

SPECIES RECOGNITION IN A VOCAL MIMIC: REPETITION
PATTERN NOT THE ONLY CUE USED BY NORTHERN
MOCKINGBIRDS IN DISCRIMINATING SONGS OF
CONSPECIFICS AND BROWN THRASHERS

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ABSTRACT.—Vocal mimics that produce large repertoires of song types, such as in the Mimidae, have unique challenges discriminating songs of conspecifics from those of other mimids in areas where these species co-occur. We investigated cues used by Northern Mockingbirds (*Mimus polyglottos*) in discriminating their songs from songs of a sympatric mimid, the Brown Thrasher (*Toxostoma rufum*). We presented territorial mockingbirds with four playback treatments in which either mockingbird song types or thrasher song types had either a standardized mockingbird repetition pattern (5 repetitions) or a standardized thrasher pattern (2 repetitions). Four measures (time within 2 m of speaker, latency to approach, closest approach, and number of flights) were used to estimate a subject's response to each playback. Subjects responded significantly more strongly to mockingbird song types in a mockingbird repetition pattern than to thrasher song types in either repetition pattern. Responses to mockingbird song types in a thrasher repetition pattern elicited intermediate responses. Thus, mockingbirds can distinguish conspecific songs from Brown Thrasher songs based on song types alone regardless of their repetition pattern, although repetition pattern still appears to have a role in conspecific recognition. Brown Thrasher song includes a significantly broader frequency range than mockingbird song, which may allow direct discrimination. Our results suggest cues used by mimids in species discrimination are not necessarily the same as those used by human observers. Received 29 October 2007. Accepted 23 April 2008.

Discriminating songs of conspecifics from vocalizations of other species is fundamentally important for territorial songbirds. This discrimination in many species is facilitated by vocal features shared by individuals within a species but distinctive from sympatric species (reviewed in Becker 1982, Catchpole and Slater 1995, Marler 2004). The structure of many species' songs, despite variation across broad geographic ranges and even between neighboring conspecifics, is easily recognized by certain species-distinctive characteristics (e.g., Walton et al. 2002, Kroodsma 2005). Discrimination in songbirds that regularly mimic the sounds of other species is not as easy (Baylis 1982). Species discrimination is likely to be especially challenging between vocal mimics that produce large repertoires of song types, particularly when multiple mimicking species include imitations of the same sounds in their repertoires.

Northern Mockingbirds (*Mimus polyglottos*) and Brown Thrashers (*Toxostoma rufum*),

Family Mimidae, provide an interesting illustration of the potential difficulties that different vocal mimics have in discriminating between each other's songs. Both species are highly versatile singers with large song repertoires (~100–400 song types/individual in mockingbirds: Wildenthal 1965; Merritt 1985; Derrickson 1987, 1988; >1,000 song types/individual in Brown Thrashers: Kroodsma and Parker 1977, Boughey and Thompson 1981), and repertoires of both species can include imitations of the same sounds (Boughey and Thompson 1976). Northern Mockingbirds and Brown Thrashers have widely overlapping geographic ranges in eastern North America, occupy many of the same habitats, and often sing during the same seasons and same times of day (Derrickson and Breitwisch 1992, Cavitt and Haas 2000). Both species defend territories, primarily against conspecifics, and there is little evidence that either species is interspecifically territorial towards the other (Howard 1974, Boughey and Thompson 1976, Cavitt and Haas 2000).

Ornithologists have long recognized that songs of Northern Mockingbirds and Brown Thrashers can be reliably distinguished in the field by their repetition patterns (e.g., Bent 1948, Walton et al. 2002). Mockingbirds typ-

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ically repeat each song type 4–5 times sequentially before producing the next song type in a sequence (range = 1–36 repetitions; Wil-denthal 1965), whereas Brown Thrashers typically repeat each song type only twice in suc-cession (range = 1–4 repetitions; Boughey and Thompson 1976). Whether these different repetition patterns are used by mockingbirds and thrashers in species discrimination is not clear. Boughey and Thompson (1976) showed that Brown Thrashers respond more strongly to normal thrasher song than to thrasher song altered to have a longer mockingbird-like rep-etition pattern, as measured by singing and ap-proaches to a speaker. However, the same sub-jects did not respond differently to unaltered Brown Thrasher and mockingbird songs, which makes these results difficult to inter-pret. Responses of Northern Mockingbirds to similar manipulations of repetition pattern have not been previously reported.

