

Ethology, 74, 21—32 (1987)
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ISSN 0179-1613

Department of Biology, University of Pennsylvania, Philadelphia

Behavioral Correlates of Song Types of the Northern Mockingbird (*Mimus polyglottos*)

KIM C. DERRICKSON

Received: April 7, 1986

Accepted: June 22, 1986 (W. Wickler)

Abstract

The primary songs of four male northern mockingbirds (*Mimus polyglottos*) were recorded along with simultaneous descriptions of behavior. Individual song types were identified spectrographically and the more commonly occurring song types in their extensive repertoires investigated for behavioral correlates. For each male, song types were distributed non randomly between categories in two behavioral dichotomies; flight versus non-flight and associating with mate versus not associating.

In species in which individuals possess large song repertoires, it commonly is assumed that all song types provide the same information. This appears not to be the case in northern mockingbirds. The difficulties in documenting behavioral correlates of song types are discussed and the various ways male mockingbirds make information available are described. These various aspects of singing differ in the specificity of information they make available and should require different time investments by the recipient to comprehend.

Introduction

Behavioral correlates for many visual displays have been well documented (see SMITH 1977, chap. 5 for review). Relatively few studies have considered the relationship between behavior and vocal displays. Although most of these studies investigate simple vocalizations such as call notes, some have studied more complex vocalizations (SMITH 1969; MORSE 1970; LEIN 1972, 1978; SMITH et al. 1978; SCHROEDER & WILEY 1983). The consensus on species in which individuals possess large repertoires is that different song types are fully redundant in the information they make available (LEMON 1971; FALLS & KREBS 1975; KREBS 1977; YASUKAWA et al. 1980). In other words, each song type is assumed to provide the same information as each other song type.

In this paper, I ask if particular song types correspond differentially with specific behavior patterns in a species, the northern mockingbird (*Mimus polyglottos*), in which individuals have extraordinarily large song repertoires. Esti-

mates of repertoire size range from 43 song types to 244 song types (WILDENTHAL 1965; HOWARD 1974; song type synonymous with "syllable pattern" of these earlier publications). Individuals I have studied have repertoires of approximately 180 distinct song types (DERRICKSON 1985). For each of four males I investigated, the common song types are not distributed randomly between categories in two behavioral dichotomies: flight versus non-flight and associating with mate versus not associating.

Methods and Procedures

Study Location

The singing behavior of 6 to 10 male northern mockingbirds was monitored each year from 1979 through 1982 at Tyler Arboretum, Lima, Pennsylvania. Approximately half of the males were banded with distinct color combinations of plastic leg streamers. I generally used the focal individual sampling technique (ALTMANN 1974; DUNBAR 1976; PAYNE & PAYNE 1977) to obtain up to a 1 h sample of singing for each male. Each male was observed in a random order during the course of the day. Occasionally, behavioral and situational circumstances did influence the order in which males were observed.

The majority of observations were made between ½ h before sunrise and noon. Occasional observations were made during the afternoon, evening, and night. The study site habitat was a grass field planted with widely spaced dogwoods (*Cornus*), spruce (*Picea*), cedars (*Thuja*), pines (*Pinus*), and holly (*Ilex*); described in more detail in DERRICKSON (1985, subm.).

Equipment and Song Type Identification

Recordings of vocalizations were made with a Marantz Superscope CD-330 professional dual-track cassette tape recorder and a Gibson P-200 parabolic microphone. A Superscope model E-5 cardioid microphone was used to concurrently record a continuous description of the bird's behavior, location, orientation and other contextual information. Major behavioral categories recorded included foraging, comfort movements, locomotion, agonistic behavior, and sexual behavior. Each of these major categories was subdivided; for example, the locomotion category included walking, running with wings folded, running with wings extended, "jump flights" (GOODPASTURE 1908; HARRINGTON 1923; LASKEY 1933; TOMKINS 1950), just took flight, gliding flight, normal flight, landing and flight intention movements such as crouching and dropping wings.

Spectrographic analyses of songs were restricted to four males that were present in both 1980 and 1981 (DERRICKSON 1985, subm.). These birds were well sampled and three of the four were neighbors in both years.

