

## VARIATION IN REPERTOIRE PRESENTATION IN NORTHERN MOCKINGBIRDS<sup>1</sup>

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**Abstract.** Male Northern Mockingbirds (*Mimus polyglottos*) have exceptionally large vocal repertoires. The manner of presenting this extensive repertoire, as described using five measures, varied with reproductive stage, among situations, and among individuals. All three versatility measures peaked during courtship, declined significantly during incubation, and then slowly increased during nestling and fledgling stages. A fourth measure, bout length, increased as the season progressed, being shortest during courtship and longest during the fledgling stage. A final measure, recurrence interval (number of intervening bouts between two bouts of a particular song type) was shorter during the nestling and fledgling stages than during courtship. Recurrence interval was shortest during patrolling and countersinging with neighboring males. Over 25% of the song types occurred only once in the sampling of singing behavior of four males each over 2 years. Mockingbirds sang these rare song types most commonly during prefemale and courtship stages, thereby increasing the recurrence interval and versatility during these stages. The patterns just described resulted in the greatest number of song types being sung per unit of time during courtship and provide circumstantial support for the hypothesis that song functions intersexually in mockingbirds. The ability to alter the manner of presentation may provide mockingbirds with the flexibility to emphasize particular functions at certain times and other functions at other times.

Males with the highest versatility measures and lowest bout length tended to be the first to acquire mates and begin to nest. However, the importance of versatility in attracting females remains speculative and requires further experimental testing because these results were from only four males. Songs sung at night were presented in a manner most similar to the period before a female arrived on a male's territory. Interestingly, under natural lighting conditions, only unmated males sang extensively at night.

**Key words:** *Song presentation; song repertoires; song types; versatility; bout length; recurrence interval; rare songs; Northern Mockingbird; Mimus polyglottos.*

### INTRODUCTION

Individuals of many bird species have vocal repertoires containing more than one song. Further, the manner of presenting such a repertoire varies among species, among individuals, and even within the same individual at different times of the day or nesting cycle (Martin 1977, Kroodsma and Verner 1978, d'Agincourt and Falls 1983, Schroeder and Wiley 1983). In addition, the way in which an individual presents its repertoire and/or selects particular song types can change with changing situations (Kroodsma and Verner 1978, Lein 1978, Smith et al. 1978, d'Agincourt and Falls 1983, Schroeder and Wiley 1983). This study describes how the manner of presentation of repertoires by male Northern Mockingbirds

(*Mimus polyglottos*) varies with reproductive stage and among social situations. How birds alter the manner of presentation is also described.

Descriptive studies of vocal repertoires of individuals provide the necessary quantitative results from which experiments can be designed to test and distinguish among the many proposed functions of repertoires. Additionally, results from descriptive studies often provide circumstantial evidence supporting some proposed functions. Hypotheses currently being investigated to explain the evolution of repertoires include sexual selection (Catchpole 1982, 1987; Searcy and Andersson 1986), antihabituation (Hartshorne 1956, 1973; Ince and Slater 1985), Beau-Geste (Krebs 1977, but see Smith 1985), differential provisioning of information (Marler 1956; Smith 1970, 1977), and the ranging hypothesis (Morton 1982, 1986). No consensus has been reached among researchers concerning the function and evolution of repertoires, perhaps

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because a general explanation is unlikely given the variety of species possessing repertoires and the range of social systems involved (Dawson 1982). In fact, the ability of an individual to alter the presentation of its repertoire could provide the flexibility that facilitates the emphasis of certain functions depending on time of year or social situation.

These hypotheses are not mutually exclusive. Several may be important at any one time and their relative importance may change depending on the time of year and social situation. For example, if song functions to attract and stimulate females, the singing behavior might differ between the courtship stage and subsequent nesting stages. This assumes that other selective forces, such as those involving male-male interactions, territorial maintenance, or antihabituation, would not also select for an identical seasonal pattern. At least for male-male interactions and territorial maintenance this is likely to be the case because these activities occur throughout the breeding season. However, a similar but not identical pattern might occur if during territorial establishment there is initially much singing with a subsequent decrement in singing as the borders become established. Regardless, I would not expect to see a change in singing behavior centered around the period of female commitment, nesting. Hartshorne (1956, 1973) suggested that species with more monotonous songs should break up their performance and thus avoid listeners habituating to it. Since the amount of singing varies seasonally in mockingbirds (Logan 1983, pers. observ.), I would predict a positive correlation between versatility and the extent of singing. Because the amount of singing is high during courtship and nest building, and low during incubation and subsequent stages, versatility should be high during courtship and nest building, and lower during later nesting stages. A discussion of information provided by particular song types in mockingbirds is presented elsewhere (Derrickson 1987a).

It takes several descriptive measures to characterize adequately the singing behavior of a species. Kroodsma and Verner (1978) describe how a song repertoire is presented and derive several estimates of versatility. "Song type versatility" is the number of distinct song types in a sequence of specified length. "Transition versatility" is the number of transitions between unlike songs in this sequence. "Total versatility"

is the product of song-type and transition versatility and, as a product, is unduly sensitive to extreme values of either. Therefore, more emphasis should be placed on the song and transition versatility measures. Furthermore, it is these measures that the bird can alter by changing the final two measures, bout length and recurrence interval. "Bout length" is the number of times a song type is repeated before changing to another song type. "Recurrence interval" is the number of bouts of other song types between two bouts of the same song type. This study documents changes in the versatility measures, bout length, and recurrence interval among breeding stages.

## METHODS

### STUDY SITE AND FIELD TECHNIQUES

Research was conducted at Tyler Arboretum, Lima, Pennsylvania, between fall 1979 and spring 1983. This 285-ha arboretum shares a boundary with 1,050-ha Ridley Creek State Park. Deciduous woodlands and mowed and uncut meadows dominate. Spring and summer observations were concentrated on the grass field which is planted with a scattering of dogwoods (*Cornus*), spruce (*Picea*), cedars (*Thuja*), pines (*Pinus*), and holly (*Ilex*). Fall and winter observations centered more around the buildings (see fig. 2.1 in Derrickson 1985).