We investigated cues used by Northern Mockingbirds, and specifically the importance of repetition pattern as a cue, in discriminating mockingbird songs from those of Brown Thrashers. A variety of vocal features other than number of song repetitions might differ consistently between these species and could be used by mockingbirds in conspecific rec-ognition, including frequency and temporal characteristics of song types, intervals be-tween sounds, song amplitude, or the presence of song types that are species-distinctive (Fletcher and Smith 1978, Baylis 1982, Becker 1982). We presented subjects with songs of both species in which song repetition patterns were manipulated but other aspects of songs, including sound amplitudes and a variety of temporal characteristics, were standardized. Our study tested whether mockingbirds pref-erentially use either song repetition patterns or characteristics of the song types in discrim-inating between species.

METHODS

Playback experiments were conducted from 25 September to 17 November 2006 on the campus of St. Mary's College of Maryland and the neighboring grounds of historic St. Mary's City, Maryland, USA (38° 11' N, 76° 25' W). The area includes abundant popula-tions of both Northern Mockingbirds and Brown Thrashers, and members of both spe-

cies defend territories in spring that can over-lap interspecifically. Mockingbirds on our study site defend territories year-round and sing from mid-September through November as well as during the spring and summer, as reported for other mockingbird populations (Derrickson and Breitwisch 1992). Thrashers sing only during spring and most individuals leave the area during late fall (Hitchner 1996). We performed our study during fall when only mockingbirds were vocalizing and actively defending territories. This may have caused some of our playback treatments (e.g., those with Brown Thrasher songs) to seem unnatu-ral, but it was unlikely to have influenced our subjects' abilities to discriminate songs of conspecifics from those of other species. Per-forming our experiments in fall also allowed us to minimize interference by Brown Thrash-ers during playback.

Songs of Northern Mockingbirds and Brown Thrashers were recorded in the field by the authors using a Marantz PMD 670 dig-ital recorder and Telinga parabolic micro-telephone or were obtained from the Macaulay Library of Natural Sounds (Cornell Labora-tory of Ornithology, Ithaca, NY, USA) or other commercially available sources (Peterson 1990, Elliot et al. 1997). Song recordings used in the study (10 of mockingbirds and 7 of thrashers) were made in a variety of geograph-ic locations and all were recorded in spring between March and July (Table 1). Mocking-birds produce repertoires of different song types in spring and in fall, and both repertoires have been shown to elicit agonistic responses in either season (Burnett 1978, Logan and Fulk 1984). We used spring songs because mockingbirds respond significantly more strongly to these vocalizations regardless of season (Logan and Fulk 1984).

We generated onscreen spectrograms for each recording (digitized at either 44.1 kHz or 48 kHz) using Audacity 1.2.4 software (Maz-zoni et al. 2000) and selected 15 unique ~30-sec song sequences from each species based on recording quality. No more than three song sequences were taken from any one recorded individual. Each sequence in all cases includ-ed unique song types, and did not contain chats or begging calls. We altered song type repetition patterns to produce two versions of each song sequence (Fig. 1): one with a stan-

TABLE 1. Song recordings used in the study.