Sonagrams from a Kay Elemetrics Corp. model 6061B sona-graph (wide band filter of 300 Hz, high shape setting) and hard copies from a Princeton Applied Research real time sound spectrum analyzer model 4212F and EPC hard copy recorder were used to construct a directory of song types for each male. A song type is defined as a single vocalization or a group of vocalizations in which the time interval between the units of the group are shorter than the time interval between groups, and which is uttered in a consistent form on every occurrence by a particular individual. These song types are organized into bouts in which each song type is repeated a few times prior to switching to another song type. An identification number was assigned to each song type for each male independently. Thus, song type 603 for one bird is not necessarily the same song as 603 for another bird. Using the directory, song types were identified by using a Unigon scan converter with the real time analyzer. A fuller description of the procedures is provided elsewhere (DERRICKSON 1985, subm.). Other information associated with the vocalizations was obtained from the tape recorded notes, including the date and time, and location, orientation and concurrent behavior of the singing individual.

The number of song types recorded from the four males over the two years ranged from 218 to 512 (South, 512; Far East, 436; GfR, 218; Barn, 310). The singing behavior of South and Far East was the most completely analyzed and accounts, in part, for the higher values attributed to them. For all

individuals, many of the song types were exceedingly rare. For all males in both years, more than 25 % of the song types identified occurred only once in my analysis. This occurred even in the most completely analyzed individual, South, in which 2698 and 3358 bouts were analyzed in 1980 and 1981, respectively. Therefore, to maintain adequate sample sizes for statistical tests (cut offs determined by inspecting the contingency table of all song types so as to maintain adequate cell values) it was necessary to use only the frequently occurring song types (≥ 31 , 12, 10 and 10 occurrences in the singing of South, Far East, GfR and Barn). Hence, 55, 54, 21, and 13 song types were used in the analyses for South, Far East, GfR and Barn, respectively.

Two behavioral dichotomies, flight versus non-flight and associating with mate versus not associating, generally had adequate sample sizes for statistical comparisons. The flight category included all songs that occurred during both normal (traveling) flight and "jump flights" (GOODPASTURE 1908; HARRINGTON 1923; LASKEY 1933; TOMKINS 1950). These all occurred within the territory. I initially planned to analyze these two subcategories separately, but small sizes required that they be combined for this preliminary analysis. The non-flight category included all songs occurring when not in flight. Associating with mate was defined operationally as the male singing within approx. 5 m of the female regardless of the female's behavior or location within the territory. Generally, but not consistently, the male was oriented toward the female. Typically, he would follow her if she moved. All songs occurring when the male was greater than 5 m away from the female were categorized as not associating.

Analyses

The log likelihood ratio test (G-statistic; SOKAL & ROHLF 1969) was used in the test of independence for all contingency tables (song types \times behavioral dichotomy categories). Also, the G-statistic was used to test the frequency of occurrence of *each* song type in the behavioral categories against the overall expected frequency of occurrence of the behavioral categories (all song types combined).

Results

Table 1 presents the frequency of occurrence of common song types in the two dichotomies for four male mockingbirds. The song types are not distributed randomly between the flight and non-flight categories in the three males with adequate sample sizes (South: $G = 193.64$, $df = 54$, $p < 0.001$; Far East: $G = 123.85$, $df = 53$, $p < 0.001$; Barn: $G = 38.99$, $df = 12$, $p < 0.001$). The remaining male, GfR, had too few flights to do any statistical testing.

Similarly, the song types were not distributed randomly between the associating and not associating with mate categories in the three males analyzed (South: $G = 105.87$, $df = 54$, $p < 0.001$; Far East: $G = 83.10$, $df = 53$, $p < 0.01$; GfR: $G = 38.57$, $df = 20$, $p < 0.02$). Statistical testing of Barn was precluded since I have not completed the analysis for the period after he paired.

Each song type was compared separately to the overall frequency of occurrence of the behavior patterns for each male using the log likelihood ratio test (G statistic; SOKAL & ROHLF 1969). In each male analyzed, there were particular song types that were used significantly more often than expected as the bird flew. Other song types occurred significantly less often in flight than expected. For example, of the 55 song types analyzed for South, 8 were positively and 11 negatively associated with flight. Similarly, 6 of the 54 song types analyzed for Far East were positively correlated with flight and four negatively. For Barn, two song types were associated positively and three negatively of the 13 song types.