Most observations were made from 0.5 hr before sunrise until noon; others were made during the afternoon, evening, and night. Vocalizations were recorded with a Marantz Superscope CD-330 stereo cassette tape recorder and a Gibson P-200 parabolic microphone. A Superscope E-5 cardioid microphone was used to record simultaneously a continuous description of the bird's behavior, location, orientation, and other salient contextual information.

Each year I recorded six to 10 mockingbird pairs, obtaining 18, 54, 112, and 72 hr of recordings in four field seasons, respectively. Half the individuals were captured in mist nets and each was banded with a U.S. Fish and Wildlife Service band and a unique color combination of plastic leg streamers. The focal-individual sampling technique (Altmann 1974, Dunbar 1976) was used. The behavior of one individual was described until it either left the vicinity, I lost track of it for several minutes, or I obtained a 1-hr sample of singing. Individuals were ob-

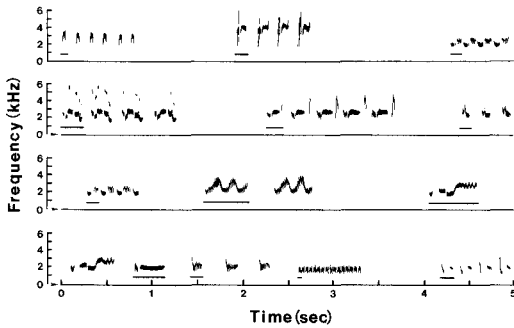


FIGURE 1. An example of early spring song by a male mockingbird. The first complete example of each song type is underlined.

served in a random order except when behavioral and situational circumstances required that one individual be monitored more closely.

Detailed analyses of singing behavior were limited to four male mockingbirds for two reasons. First, it was necessary to limit the number of birds analyzed intensively because large samples of song are required to describe the singing behavior adequately. Second, these particular birds were sampled intensively over two consecutive breeding seasons, 1980 and 1981, and three of the four males were neighbors in both years (see fig. 2.1 in Derrickson 1985). Thus, details of their social histories were known, and I could monitor changes in their singing behavior between years.

#### TERMINOLOGY AND CLASSIFICATION OF SONG TYPES

I define singing as a regularly patterned sequence of songs. Figure 1 depicts 58 songs as an example of singing by a male Northern Mockingbird during early spring. They are organized into 13 bouts of 12 different "types" (upper right song type occurs again on third line). A "song type" is defined as a single vocalization or a group of vocalizations in which the time intervals between the units of the group are shorter than the time intervals between groups, and that is always uttered in a *consistent* (although not completely identical) form by a particular individual. That a particular song type might be repeated two times in one bout and three times in a subsequent bout made identifying what constituted the song type very easy. Song types, as defined here, appear to be a category comparable to "syllable patterns" of earlier investigators of mockingbird repertoires (e.g., Howard 1974).

Song types are of unequal duration (see Fig. 1) and this increased the variation in the calculated diversity indices. However, it does not alter the conclusions derived from these indices because song types of short duration were not sung preferentially during particular reproductive stages (see below). Obviously, an analysis incorporating time would be preferable, but data were collected in a manner that precluded incorporating time into the calculation of the indices.

Northern Mockingbirds imitate songs of many other species (Bailey 1911, Mayfield 1934, Laskey 1944, Borror and Reese 1956, Baylis 1982) and this can cause some confusion in categorizing song types. What is considered a song type in some imitated species can contain several repetitions of a group of elements (continuous traces on a sound spectrogram). In my classification, the group of elements is recognized as being the song type and the "source song type" as being a bout of the mockingbird's song type. For example, in Figure 1 the collection of elements at the beginning of the second line represents one rendition of an imitated Carolina Wren (*Thryothorus ludovicianus*) song. In my classification this collection of elements would be a bout of four songs of a particular song type (underlined in Fig. 1). I feel this classification system is appropriate because there is no reason to assume that mockingbirds classify vocalizations in the same manner as do the imitated species. Further, mockingbirds show more variation in the number of repetitions of the group of elements than do the imitated species. In addition, they rarely imitate long and complex songs, such as songs by Indigo Buntings (*Passerina cyanea*), in their entirety. Of the almost 1,500 song types identified only eight (0.54%) were imitations of complex songs, and these accounted for only 15 bouts of over 10,000 bouts analyzed. More often, mockingbirds include in their repertoires fragments of the complex songs of other species in a manner similar to the Marsh Warbler (*Acrocephalus palustris*; Lemaire 1974, Dowsett-Lemaire 1978).

Typically, mockingbirds repeat a song type several times prior to switching to another song type. In other words, each song type is presented in a bout. Bout length is defined as the number of repetitions of a song prior to switching to another type. In Figure 1, the bout lengths are 6, 4, 4, 4, 5, 3, 4, 2, 2, 1, 3, 16, and 4 for the 13 bouts. Another term used to describe the orga-

nization of song types is recurrence interval, the number of other song types occurring between two bouts of the same song type.

Slight differences among renditions of a given song type can be seen in several songs depicted in Figure 1. For example, the duration of the song type shown in the center of the second axis increases with each rendition, and the first song type in the third row is rendered only 3½ times. It was characteristic of a limited number of song types that they were not always completed.

Spectrograms from a Kay Elemetrics model 6061B Sona-Graph (wide band filter of 300 Hz, and high-shape setting) and hard copies from a Princeton Applied Research real-time sound spectrum analyzer model 4212F and an EPC hard copy recorder were used to depict song types. From these individually identified songs a poster with representatives of each song type for each male was constructed and song types were arranged by a classification scheme that allowed quick identification. After a relatively complete repertoire list was constructed, song types were identified and recorded by number directly onto a data sheet along with their bout lengths. Data collection was facilitated greatly by using the video monitor associated with the real-time analyzer. Of 10,734 bouts analyzed, approximately 80% were identified by using the video monitor.

#### MEASURES OF SONG PRESENTATION

One method of measuring the versatility or perceived diversity of songs uttered by an individual male was developed by Kroodsma and Verner (1978) and modified by d'Agincourt and Falls (1983). Techniques used here in calculating song, transition, and total versatility are identical to those in d'Agincourt and Falls (1983). My versatility measures were based on samples of 25 songs. Only those portions of my data that included sequences long enough to get several estimates (so as to provide a variance measure) of the versatility measures were used.