Species	Recording source
<i>Mimus polyglottos</i>	Peter P. Kellogg, Richmond Air Force Base, FL, May 1950
<i>Mimus polyglottos</i>	Robert C. Stein, Rock Springs, TX, April 1961
<i>Mimus polyglottos</i>	William W. Gunn, Homestead, FL, March 1968
<i>Mimus polyglottos</i>	Wilbur L. Hershberger, Frederick, MD, July 1997
<i>Mimus polyglottos</i>	Peterson (1990)
<i>Mimus polyglottos</i>	Elliot et al. (1997)
<i>Mimus polyglottos</i>	Authors, St. Mary's City, MD, April 2006
<i>Mimus polyglottos</i>	Authors, St. Mary's City, MD, April 2006
<i>Mimus polyglottos</i>	Authors, St. Mary's City, MD, April 2006
<i>Mimus polyglottos</i>	Authors, St. Mary's City, MD, April 2006
<i>Toxostoma rufum</i>	Geoffrey A. Keller, Ocala National Forest, FL, May 1994
<i>Toxostoma rufum</i>	Wilbur L. Hershberger, Frederick, MD, March 2000
<i>Toxostoma rufum</i>	Peterson (1990)
<i>Toxostoma rufum</i>	Elliot et al. (1997)
<i>Toxostoma rufum</i>	Authors, St. Mary's City, MD, April 2006
<i>Toxostoma rufum</i>	Authors, St. Inigoes, MD, May 2006
<i>Toxostoma rufum</i>	Authors, St. Inigoes, MD, May 2006

standardized mockingbird pattern (5 repetitions/bout) and one with a standardized thrasher pattern (2 repetitions/bout). We follow Derrickson and Breitwisch (1992) in defining a "song type" as an acoustically distinct sound pattern, usually repeated more than once sequentially, and in defining a "bout" as a group of repeated song types. Intervals between song types and between bouts were not altered in these manipulations, and sounds that were not repeated in these recordings (short sounds that occurred in <25% of recordings) were deleted. All recordings were passed through a 10-band equalizer to remove low frequency background noise below 320 Hz and normalized to the same peak amplitude using Sound Studio 2.2.4 (Freeverse Inc., New York, NY, USA). Each song sequence used in playback experiments was repeated several times sequentially for a total playback duration of 3 min (mean \pm SE number of song types/playback: NM = 14.2 ± 0.9 , BT = 18.6

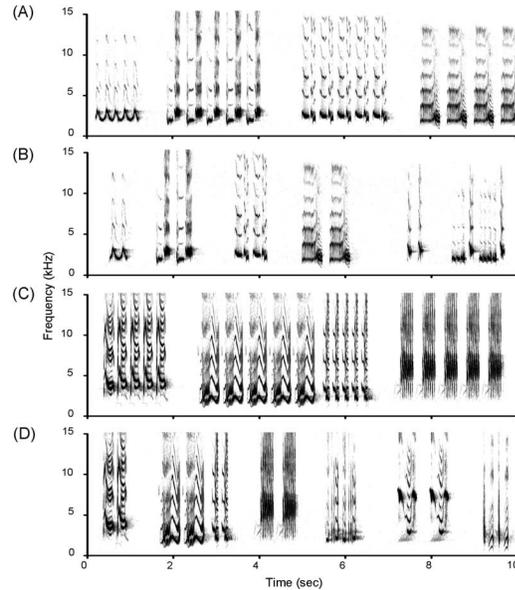


FIG. 1. Spectrograms of the four types of song sequences presented to Northern Mockingbird subjects: (A) mockingbird song types in a standardized mockingbird repetition pattern (5 repetitions), (B) mockingbird song types in a standardized Brown Thrasher pattern (2 repetitions), (C) thrasher song types in a mockingbird pattern, and (D) thrasher song types in a thrasher pattern.

± 0.9 ; mean \pm SE number of bouts/3 min playback: NM/NM = 73.5 ± 5.6 , NM/BT = 136.7 ± 9.4 , BT/BT = 128.9 ± 5.6 , BT/NM = 66.9 ± 3.5). Each initial recording was used to create two treatment stimuli, one for each repetition pattern type, but both variations from the same original recording were not played to the same subject. Precautions were also taken to ensure that subjects would not hear their own songs or the songs of a nearby neighbor. Thus, each subject heard four song sequences with different song types.