Table 1: The frequency of occurrence of common song types (arranged in decreasing order of occurrence for each male) in two behavioral dichotomies, flight versus non-flight and associating with mate versus not associating, for four male northern mockingbirds. p-value obtained from G statistic comparing each song type's distribution to the overall frequency of occurrence of the behavior patterns within each male. Blank p-value represents not significant, (+) song type occurs significantly more frequently than expected, (-) song type occurs significantly less frequently than expected

Song ID	Frequency		p-value	Frequency		p-value
	Flight	Non-Flight		Assoc.	Not Assoc.	
South						
603	24 (+)	69	< 0.001	18	75	
525	21 (+)	69	< 0.005	15	75	
220	12	75		19	68	
070	2 (-)	69	< 0.01	16	55	
159	3 (-)	66	< 0.05	19	50	
073	8	61		19	50	
155	8	56		16	48	
523	13 (+)	49	< 0.05	9	53	
500	5	57		21 (+)	41	< 0.025
530	12 (+)	46	< 0.05	5 (-)	53	< 0.025
261	4	54		10	48	
208	3	55		6 (-)	52	< 0.05
511	1 (-)	55	< 0.01	9	47	
506	2	49		12	39	
206	3	48		10	41	
108	10	41		11	39	
218	4	43		11	36	
023	6	41		5	42	
328	3	43		15	31	
272	1 (-)	42	< 0.05	7	36	
600	5	37		9	33	
286	2	40		6	36	
539	3	38		11	30	
535	6	35		5	36	
080	0 (-)	41	< 0.005	8	33	
228	9 (+)	31	< 0.05	10	30	
544	6	33		15 (+)	24	< 0.025
501	3	36		9	30	
156	1 (-)	38	< 0.05	8	31	
518	4	34		6	32	
327	7	31		6	32	
281	3	35		6	32	
154	3	35		13	25	
022	3	35		12	26	
294	7	30		6	31	
244	8	29		11	26	
534	3	33		17 (+)	19	< 0.001
400	0 (-)	36	< 0.005	11	25	
309	0 (-)	35	< 0.005	8	27	

Table 1: Continued

Song ID	Frequency		p-value	Frequency		p-value
	Flight	Non-Flight		Assoc.	Not Assoc.	
152	4	31		1 (-)	34	< 0.005
038	2	33		7	28	
909	12 (+)	22	< 0.001	4	30	
201	1	33		8	26	
081	0 (-)	34	< 0.005	9	25	
057	5	29		8	26	
026	2	31		2	30	
926	0 (-)	32	< 0.01	2 (-)	30	< 0.025
900	9 (+)	23	< 0.01	4	28	
550	2	30		5	27	
524	2	30		13 (+)	19	< 0.025
221	13 (+)	19	< 0.001	6	26	
507	3	28		3	28	
227	1	30		5	26	
092	0 (-)	31	< 0.01	6	25	
062	3	28		10	21	
Far East						
022	2	47		20	28	
266	1	37		19	19	
203	0 (-)	36	< 0.025	22	14	
406	0 (-)	34	< 0.025	24 (+)	10	< 0.005
082	1	28		15	13	
600	7 (+)	20	< 0.005	11	16	
506	2	25		6 (-)	20	< 0.025
528	0 (-)	26	< 0.05	16	10	
527	0 (-)	26	< 0.05	12	14	
280	1	24		11	14	
006	2	22		11	13	
408	0	23		17 (+)	6	< 0.005
405	5 (+)	18	< 0.05	5 (-)	17	< 0.05
017	1	22		7	16	
315	3	19		8	14	
014	0	22		10	12	
525	0	21		11	10	
512	0	21		10	11	
262	4	17		6	14	
251	1	20		11	10	
073	4	17		8	13	
400	3	17		10	10	
213	0	20		7	13	
533	6 (+)	13	< 0.005	4 (-)	15	< 0.05
281	2	17		9	10	
226	1	18		10	9	
153	0	19		7	12	