Two additional measures were used to describe song presentation, bout length, and recurrence interval. The entire data set was used in the analysis of bout length. A subset of my total data was used in calculating recurrence intervals. All samples used were sequences that had 75 successive bouts; longer sequences were curtailed after 75 song types. This arbitrary sampling protocol attempted to balance two conflicting constraints. Longer sequences would provide a more

accurate estimate of recurrence interval, especially since recurrence intervals greater than 75 are not uncommon in mockingbird song. However, using longer sequences reduced the number of samples analyzed and precluded determining how recurrence interval varied through the breeding season.

Seven periods in the annual cycle of the mockingbird were recognized. "Prefemale" was the period when a male was on his breeding territory prior to arrival of a female or periods between successive mates when no female was observed on his territory (only male A). The courtship stage began when a female arrived and ended when she began to assist in nest building. Incubation, nestling, and fledgling stages are self explanatory. Two remaining categories were songs performed at night by unmated males ("night"), and songs that occurred immediately after a nest was destroyed by a predator or just prior to desertion of the territory in late summer ("pre-desertion").

Long singing sessions do not occur during certain stages of the breeding season in mockingbirds (Logan 1983), making it difficult to estimate recurrence intervals for all stages because 75 successive bouts are uncommon during certain breeding stages. Therefore, slightly different criteria were used to define situations when estimating recurrence intervals. Prefemale, courtship, and night singing categories remained unchanged. Two new categories were (1) singing associated with nest building by the male in the presence of the female and (2) singing while patrolling and/or countersinging. Nestling and fledgling stages were combined.

#### STATISTICAL ANALYSES

The Statistical Analysis System (SAS) package (Ray 1982) was used to produce the majority of statistical analyses reported. The General Linear Model (GLM) procedure was used to examine variation in singing behavior between years, among individuals, and among situations. Ray (1982) recommended using GLM, a parametric analysis of variance procedure, whenever the data are unbalanced (unequal cell sample sizes), which was always the case in my analyses. The extremely large sample sizes made testing for normality problematic. Obviously, the data used to analyze recurrence interval (see above) produced a truncated distribution that was not distributed normally. Further, tests of random subsamples

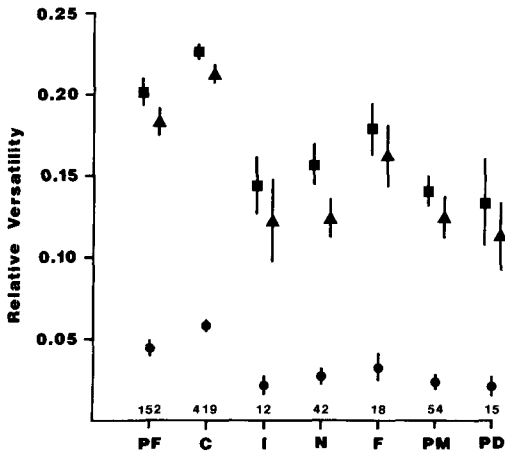


FIGURE 2. Relative Versatility: changes in song (square), transition (triangle), and total (circle) versatility ( $\bar{x} \pm SE$ ) among seven situations (first five being breeding stages). Situations are as follows: PF = pre-female, C = courtship, I = incubation, N = nestlings, F = fledglings, PM = night, PD = pre-desertion. Sample sizes below total versatility.

from the other data sets occasionally showed them to be nonnormally distributed. Thus, all parametric analyses of variance and covariance were done on both nontransformed and rank-transformed data (see Conover and Iman 1981 for use of parametric tests on ranked data to simulate nonparametric tests). The results from the unranked data are presented throughout the paper. In all comparisons between the two approaches, the results were identical with insignificant changes in the *F*-values. In most instances, a greater proportion of the variance was explained

when using ranked data and, thus, the reported values are probably conservative estimates.

Tukey's studentized range test and *t*-test were used to compare the means of several measures between years, among individuals, or among stages. The Tukey procedure in SAS appears to be a powerful procedure, has fared extremely well in Monte Carlo studies, and is recommended for analyses with unequal cell sizes (Ray 1982). As described above, these procedures were done on both unranked and ranked data with no differences in their outcome. The Kruskal-Wallis test (Sokal and Rohlf 1969) was used to determine if stages differed in the number of recurrence intervals occurring during samples.

RESULTS

VERSATILITY

Song, transition, and total versatility did not differ between years (Song: *F* = 3.12, ns; Transition: *F* = 0.54, ns; Total: *F* = 0.00, ns). However, differences among males were significant for all three measures (Song: *F* = 14.87, *P* < 0.001; Transition: *F* = 13.22, *P* < 0.001; Total: *F* = 9.68, *P* < 0.001). In addition, the interaction between year and male was highly significant (*P* < 0.001) for all measures, and was due to a change in versatility in one male between years. Male B sang with the highest versatility of all males in 1980 and the lowest in 1981. The remaining males were ranked similarly in both years. When the analysis was repeated with male B removed, the interaction term was not significant for all measures. The former two-way AN-

TABLE 1. Relative versatility: two-way ANOVA results for changes in versatility measures among breeding stages (prefemale, courtship, incubation, nestling, and fledgling stages) and two other situations (song performed at night and song that occurred prior to territory desertion).

	Source	Sum of squares	df	Mean square	<i>F</i>
Song	Bird	0.308	3	0.1027	14.34***
	Stage	0.856	6	0.1427	19.95***
	Bird × Stage	0.112	1	0.1124	15.72***
	Error	5.014	701	0.0072	
Transition	Bird	0.400	3	0.1332	12.97***
	Stage	1.001	6	0.1668	16.24***
	Bird × Stage	0.143	1	0.1430	13.93***
	Error	7.199	701	0.0103	
Total	Bird	0.066	3	0.0221	9.47***
	Stage	0.200	6	0.0333	14.29***
	Bird × Stage	0.021	1	0.0209	8.96**
	Error	1.635	701	0.0023	

\*\* *P* < 0.01; \*\*\* *P* < 0.001.