Fifteen territorial mockingbird subjects were each presented with four different treatments: (1) Northern Mockingbird song types in a standardized mockingbird repetition pattern (NM/NM), (2) mockingbird song types in a standardized Brown Thrasher repetition pattern (NM/BT), (3) thrasher song types in a standardized mockingbird repetition pattern (BT/NM), and (4) thrasher song types in a standardized thrasher repetition pattern (BT/BT). Treatments for each subject were presented in random order on the same day at

different locations in the territory, separated by a minimum of 15 min of silence to minimize habituation and fatigue. The speaker was relocated during these intervals within the subject's territory for the next treatment. Small shrubs and trees with similar branch densities were chosen for each speaker location, and speaker locations were approximately equidistant from one another as well as from estimated territorial boundaries to control for speaker movement. Territorial boundaries were estimated by a non-invasive observation period of 15–30 min the day before playback was performed. Researchers measuring the responses of subjects did not know the order in which treatments were presented at the time of playback to minimize observer bias, although the repetition pattern was likely discernable after the first few song types were heard.

Each treatment began only when the bird was visible, and a trial (playback of all 4 treatments) was aborted if the subject was lost from view for >15 min. Birds were not color banded for individual identification in our study; however, subjects were followed visually throughout each trial to ensure the same individual was observed in all four treatments. Males and females are visually indistinguishable in mockingbirds, and females are known to sing occasionally during fall (Derrickson and Breitwisch 1992). We attempted to focus on males by identifying them by their more frequent singing behaviors before each experiment. Songs were broadcast using an SME-AFS amplified field speaker (Saul Mineroff Electronics Inc., Elmont, NY, USA) connected to a 6 GB iPod Mini (Apple Inc., Cupertino, CA, USA). We standardized the volume of playback using a Realistic digital sound pressure level meter (fast response, C weighting) to approximate that of naturally singing birds. All experiments were conducted during the period of highest bird activity between 0700 and 1030 hrs EST and only under favorable weather conditions.

We measured responses of subjects during each 3-min playback period by recording four measures: (1) the amount of time, in seconds, each bird spent within 2 m of the speaker, (2) the latency, in seconds, to approach towards the speaker >1 m after playback began, (3) the closest approach to the speaker, and (4)

TABLE 2. Loadings of individual response measures on the first principal component for playback treatments.

Response measure	Loading score
Time within 2 m of speaker	-0.769
Latency to approach	0.827
Closest approach to speaker	0.894
Number of flights	-0.711

the number of flights >1 m. We conducted a principal components analysis using these four behavioral response measures as variables to assess the overall strength of response to each treatment. The response measures loaded about equally on the first principal component (Table 2), which explained 64.5% of the total variation. We analyzed the resulting response scores (PC I) with a one-way ANOVA and a Tukey's HSD post hoc test to compare responses between the four treatments. We also compared each response measure individually between treatments using a one-way repeated measures ANOVA with a Bonferroni post hoc test.

We analyzed the song sequences used in playback following these experiments to investigate the possibility that our treatments differed in aspects other than song type repetition pattern. We measured mean song type durations, bout durations, intervals between bouts, and song type repetition rates for each song sequence used in playback using Raven, Version 1.2.1 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). Five bouts were chosen randomly from each recording for these measurements, which were used to calculate a mean measurement for each song sequence. We also measured the highest and lowest peak frequencies ("maximum frequency" in spectrogram slices in Raven) that occurred in each song sequence to calculate the range of frequencies used (following Price et al. 2006). These data were analyzed using a two sample *F*-test for variances and an independent measures *t*-test.

RESULTS

A principal components analysis including time spent within 2 m of the speaker, latency to approach, closest approach, and number of flights (Fig. 2A) revealed significantly differ-

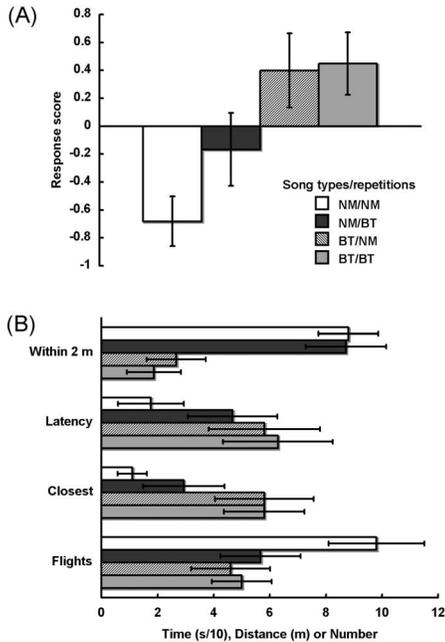


FIG. 2. (A) Mean (\pm SE) scores from a principal components analysis of mockingbird responses to playback treatments in which either Northern Mockingbird (NM) or Brown Thrasher (BT) song types were presented in either a NM or BT repetition pattern. (B) Mean (\pm SE) response measures included in the principal components analysis: time spent within 2 m of the speaker (Within 2 m), latency to approach >1 m towards the speaker (Latency), closest approach to the speaker (Closest), and number of flights (Flights) ($n = 15$ subjects).