Table 1: Continued

Song ID	Frequency		p-value	Frequency		p-value
	Flight	Non-Flight		Assoc.	Not Assoc.	
580	2	16		9	9	
513	4 (+)	14	< 0.05	7	11	
403	1	17		8	10	
089	0	18		7	11	
806	0	17		11	6	
205	2	15		6	11	
202	0	17		6	11	
021	0	17		6	11	
532	4 (+)	12	< 0.05	2 (-)	14	< 0.01
284	0	16		7	9	
815	3	12		7	8	
800	1	14		7	8	
610	0	15		5	10	
575	1	14		9	6	
534	0	14		8	6	
409	1	13		4	10	
216	0	14		9	5	
212	2	12		3	11	
208	0	14		6	8	
150	0	14		8	6	
522	4 (+)	9	< 0.025	5	8	
268	0	13		9	4	
263	2	11		8	5	
214	0	13		2	11	
057	2	11		5	8	
013	1	12		6	7	
010	2	11		7	6	
GfR						
527	0	17		7	10	
400	0	17		9	8	
280	0	16		7	9	
052	1	15		12	4	
408	0	15		10	5	
070	1	14		5 (-)	10	< 0.05
602	0	14		6	8	
406	0	14		5	9	
057	0	14		6	8	
411	1	12		9	4	
403	0	13		8	5	
807	0	12		9	3	
224	0	12		10	2	
203	0	12		10	2	
806	1	9		4	6	
601	0	10		7	3	

Table 1: Continued

Song ID	Frequency		p-value	Frequency		p-value
	Flight	Non-Flight		Assoc.	Not Assoc.	
286	0	10		9 (+)	1	< 0.05
221	0	10		6	4	
201	0	10		5	5	
089	0	10		8	2	
050	0	10		9 (+)	1	< 0.05
Barn						
504	5	13				
400	1 (-)	17	< 0.025			
054	6	11				
541	7	9				
219	6	8				
524	7 (+)	6	< 0.05			
603	1	11				
557	7 (+)	5	< 0.025			
079	1	11				
070	2	9				
008	0 (-)	11	< 0.01			
538	0 (-)	10	< 0.025			
410	4	6				

At the same time, there were particular song types that were used significantly more often than expected when associating with a mate. Conversely, other song types were used significantly more often than expected when not associating with a mate. This was consistent among all males. For example, of the 55 song types analyzed for South, four were used significantly more and four less often when associating with his mate. In Far East, two of 54 song types were used more often when associating with his mate and four less. For GfR, two of the 21 song types were used significantly more often while one song type was used less frequently.

6 of the 143 song types showed a significant departure from expected values in both dichotomies; two for South and four for Far East. Four of the 6 were positively correlated with flight and negatively correlated with associating with mate. Of the remaining two, one song type was negatively correlated with flight and associating with mate and the remaining song type was negatively correlated with flight and positively correlated with associating with mate.

When analyzing a large number of song types for behavioral or situational correlates, a proportion of them would deviate significantly from expected values solely due to chance. (For example, 5 % at a significance level of 0.05.) Table 2 summarizes the significance levels obtained for the song types of the four males in both dichotomies. Within each male in both dichotomies, consistently over 10 % of the song types showed a significant departure from random expectations. For

Table 2: Summary of the significance levels (numbers are cumulative totals) obtained for the song types of four male northern mockingbirds in two dichotomies, flight versus non-flight and associating with mate versus not associating. Percentage of song types showing a significant departure ($p < 0.05$) from random expectations are in parentheses

	< 0.001	< 0.01	< 0.05	n.s.	Total number Song types
a. Flight versus Non-flight:					
South	3	13	19 (34.55)	36	55
Far East	0	2	10 (18.52)	44	54
GfR	0	0	0	21	21
Barn	0	1	5 (38.46)	8	13
b. Associating with mate versus not:					
South	1	2	8 (14.55)	47	55
Far East	0	3	6 (11.11)	48	54
GfR	0	0	3 (14.29)	18	21

example, for the flight dichotomy, between 18.5 % and 38.5 % of the song types within a male had a departure from expected values at a significance level of less than 0.05. Furthermore, certain song types departed from random expectations at significance levels less than 0.001 — a very unlikely random event. Therefore, results obtained in this study are not simply artifacts of the large number of comparisons.