TABLE 2. The mean and standard error for song, transition, and total versatility for four male mockingbirds.

Bird	n	Versatility		
		Song	Transition	Total
C	81	0.240 ± 0.0077 a <sup>1</sup>	0.238 ± 0.1255 a	0.060 ± 0.0039 a
B	180	0.229 ± 0.0077 a	0.209 ± 0.0088 a,b	0.063 ± 0.0054 a
D	106	0.216 ± 0.0091 a	0.199 ± 0.0101 b,c	0.052 ± 0.0052 a,b
A	330	0.184 ± 0.0048 b	0.167 ± 0.0057 c	0.039 ± 0.0021 b

<sup>1</sup> Values with the same letter are not significantly different within the versatility measure at the  $P = 0.05$  level by Tukey's studentized range test.

OVA, with male B included, explained approximately 20% of the total variation.

All three versatility measures showed a similar pattern of change through the breeding season (Fig. 2). Song, transition, and total versatility were high before a female arrived. During courtship all three measures of versatility peaked. A significant decline occurred in all measures between courtship and incubation. All measures rose to above the incubation stage level during the fledgling stage. The versatility of singing that occurred during two other situations is also presented in Figure 2. Versatility measures of singing at night were similar to those during incubation. Singing that occurred shortly after a nest was destroyed or shortly before the territory was deserted showed the lowest values for all measures. That these latter situations arose late in the breeding season could account for the low values (see below).

Two-way ANOVAs (Table 1) indicated that all versatility measures changed across the breeding season (same stages as above). There were differences among stages ( $P < 0.001$ ) and among individuals ( $P < 0.001$ ), along with a significant interaction. The interaction resulted from two birds switching their ranking among stages. Birds differed significantly when analyses were performed on each stage. In addition, stages differed significantly for each male. The two-way ANOVAs explained 20.3%, 17.6%, and 15.0% of the variation in song, transition, and total versatility, respectively.

Since two of the four birds did not reach the nestling stage in one of 2 years and sample sizes were rather small for a few stages in particular birds, I combined the stages in the following way for an analysis to compare prefemale, courtship, and postfemale-commitment singing behavior. Prefemale and song performed at night were pooled. This was done because only males without a female sang for extensive periods at night under natural lighting conditions. In addition,

night song was very similar to prefemale singing behavior in certain aspects (see below). Incubation, nestling, and fledgling stages were combined and represent the postfemale-commitment stage. The courtship stage remained unchanged. The categories for loss of nest and preterritory desertion were deleted. ANOVA of three main effects, bird, year, and stage (prefemale, courtship, and postfemale-commitment) revealed significant differences among stages (Song:  $F = 52.67$ ,  $P < 0.001$ ; Transition:  $F = 42.05$ ,  $P < 0.001$ ; Total:  $F = 37.32$ ,  $P < 0.001$ ) as well as among individual birds (Song:  $F = 16.38$ ,  $P < 0.001$ ; Transition:  $F = 14.01$ ,  $P < 0.001$ ; Total:  $F = 11.03$ ,  $P < 0.001$ ). Years did not differ in transition or total versatility ( $F = 1.81$ , ns;  $F = 0.25$ , ns), but did differ significantly ( $F = 6.13$ ,  $P < 0.05$ ) in song versatility.

The mean and standard error for song, transition, and total versatility measures for the four males are shown in Table 2. Of particular interest is which individuals differ. Male A had the lowest versatility and was significantly different ( $P < 0.05$ ) from males B and C on all three versatility measures. Male D consistently showed the next to lowest versatility, being classified with male A in transitional and total versatility, and males B or C in all three versatility measures. This ranking was the inverse of the order in which males acquired mates.

Prefemale, courtship, and postfemale-commitment stages have different ( $P < 0.05$ ) mean song and transition versatility (Table 3). Mean song and transition versatility were highest during courtship, lowest for the postfemale-commitment stage, and intermediate for the prefemale stage. For total versatility, means for prefemale and postfemale-commitment stages could not be distinguished statistically. However, both stages differed from the courtship stage. Overall, total versatility showed the same pattern as song and transition versatility, rising sharply

TABLE 3. The mean and standard error for song, transition, and total versatility for three stages (prefemale, courtship, and postfemale commitment).

Stage	n	Versatility		
		Song	Transition	Total
Prefemale	206	0.186 ± 0.0063 a <sup>1</sup>	0.168 ± 0.0072 a	0.040 ± 0.0032 a
Courtship	419	0.226 ± 0.0045 b	0.212 ± 0.0055 b	0.058 ± 0.0028 b
Postfemale commitment	72	0.159 ± 0.0092 c	0.133 ± 0.0098 c	0.027 ± 0.0033 a

<sup>1</sup> Values with the same letter are not significantly different within the versatility measure at the *P* = 0.05 level by Tukey's studentized range test.

once a female arrived on the territory and then declining once she began to assist the male in building the nest.

SINGING AT NIGHT

Singing at night was typical of unmated males. It regularly occurred during full-moon periods and less commonly during other lunar phases. Under natural lighting conditions, mated males rarely sang at night. If they sang at all, it was extremely brief (one to 10 bouts). This pattern was disrupted in more developed areas with artificial lighting.

Singing at night was similar to singing during prefemale and courtship stages (Table 4). Only one male, male A, was used in this analysis since only he was unmated during three separate full-moon periods. There was no difference among these stages in mean song (*F* = 2.38, *P* > 0.05), transition (*F* = 1.57, *P* > 0.10), or total (*F* = 1.87, *P* > 0.10) versatility in 1980. However, in 1981 stages did differ (*P* < 0.05). For all versatility measures, courtship was statistically indistinguishable from the prefemale stage but different from song given at night. The prefemale stage was intermediate, and was not statistically distinct from either remaining stage.