ent responses to mockingbird song types in a mockingbird repetition pattern (NM/NM) than to Brown Thrasher song types with either repetition pattern (one-way ANOVA with Tukey's HSD post hoc, $n = 15$, $F_{3,56} = 5.177$; BT/BT, $P = 0.006$; BT/NM, $P = 0.01$). Birds responded similarly to Brown Thrasher song types regardless of repetition pattern ($P > 0.99$). Mockingbird song types in a thrasher repetition pattern (NM/BT) elicited an intermediate response that was not significantly different from responses to any of the other three treatments (BT/BT, $P = 0.26$; BT/NM, $P = 0.33$; NM/NM, $P = 0.41$).

Mockingbirds generally responded more strongly to playback of conspecific song types than to Brown Thrasher song types, comparing individual response measures among treatments (Fig. 2B). For example, subjects spent

significantly more time within 2 m of the speaker during both treatments with mockingbird song types than during treatments with Brown Thrasher song types (one-way repeated measures ANOVA with Bonferroni post hoc, $F_{3,42} = 13.328$, NM/NM vs. BT/BT, $P = 0.001$; NM/NM vs. BT/NM, $P = 0.002$; NM/BT vs. BT/BT, $P = 0.011$; NM/BT vs. BT/NM, $P = 0.048$). Responses to the same song types with different repetition patterns did not differ in time spent near the speaker (NM/NM vs. NM/BT, $P > 0.99$; BT/BT vs. BT/NM, $P > 0.99$). Latency to approach did not differ significantly among treatments ($F_{3,42} = 2.106$, $P = 0.13$); however, 13 of 15 subjects responded in 10 sec or less to NM/NM songs, whereas only 7 of 15 responded as quickly during NM/BT songs and 6 of 15 during both BT/NM and BT/BT treatments. Subjects approached the speaker somewhat more closely during NM/NM playback than during treatments with BT/BT songs ($F_{3,42} = 2.997$, $P = 0.03$) or BT/NM songs ($P = 0.098$). Subjects also performed significantly more flights in response to NM/NM songs than to Brown Thrasher song types with either repetition pattern ($F_{3,42} = 5.773$; BT/BT, $P = 0.031$; BT/NM, $P = 0.029$). No behavioral measures differed significantly in response to the two treatments with Brown Thrasher song types (BT/NM and BT/BT).

Measurements of the song sequences used in our playback experiments revealed no significant differences in mean song type durations between Northern Mockingbirds and Brown Thrashers (t -test: two sample assuming unequal variances, $n = 15$, $P = 0.28$). There was no significant difference in bout duration between treatments with the same repetition pattern ($P = 0.88$), but bout duration was significantly different between treatments with two repetitions/song type and five repetitions/song type ($P = 0.003$). We found no differences in the mean intervals between bouts with different repetition patterns ($P = 0.61$). Songs with different song types but the same repetition patterns did not differ in their mean song repetition rates (NM/NM vs. BT/NM, $P = 0.48$; NM/BT vs. BT/BT, $P = 0.32$) or in the total number of bouts included in each playback (NM/NM vs. BT/NM, $P = 0.48$; NM/BT vs. BT/BT, $P = 0.32$). Songs with mockingbird song types, however, exhibited a

significantly narrower range of mean peak frequencies (800–6,700 Hz) than songs with thrasher song types (600–9,250 Hz; $P < 0.001$). Brown Thrasher songs included both significantly lower frequencies ($P = 0.008$) and significantly higher frequencies ($P < 0.001$) than mockingbird songs, on average, which may be attributed to more energy in the upper harmonics of thrasher song (Fig. 1).

