frequency limits of the syllable (or syllable pattern) and the duration of the syllable (or syllable pattern) showed dependence. In other words, the difference between the highest and lowest frequency excursion of a syllable predicts the length of that syllable. Most syllables had a characteristic frequency excursion of 4 kHz.

DISCUSSION

Our playback experiments and the descriptive analysis of the catbird song revealed several parameters that appear to be important in conspecific recognition by catbirds. One important parameter is the frequency excursion or sweep of normally occurring syllables. Harcus (1973) found, and our results confirm (Playback Type 3), that a second important characteristic of song for species recognition is a lack of monotony (high syllable diversity) in the syllable patterns.

The response of the catbirds to the "backwards" (Type 2) and "added randomized time" (Type 4) playbacks did not differ significantly from the responses to the "normal" (Type 1) playbacks. These results are in agreement with Harcus' (1973) findings that changes in the gross temporal organization of the song had little effect on the elicited aggressive response of the catbird. He noted too that in the wild, individual catbirds often vary the temporal arrangement of their song from discontinuous to continuous. The catbird's similarly strong response to songs played forward or backward may be explained in at least two ways. Some structural aspect (e.g. harmonics) of the syllables and syllable patterns may be important rather than their specific morphology. If the morphology of the syllable is important, one would predict that the symmetrical shape of many of the syllables should result in it making little difference in how they sound when they are played forward or backward. It is not possible from our results to tell whether quality or morphology is most important.

Thompson and Jane (1969) concluded from their analysis that there is no fixed order of syllables or syllable patterns in catbird song. We tested this parameter but since there were only three playbacks in which the order of the syllables was randomized (Type 3) they were not treated statistically. The responses to Type 3 are strong, however, and imply that the catbirds do not discriminate them from "normal" (Type 1) playbacks. Other bird species apparently ignore sequence information (Bremond 1968, Emlen 1972). Because the specific order of syllables or syllable patterns, the temporal organization, or the direction in which syllables were played did not appear to be crucial in species recognition by catbirds, we altered song in ways that affected the tonal quality of the syllables. These included Types 5, 5a, 6, and 7. However, several problems existed with the 1974 playbacks that used frequency filtering. When a frequency filter is used to filter a normal song, the duration of some syllables is decreased, and the interval between these syllables is increased. Sound energy falling outside of the 2–4-kHz bandwidth is strongly attenuated, and if the energy that begins or ends a syllable is attenuated, then the syllable length and the interval associated with it are altered. This means that several parameters will co-vary, making interpretation of the results even more difficult. Because of these considerations, different kinds of bandwidth excursion playbacks were used in 1975. The significantly stronger response of the catbirds to the "normal" (Type 1) playback than to Types 7 or 5a indicates that some parameter of the song other than the bandwidth excursion is also important. That parameter is almost surely the increased variety of syllables and syllable patterns characteristic of the Type 1 playback. It is important to note that Types 5, 5a, and 7 are all significantly poorer in eliciting measured responses from catbirds. When compared to Type 5a, Type 7 elicits a significantly stronger response.

In general, the responses to the normal playbacks in 1975 were stronger than to the 1974 normal playbacks. We believe that this is most likely due to the change in procedure in 1975. In the 1974 playbacks we found that when a bird was used more than once its response declined, regardless of what type of playback was used. Therefore, during the spring and summer of 1975 each bird was used for only one set of playbacks. The playbacks used during 1975 are also 2 min longer, providing more response time.

Besides doing playback experiments in the field, normal catbird song recordings were analyzed. Measurements of naturally occurring song show that all measured parameters are highly variable and therefore unlikely to be used as cues in conspecific recognition. It is interesting to note that we found essentially the same mean duration of syllables as those reported by Thompson and Jane (1969).

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