BOUT LENGTH

Mean bout length generally increased over the season (Fig. 3). There was a slight nonsignificant decrease (*P* > 0.05) in mean bout length during the fledgling stage which corresponded to the increase in versatility at this stage. A two-way ANOVA for changes in bout length across the breeding season revealed a significant difference among stages (*F* = 25.18, *P* < 0.001) and among males (*F* = 57.42, *P* < 0.001). The interaction term was significant (*F* = 10.37, *P* < 0.001), and once again a single bird was responsible. When the analysis was repeated with male B removed, the interaction term was not significant. However, this ANOVA explained only 5.1% of the variance in bout length.

Variation in bout length *within* a song type over the course of the breeding season was not addressed in the above analyses. Each song type, regardless of its frequency of occurrence, was weighted equally. To understand more fully the determinants of bout length and seasonal variation in bout length, along with maintaining adequate sample sizes, an analysis was performed on the 11 most frequently occurring song types for three males and 13 most common song types of the remaining male (Table 5). Song types dif-

TABLE 4. Mean and standard error for song, transition, and total versatility for three stages (prefemale, courtship, and night-time singing) for one male over 2 years.

Stage	n	Versatility		
		Song	Transition	Total
1980				
Prefemale	24	0.120 ± 0.0131 a <sup>1</sup>	0.103 ± 0.0155 a	0.016 ± 0.0035 a
Courtship	66	0.156 ± 0.0100 a	0.142 ± 0.0133 a	0.029 ± 0.0044 a
Night	39	0.132 ± 0.0104 a	0.119 ± 0.0156 a	0.022 ± 0.0043 a
1981				
Prefemale	32	0.195 ± 0.0136 a,b	0.169 ± 0.0142 a,b	0.039 ± 0.0058 a,b
Courtship	154	0.220 ± 0.0069 a	0.202 ± 0.0080 a	0.052 ± 0.0033 a
Night	15	0.158 ± 0.0172 b	0.136 ± 0.0220 b	0.027 ± 0.0075 b

<sup>1</sup> Values with the same letter are not significantly different within the versatility measure at the *P* = 0.05 level by Tukey's studentized range test.

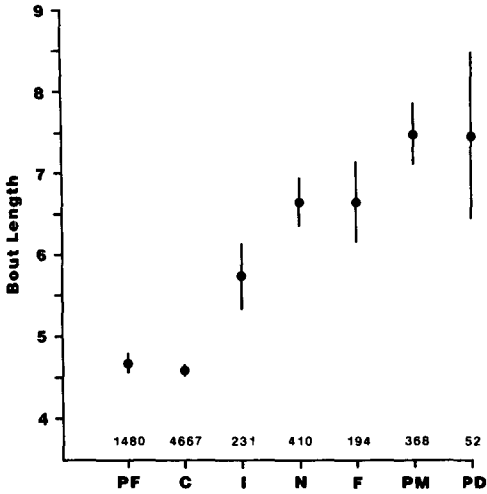


FIGURE 3. Changes in average bout length ( $\bar{x} \pm SE$ ) among seven situations (first five being breeding stages). Situations as in Figure 2. Sample sizes above abscissa.

ferred significantly ( $P < 0.001$ ) in bout length for each male. In the two males that were analyzed most intensely, date (days numbered consecutively; day 1 being March 18) was a significant factor ( $P < 0.001$ ) in determining bout length. The remaining two males were sampled over a shorter period and date was not a significant factor ( $P > 0.05$ ). Bout length did not differ ( $P > 0.10$ ) between years within each male. The amount of total variation in bout length explained by these analyses of covariance was 58.0%, 39.9%, 59.6%, and 62.9% for males A, B, C, and D, respectively.

It was deemed important to identify what determined bout length for a particular song type because bout length differed among song types. Was the bout length of a song determined individually for each song or was there a common rule or principle? The latter appears to be the case. Figure 4 shows a plot of log mean bout length (LMBOU TL) as a function of log mean duration (LMDUR; duration is the time between onset of one song and onset of its subsequent presentation within a bout) for the commonly used songs. The regression ( $LMBOU TL = -0.6923 LMDUR + 1.5816$ ) is significant ( $F = 38.61$ ,  $df = 1$ ,  $P < 0.001$ ,  $r^2 = 0.467$ ). Songs of short duration were repeated more often prior to switching than were longer songs. The slopes of the four males were not significantly different (interaction term:  $F = 0.87$ ,  $P > 0.45$ ). Male D's slope, however, did appear to be distinct. In paired

TABLE 5. Bout length: analysis of covariance results for changes in bout length among song types, between years, and across the breeding season for four male mockingbirds.

Source	Sum of squares <sup>1</sup>	df	Mean square	F
<b>Male A</b>				
Song type	32,960.29	12	2,746.69	71.93***
Year	13.54	1	13.54	0.35
Date	1,119.33	1	1,119.33	29.31***
Error	33,678.20	882	38.18	
<b>Male B</b>				
Song type	4,754.87	10	475.49	16.78***
Year	28.70	1	28.70	1.01
Date	778.41	1	778.41	27.46***
Error	9,296.87	328	28.34	
<b>Male C</b>				
Song type	849.38	10	84.94	20.73***
Year	0.97	1	0.97	0.24
Date	3.25	1	3.25	0.79
Error	618.67	151	4.10	
<b>Male D</b>				
Song type	813.97	10	81.40	23.34***
Year	1.82	1	1.82	0.52
Date	1.35	1	1.35	0.39
Error	491.70	141	3.49	

\*\*\*  $P < 0.001$ .  
<sup>1</sup> Type III sum of squares.

comparisons, the intercept for this male differed significantly from the intercepts of males A and B (least squares means;  $P < 0.05$ ), when slopes were assumed to be similar among males.

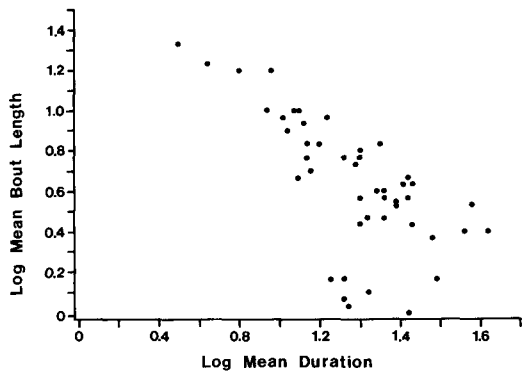


FIGURE 4. Changes in mean bout length as a function of song type duration. Thirteen most common song types used for male A, and 11 most common song types used for the remaining three male mockingbirds.