DISCUSSION

Our results indicate that Northern Mockingbirds can distinguish between conspecifics and Brown Thrashers based on their song types alone, regardless of the repetition pattern in which these songs are presented. Subjects responded strongly to playback of mockingbird song types in a standardized mockingbird repetition pattern, but responded relatively little to Brown Thrasher song types even when these sounds were played in exactly the same pattern of five repetitions/bout. Mockingbird song types with a Brown Thrasher repetition pattern elicited intermediate responses, generally stronger than responses to Brown Thrasher song types but not as strong as the responses to normal mockingbird song. Thus, although repetition pattern was not the principal cue used by our subjects to discriminate their own species' songs from thrasher songs, it appeared to have a role in conspecific recognition.

Most North American field guides indicate that songs of species in Family Mimidae (e.g., Northern Mockingbirds, Brown Thrashers, Gray Catbirds [*Dumetella carolinensis*]) can be most easily distinguished by their distinctive repetition patterns (e.g., Bent 1948, Cimprich and Moore 1995, Cavitt and Haas 2000, Walton et al. 2002); this cue is widely used by human observers in recognizing songs of these three species. Our results are surprising in demonstrating that mockingbirds preferentially use different vocal cues than what we typically use in discriminating species. None of our playback songs differed consistently in song type durations, amplitudes, or in intervals between song types or bouts. Our subjects appeared to recognize conspecific vocalizations based on acoustic features of the song types themselves.

Mockingbirds apparently have the ability to distinguish between two and five items, based

on a study by Farnsworth and Smolinski (2006) which focused on visual discrimination. In mockingbird song, however, the number of times in which song types are repeated can potentially vary over a relatively wide range (1–36 times according to Wildenthal 1965), which could explain in part why repetition pattern is not used as a primary cue in conspecific recognition.

Northern Mockingbirds increase the number of repetitions/bout during countersinging between territorial males (Derrickson 1988). Experiments with a closely related species, Tropical Mockingbird (*Mimus gilvus*), show that territorial males respond more strongly to a higher number of repetitions/bout during playback (Botero and Vehrencamp 2007). Playing mockingbird song types with a higher number of repetitions in our study elicited a stronger response, but increasing the repetition number of thrasher song types had no measurable effect on mockingbird responses. Repetition pattern in mockingbirds might have an important role in communication between territorial males rather than simply advertising species or individual identity. Mockingbirds are also known to decrease repetitions/bout during courtship and intersexual singing (Derrickson 1988). It is possible that our treatment of only two repetitions/bout was recognized as a mockingbird repetition pattern, although one atypical for the season. This may explain the intermediate response of our subjects to this treatment.

Our findings agree somewhat with results of previous playback studies in which other mimid species were tested using songs with artificially altered patterns (Boughey and Thompson 1976, Fletcher and Smith 1978). For example, Gray Catbirds apparently do not distinguish their songs from those of other mimids based on repetition pattern alone. Altering repetition patterns of catbird, thrasher, or mockingbird songs has no apparent effect on a catbird's ability to recognize species (Boughey and Thompson 1976); changing the order of catbird song types or even playing their songs backwards also has no effect (Fletcher and Smith 1978). Boughey and Thompson (1976) demonstrated that Brown Thrashers respond similarly to mockingbird song types with different repetition rates, including a thrasher-like repetition pattern.

Brown Thrashers respond more strongly to Brown Thrasher songs in the normal repetition pattern than to thrasher songs in a mockingbird pattern, suggesting that repetition pattern is important for species recognition in thrashers. However, these experiments also showed that Brown Thrashers do not discriminate between normal conspecific song and normal mockingbird song, which makes these results difficult to interpret.