Discussion

The significance of song repertoires has received much attention. Many investigators describe how the presentation of the repertoire (birds can vary how a repertoire is presented by altering the bout length or recurrence intervals of each song type) differs among stages of the breeding season or in different social situations. For example, large repertoire size augments the versatility of singing behavior during certain breeding stages in the sedge warbler (*Acrocephalus schoenobaenus*: CATCHPOLE 1980), marsh warbler (*A. palustris*: LEMAIRE 1974), eastern meadowlark (*Sturnella magna*: D'AGINCOURT & FALLS 1983), and northern mockingbird (DERRICKSON 1985, subm.). YASUKAWA et al. (1980) thought this might occur in the red-winged blackbird (*Agelaius phoeniceus*), in which males of some populations have approximately five different songs. Changes in singing behavior among different social situations have been documented for the red-winged blackbird (SMITH & REID 1979), sedge wren and Bewick's wren (*Cis-tothorus platensis*; *Thryomanes bewickii*: KROODSMA 1977), eastern meadowlark and western meadowlark (*Sturnella neglecta*: FALLS & KREBS 1975; FALLS & D'AGINCOURT 1982), yellow-throated vireo (*Vireo flavifrons*: SMITH et al. 1978), warbling vireo (*Vireo gilvus*: HOWES-JONES 1985), tufted titmouse (*Parus bicolor*: SCHROEDER & WILEY 1983), plain titmouse (*Parus inornatus*: DIXON 1969), northern cardinal (*Cardinalis cardinalis*: LEMON 1968), and northern mockingbird (DERRICKSON 1985, subm.).

Other authors have suggested that having more song types facilitates individual recognition (ARMSTRONG 1963; EMLEN 1971; LEMON 1971; GOLDMAN 1973; BROOKS & FALLS 1975 a, b), lessens individual recognition (KREBS & KROODSMA 1980; FALLS 1982) or facilitates vocal interactions with neighbors (KROODSMA 1979).

KREBS (1977) reviewed "the major current hypotheses which have been put forward to explain the apparently redundant song repertoires of many oscine birds" and added another, the Beau Geste hypothesis, in which individuals misrepresent the density of territorial males by singing a repertoire. Other authors have also assumed that the different song types are fully redundant in the information they make available to recipients and emphasize that information is provided by the rate of singing or pattern of presentation. For example, FALLS & KREBS (1975, pp. 1176—1177) state, "since the different song types usually carry the same message, why the need for so much redundancy?" Similarly, KREBS (1977, p. 475) noted that "in most cases (an exception: MORSE 1970) it seems that all the songs in a repertoire carry the same message — they are used at the same time of year and in the same contexts — so that the variability in song appears to be redundant." Undoubtedly this is true for some species. For example, it appears to be in the Carolina wren (*Thryothorus ludovicianus*: SIMPSON 1985). However, I caution against tacit acceptance of this assumption for species in which individuals have large repertoires. I feel the lack of evidence for behavioral or situational correlates with particular song types may be attributable to our inability to define correctly the situations and behavior patterns that are biologically important to the birds. Even if correctly identified, adequate sample sizes of renditions of song types and occurrences of particular behavior patterns or situations are hard to obtain. This sampling problem becomes awesome in species in which males have large repertoires. To maintain sample sizes adequate for statistical evaluation required extensive sampling of the singing behavior (over 10,000 bouts analyzed) of a few individual males. In addition, analyses were limited to a subset of the song types (the most commonly occurring song types) and two obvious dichotomies, flight versus non-flight and associating with mate versus not associating.

In the northern mockingbird, a species in which males have very large repertoires, I have shown that the utterance of some song types is correlated with, but not restricted to, particular kinds of behavior: flight or associating with mate. Providing information about concurrent or future behavior should be advantageous to both signaller and recipients in these situations. For example, information about potential or actual movements of a neighboring territorial male makes it less urgent to investigate a male subsequently singing from a new location in the same general area since it is *probably* still your neighbor. Responding inappropriately to your neighbor's new location by flying toward the singing male wastes time and energy and could increase the likelihood of injury to either individual if a fight were to occur.