TABLE 6. Mean and standard error for recurrence intervals for seven situations.

Situation/stage	<i>n</i>	Recurrence interval
Nest building in presence of female	130	24.785 ± 1.673
Night singing	51	24.235 ± 2.738
Courtship	240	22.658 ± 1.199
Prefemale	82	21.927 ± 2.127
Nestling and fledgling	77	20.948 ± 1.969
Patrolling in presence of female	47	19.170 ± 2.118
Patrolling and countersinging	200	18.180 ± 1.292

An analysis of covariance was performed to determine the effects of bird, mean duration, and mean date (average of the dates on which a song type occurred) on mean bout length. Mean bout length differed significantly among birds ( $F = 10.84$ ,  $P < 0.001$ ), and is dependent upon mean duration ( $F = 39.57$ ,  $P < 0.001$ ), and mean date ( $F = 4.74$ ,  $P < 0.05$ ). All first-order interactions were not significant. The second-order interaction was significant ( $F = 3.07$ ,  $P < 0.05$ ) and was due to an individual bird, male D. In an otherwise identical analysis that excluded this male, all first-order interactions and the second-order interaction were not significant. Furthermore, in this analysis mean date barely missed significance ( $P = 0.06$ ) and differences among birds, while still significant ( $P < 0.05$ ) did not explain as much of the total variation in bout length as when male D was included in the analysis. The analysis of covariance which included all four males explained 76.82% of the total variation in bout length. Mean duration accounted for the largest portion of variation in bout length.

To summarize, the duration between the onset of one utterance of a particular song and the onset of its subsequent presentation within a bout was correlated with how often a song was repeated prior to switching. In other words, songs of short duration have longer bout lengths than do songs of longer duration.

Not only did bout length differ according to song duration, but individual song types also showed different trends. Bout length increased through the season (positive slope) for many song types, remained unchanged for some, and declined (negative slope) for a few song types. Overall, bout length increased as the season progressed (1980: Bout = 0.0348 Day + 0.6789; 1981: Bout = 0.0215 Day + 2.426; days num-

bered as above; both slopes and both intercepts were significantly different from zero at  $P < 0.001$ ).

#### RECURRENCE INTERVAL

Results from a two-way ANOVA revealed no significant difference among males ( $F = 0.18$ ,  $df = 3$ ,  $P > 0.10$ ) or between years ( $F = 0.01$ ,  $df = 1$ ,  $P > 0.10$ ) in the length of the recurrence interval. The interaction was not significant.

A one-way ANOVA revealed that stages (categories slightly different from above, see Methods) were significantly different ( $F = 2.27$ ,  $df = 6$ ,  $P < 0.05$ ). However, it explained less than 5% of the total variance. Furthermore, Tukey's studentized range test could not distinguish among mean recurrence intervals for the stages. Table 6 presents means and standard errors for recurrence interval of different stages. Particular groups of these stages resulted in significant difference among means as measured by Tukey's studentized range test. The combination of nest building and courtship was statistically different from the patrolling and countersinging category. Songs presented at night could not be distinguished from other categories when they were combined. However, a comparison among night song, courtship and nest building, and patrolling and countersinging did produce significant results. The mean recurrence interval of night singing could not be distinguished from that of courtship and nest building, but was significantly different ( $P < 0.05$ ) from patrolling and countersinging. I feel this was due partially to the sampling limit of only 75 successive song types because this severely limited the range over which recurrence intervals could occur. In effect, it only sampled the tail of the distribution, and gaining information from this portion alone is difficult.

If this limitation was important, I predicted that categories with larger mean recurrence intervals should have fewer recurrence intervals occurring in this tail portion (i.e., in my standardized samples). To test this I ranked the categories by number of recurrence intervals that occurred in the sample of 75 successive song types. The distribution was not random as measured by the Kruskal-Wallis H test ( $adjH = 22.31$ ,  $df = 6$ ,  $P < 0.005$ ). The courtship and nest-building categories had very few recurrence intervals per sample while the patrolling and countersinging, and song delivered at night had many recurrence intervals occurring during a

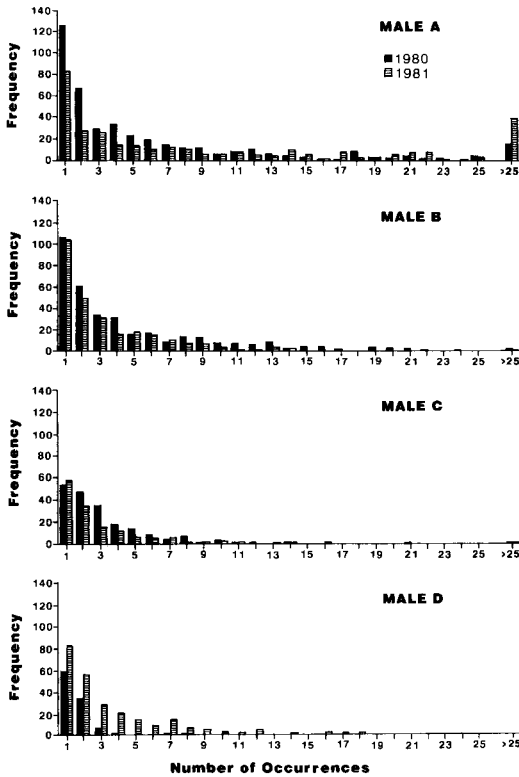


FIGURE 5. Frequency with which song types occur in the sampling of vocal behavior of four male mockingbirds during 1980 and 1981 (male A: 1980, 412 song types, 1981, 319 song types; male B: 346, 263; male C: 196, 145; male D: 102, 244).

sample of 75 successive song types. Singing behavior at night was unique, in that it had many recurrence intervals per sample but they were consistently large intervals. It appears that short recurrence intervals were avoided when singing at night.

IMPORTANCE OF RARE SONGS IN GENERATING VERSATILITY

Figure 5 shows the frequency with which song types occurred in my sampling of vocal behavior of four males during 1980 and 1981. Some song types were quite common. Many song types were recorded only once. The percent of song types that occurred only once never fell below 25, even in intensely sampled individuals.

Table 7 shows the stages in which song types recorded only once occurred, combining both years and all birds. These song types were not distributed randomly among the stages ( $G = 268.67, df = 9, P < 0.001$ ). Significantly more

TABLE 7. The frequency of occurrence of singlets (song types occurring only once in the sample) and more common song types during several breeding stages and situations.

Stage/situation	Frequency of occurrence	
	Singlets	Other
Prefemale	104	439
Courtship	305	3,093
Nest building/near nest	85	1,468
Incubation	10	84
Nestling	16	267
Fledgling	20	221
Night	3	238
Patrolling/countersinging	68	2,823
Other	78	1,392
	689	10,025

of these song types occurred during prefemale and courtship stages than would be expected if they had been distributed proportionately over all stages. In contrast, significantly fewer occurred during the patrolling and countersinging stage. These results remained when the years were analyzed separately. All males in 1980 and three of the four males in 1981 showed the same significant ( $P < 0.05$ ) nonrandom distribution of song types recorded once among stages.

DISCUSSION

VERSATILITY, BOUT LENGTH AND RECURRENCE INTERVAL

I have shown by using several descriptive measures that the manner in which a Northern Mockingbird presents his repertoire depends on the breeding stage. All versatility measures peaked during courtship. This is also the stage when bout length was shortest and recurrence interval longest, as expected for these two measures that influence versatility. Versatility declined significantly during incubation and then slowly increased during nestling and fledgling stages. Bout length showed a different pattern. It rose gradually as the season progressed, being shortest during courtship and longest during the fledgling stage. Recurrence interval was shorter during the nestling and fledgling stage than during the prefemale and courtship stages.

Overall, these patterns result in the greatest number of song types being presented per unit of time during courtship. This is also the stage when mockingbirds sing the most (Logan 1983, pers. observ.). That these changes are centered on the courtship stage provides circumstantial

support for the hypothesis that song functions intersexually in mockingbirds. Presentation of the repertoire during subsequent stages is altered, possibly emphasizing other functions, by repeating songs more often before switching (longer bout lengths), and by repeating separate bouts of each song with fewer intervening song types (i.e., shorter recurrence interval).

The most drastic change in singing behavior occurs during the nest-building period. The nest is built by both sexes (Goodpasture 1908; Laskey 1935, 1962; Gage 1961). At my study site, males construct the outside portion of the nest by depositing many twigs at potential nest sites. Several nests may be initiated by a male before his female begins to assist, and she builds the inner cup from dried grass and rootlets. The male's presentation of his repertoire changes most dramatically once the female has committed herself to a breeding attempt by assisting in nest building.

Mockingbirds alter the versatility of song presentation in part by changing bout length. A similar mechanism has been described for the Eastern Meadowlark (*Sturnella magna*, d'Agincourt and Falls 1983), and is probably used to alter the versatility of the singing behavior of Sedge Wrens (*Cistothorus platensis*) and Marsh Wrens (*C. palustris*, Kroodsma and Verner 1978).

A second mechanism to increase the versatility of singing behavior is to increase the recurrence number. This can be done in two ways. One, a bird could sing in long stereotyped sequences, thus interposing the majority of its other song types between renditions of a given song. Mockingbirds do increase the recurrence interval by avoiding a quick return to a given song type, but they do not push this to Marsh Wren-like extremes by resorting to fixed sequences.

A second method, not yet described in any other species, involves singing novel song types. The percent of song types occurring only once never fell below 25. There are several possible explanations for this high percentage of song types occurring a single time. First, they may represent mistakes by the bird. Second, they may be misclassifications by me. Third, song types occurring once could be attributed to improvisation during song learning periods. Finally, these rare song types could function in generating versatility. All four factors could be involved to varying degrees. To estimate their relative importance I predicted when these song types would be expected to oc-

cur during the breeding season for each possible explanation. If they represented mistakes, either by the bird or by myself, they should occur randomly throughout the season (i.e., proportionately to the number of songs sampled in the different stages). If they were attributed to song learning, they should be more common early or late since song development appears to be controlled physiologically (Nottebohm 1968). If song learning is a continuous process in mockingbirds (Derrickson 1985), then song types recorded only once should occur randomly throughout the breeding season. If, on the other hand, they are employed by males to increase versatility, they should occur in association with specific events in which versatility is high. The last is the case. Mockingbirds sang these song types most commonly during prefemale and courtship periods. Use of these singly or, at least, rarely-performed song types increased the recurrence interval and thereby increased the versatility. Therefore, I feel these song types function to generate versatility.

In mockingbirds, bout length is negatively correlated with the durations of the song. For song types of short duration, the song may be repeated many times prior to switching. Conversely, for the longest songs, bout length may be reduced to only one or two renditions. This correlation implies that mockingbirds are using the total time interval over which a song is sung (i.e., bout duration, as distinct from what I am calling bout length, which measures the number of repetitions of a given song type within a bout) as at least one factor governing when a new song should be introduced.

Seasonal changes in bout length could be accounted for as follows. Early in the breeding season all bouts, even of different song types, are approximately equal in duration. A song type's bout length is determined by how many renditions can be sung in that time interval. As the season progresses this time interval increases, allowing more renditions to be uttered, thereby generating longer bout lengths (more songs/bout). The rate at which a particular song type's bout length changes through the season is dependent, in part, on the song's duration. Since songs differ in duration they will also differ in the rate at which their bout length increases over the breeding season. More specifically, I would predict that briefer songs would change through the season at a faster rate.

An alternative explanation involves singing

briefer songs preferentially later in the season. The bout length could be increased in this fashion without altering the average duration of bouts and thus the time allocated to each type. There was no seasonal trend in the duration of preferred songs. Regression analyses performed for each bird in both years resulted in slopes that were not significantly ( $P > 0.10$ ) different from zero.