No obvious differences in structural detail or complexity were apparent when song types frequently occurring in one category were compared visually to the song types frequently occurring in the other category of the dichotomy. This

was true of both dichotomies. Also, in both dichotomies, the average duration of song types in the two categories did not differ. Suggestively, within each male's song some similarities were noticed. For example, within each male the number of component parts and frequency changes in song types appear to be similar within a category and different from characteristics typical of the song types in the other category. However, these are not consistent among males. More detailed analyses are required.

A male mockingbird makes information available in several ways as it sings: through the fashion in which a male mockingbird presents its repertoire, how much it sings, and the particular song types sung. A northern mockingbird can vary the presentation of its repertoire by altering the number of times a given song type is repeated prior to switching to another song type and by changing the sequence of song types. The manner in which a mockingbird presents its repertoire varies seasonally. Males sing in a way that produces the highest diversity of songs in a given time interval during the courtship period. The singing behavior becomes less diverse when a female begins to assist in nest building, or in other words, makes a commitment to the male. Other breeding stages and situations are also typified by distinct singing behavior (DERRICKSON 1985, *subm.*). LOGAN (1983) showed that the amount of song increased substantially while the male was nest building and decreased significantly during incubation and care of offspring. This pattern was repeated on subsequent nesting attempts — of which there may be many during a breeding season. Additional information is made available by the transitions between certain song types. The sequencing of song types in mockingbird song is not completely random (DERRICKSON 1985). Transitions between particular song types occur more frequently than expected. Such transitions are common and noticeable features of the singing behavior. The song types used in them differ among males and thus, could provide information about individual identity. Finally, as shown here, at least some song types differentiate between categories of behavior. Thus, the singing behavior of northern mockingbirds provides much information. However, just how informative all this is to other mockingbirds remains to be shown.

Interestingly, comprehension of the information made available by these different aspects of singing should require different time investments by the recipient. For example, the approximate amount of time another male is singing can be obtained easily and it provides some information about the stage of nesting even to recipients with no previous knowledge of particular song types. To estimate singing versatility would require more attention be paid to transitions among song types and therefore, probably would require a larger investment in time than required to estimate amount of singing. However, more information would be potentially attainable. Finally, if it is necessary to learn the association between particular song types and behavior patterns the largest investment of time would be needed since not only must individual song types be recognized but the singer's concurrent behavior must be monitored. But potentially the most detailed information about another's behavior or future behavior could be obtained, thus allowing for more efficient interactions.

The potential costs and benefits of investing the time learning (assumption, see next paragraph for alternative possibility) these associations is unknown. However, for long-lived species in which males maintain or return to the same territories, as in the northern mockingbird, the cost of the initial investment in time and energy may be small in comparison to the benefits received by the more efficient handling of interactions with well established "known" neighbors. That the song types appear to be "faithful" to their particular behavioral association between years (no obvious reversals in behavioral association in the common song types; however, small samples preclude statistical testing) would be such a benefit to an old neighbor. This might also explain why the amount of singing increases and particular behavior patterns occur more often when a new territorial neighbor first appears as compared to when old neighbors reoccupy the same territories. For example, the jump flight occurred at a very low frequency when the three neighboring males returned to their respective territories in 1980. When new males began to occupy some of these territories in 1981 and 1982, the incidence of jump flights increased.

On the other hand, the correlates of particular song types need not be learned by the recipient. If there are species-specific rules such that a northern mockingbird is born knowing that song types with particular characteristics are associated with flight while those song types with other characteristics predict associating with mate, then the investment by the recipient is limited to learning the song types of the neighbor and possibly attending to the sequencing of song types. Thus the behavioral correlates of this paper may be either the most expensive (if correlates learned) or the least expensive information to garner (species-specific rules).

Acknowledgements

This research was supported by a NIH Theoretical Biology Training Grant NIH T32GM07517, a Frank M. Chapman Grant in Aid of Ornithological Research, the Department of Biology, University of Pennsylvania, the National Zoological Park, and a Smithsonian Postdoctoral Fellowship. I wish to thank W. John SMITH and Eugene MORTON for their critical comments on earlier drafts of the manuscript along with Richard D. HOWARD and an anonymous reviewer for further constructive suggestions. I also thank the administration and staff of Tyler Arboretum, Lima, Pennsylvania for their cooperation and assistance.

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Author's address: K. C. DERRICKSON, Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008 U.S.A.