Two caveats should be mentioned. First, obtaining estimates of recurrence intervals can be difficult. A bird with a large repertoire singing with eventual variety commonly has recurrence intervals that exceed 100 song types. Therefore, to depict accurately the recurrence interval distribution would require sampling extremely long sequences of songs. Such sequences occurred only six times in my data. To determine how recurrence intervals differed among breeding stages required the use of shorter sequences, thus effectively eliminating the righthand portion of the distribution. From the remaining portion of the distribution, I not only compared mean recurrence interval for the various stages from the sequences set at 75 successive song types, but also monitored the number of recurrence intervals occurring during each sequence (see Results). This analysis showed that, in comparison to other stages or situations (especially patrolling and countersinging), courtship singing had fewer recurrence intervals occurring during sequences of 75 successive song types. Further, those that did occur were longer.

Second, ANOVAs consistently explained 20% or less of the total variance. Occasionally analyses performed on individual males explained up to 60% in a given year. Similar analyses performed on the versatility measures and bout length by d'Agincourt and Falls (1983) on the Eastern Meadowlark's smaller repertoire (50 to 100 song types) explained approximately 80% of the total variance.

The large variation with which mockingbird males present their song repertoire could be due to two mutually compatible factors. First, high variance may be an inherent feature of presenting a very large repertoire. Northern Mockingbirds have well over 150 song types and these are very diverse in structure (Wildenthal 1965; Derrickson 1985, 1987b). The smaller repertoire and acoustically simpler songs might allow Eastern Meadowlarks to regulate (i.e., show less variance in) their singing behavior more closely than can mockingbirds. Second, the methodology (cer-

tainly the number of utterances analyzed per sample) used to estimate versatility was more appropriate for the singing behavior of Eastern Meadowlarks. Eastern Meadowlark songs are approximately five times the duration of mockingbird song types and show much less variation in duration among songs. Furthermore, mockingbirds sing more continuously, producing more songs in a given time. In mockingbirds, brief songs are repeated more often within a bout than longer songs, introducing much variation into the measures of versatility, which are based on the number of repetitions and take no account of time.

If my data were organized temporally and the arbitrary "intervals" for calculating versatility were based on time instead of number of songs sampled, total variation would probably decrease and more of the total variance would be explained in the ANOVAs. Furthermore, a temporal interval would be a more appropriate measure, since birds themselves probably measure diversity over time instead of during an arbitrary number of songs.

#### INDIVIDUAL DIFFERENCES

All males that acquired mates and bred showed a similar pattern in the changes in versatility of their singing behavior over the breeding season. However, individual males did differ in song, transition, and total versatility measures. In addition, males differed in bout length but not recurrence interval. This partially could be due to some males being sampled later in the breeding season when bout lengths are longer.

Wildenthal (1965) showed that the mean bout lengths of two individuals differed. A mockingbird from Kansas had a mean bout length of 7.0 while a mockingbird from Florida had a mean of only 5.6. While this could be due to population or geographic differences, another possible explanation is seasonal or situational differences in sampling. Her Florida mockingbird was recorded in March (some song recording might have been done as late as May). The Kansas bird was recorded later, in June to July, which could account for its larger mean bout length.

The males I studied acquired mates and began to nest in the same order as their versatility measures (arranged high to low) and bout length (low to high). These results suggest that the most versatile songsters acquire females and initiate nesting first. However, because of the limited sample

size this relationship is at this point strictly suggestive and requires further study.

#### PRESENTATION DURING SPECIFIC SITUATIONS

Songs sung at night were presented in a fashion more similar to the presentation of song during the prefemale stage than singing at any other stage. Interestingly, singing at night is characteristic of unmated males. Song, transition, and total versatility did not differ statistically between these two situations, but did differ significantly from other stages of the breeding season. However, versatility was produced in different ways. During the prefemale stage bout length was short and the recurrence interval intermediate in relation to other stages. In contrast, night singing was typified by the longest bout lengths and large recurrence intervals; its versatility arose from the latter.

Mean recurrence interval also differed between male-female and male-male interactions. In male-male interactions the recurrence interval was at its lowest value. This was in contrast with night singing and prefemale stages, during which intersexual aspects were most likely emphasized. In addition, countersinging situations had the second highest mean bout length (calculated from entire data set). Again, this could be due partially to more countersinging occurring late in the breeding season when bout lengths were generally longer regardless of activity.

A number of species have been observed to increase switching (reduce bout length) during agonistic encounters (Plain Titmouse, *Parus inornatus*, Dixon 1969; Sedge Wren, Kroodsma and Verner 1978; Bewick's Wren, *Thryomanes bewickii*, Kroodsma 1977; Western Meadowlark, *Sturnella neglecta*, Falls and d'Agincourt 1982), during courtship (Red-winged Blackbird, *Agelaius phoeniceus*, Smith and Reid 1979), or during both situations (Eastern Meadowlark, Falls and d'Agincourt 1982). An increase in switching during courtship is the pattern observed in Northern Mockingbirds. In the case of mockingbirds, the relatively long distance between established male neighbors may require more redundancy to improve detectability (Wiley and Richards 1982). Moreover, mockingbirds will match (the temporally associated singing of acoustically similar song types by both males) during these countersinging sessions. Longer bout lengths provide more time for neighboring males

to respond with the same song type (Ince and Slater 1985), thus providing accurate distance information through the use of degradation assessment mechanisms and in this way more effectively threaten one another (Morton 1986).

The organization of Northern Mockingbird singing is not explained simply as an antihabituation procedure. The singing behavior is consistent with the antihabituation hypothesis (Hartshorne 1956, 1973) and also with the hypothesis proposed by Catchpole (1982) and Ince and Slater (1985) that continuous and varied song evolved through sexual selection to attract mates, while the major role of discrete and simple songs is in communication between males. Interestingly, although Ince and Slater (1985) used these singing behavior patterns to differentiate among *Turdus* species, both patterns occur in the mockingbird. Early in the breeding season a male mockingbird sings varied song and sings continuously (Logan 1983, pers. observ.). When males are countersinging with each other, typically later in the breeding season, they sing with less versatility and less continuously. Furthermore, information about mated status and nesting stage of a singing male is provided by changes in the manner in which a repertoire is presented. In addition, these differences in presentation can provide information about the current activity (courtship vs. patrolling) of the singing male.

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