How our mockingbird subjects were able to distinguish mockingbird song types from Brown Thrasher song types with the same repetition pattern is not clear. One possibility is that our subjects were familiar with song types we included in the study or that mockingbird songs generally include song types that are species-specific and indicate species identity. This seems unlikely, however, as most of our subjects appeared to make this discrimination after hearing only a few different song types (i.e., within the first 10 sec of playback). Furthermore, mockingbirds include an extensive variety of mimicked sounds in their song repertoires (Derrickson and Breitwisch 1992) and composition of these repertoires can vary geographically (Thompson et al. 2000), with age and social context (Derrickson 1987, 1988), and even seasonally between spring and fall (Burnett 1978). Our study was conducted in fall and included mockingbird songs recorded in spring from widely different locations and different years (Table 1). Some songs used in our study had been recorded from birds in our study population (4 Northern Mockingbird songs and 1 Brown Thrasher song), but we made sure that subjects did not hear their own song types or song types recorded from a nearby territory.

A more likely explanation for our results is that mockingbird and Brown Thrasher song types differ consistently in certain acoustic characteristics. We found that Brown Thrashers use a significantly wider range of sound frequencies than mockingbirds, as has been noted in previous studies (Wildenthal 1965, Boughey and Thompson 1976; Fig. 1). It is possible that mockingbirds are unable to produce the extremely high and low frequency whistles of which Brown Thrashers are capable, and studies investigating the limitations on song performance in mockingbirds are consistent with this possibility (ca. 750 Hz –

ca. 7,000 Hz in Zollinger and Suthers 2004). Other attributes that might differ between these species, not investigated in our study, include rate and pattern of frequency changes within song types, production of two sounds simultaneously, relative amplitudes of harmonics, and overall song amplitude. Further studies will be needed to identify the principal cues used by these birds and by other vocal mimics in recognizing conspecifics by song.

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LITERATURE CITED

- BAYLIS, J. R. 1982. Avian vocal mimicry: its function and evolution. Pages 51–83 in *Acoustic communication in birds*. Volume 2 (D. E. Kroodsma and E. H. Miller, Editors). Academic Press, New York, USA.
- BECKER, P. H. 1982. The coding of species-specific characteristics in bird sounds evolution. Pages 213–252 in *Acoustic communication in birds*. Volume 1 (D. E. Kroodsma and E. H. Miller, Editors). Academic Press, New York, USA.
- BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. National Museum Bulletin. Number 195.
- BOTERO, C. A. AND S. L. VEHRENCAMP. 2007. Responses of male Tropical Mockingbirds (*Mimus gilvus*) to variation in within-song and between-song versatility. *Auk* 124:185–196.
- BOUGHEY, M. J. AND N. S. THOMPSON. 1976. Species specificity and individual variation in the songs of the Brown Thrasher (*Toxostoma rufum*) and Catbird (*Dumetella carolinensis*). *Behaviour* 57:64–90.
- BOUGHEY, M. J. AND N. S. THOMPSON. 1981. Song variety in the Brown Thrasher (*Toxostoma rufum*). *Zeitschrift für Tierpsychologie* 56:47–58.
- BURNETT, L. J. 1978. Mockingbird song (*Mimus polyglottos*): an investigation within and across seasons. Thesis. University of North Carolina, Greensboro, USA.
- CATCHPOLE, C. K. AND P. J. B. SLATER. 1995. *Bird song: biological themes and variations*. Cambridge University Press, New York, USA.
- CAVITT, J. F. AND C. A. HAAS. 2000. Brown Thrasher (*Toxostoma rufum*). *The birds of North America*. Number 557.

- CIMPRICH, D. A. AND F. R. MOORE. 1995. Gray Catbird (*Dumetella carolinensis*). The birds of North America. Number 167.
- DERRICKSON, K. C. 1987. Yearly and situational changes in the estimate of repertoire size in Northern Mockingbirds (*Mimus polyglottos*). *Auk* 104:198–207.
- DERRICKSON, K. C. 1988. Variation in repertoire presentation in Northern Mockingbirds. *Condor* 90:592–606.
- DERRICKSON, K. C. AND R. BREITWISCH. 1992. Northern Mockingbird (*Mimus polyglottos*). The birds of North America. Number 7.
- ELLIOT, L., D. STOKES, AND L. STOKES. 1997. Stokes field guide to bird songs, eastern region. Time Warner Audiobooks, New York, USA.
- FARNSWORTH, G. L. AND J. L. SMOLINSKI. 2006. Numerical discrimination by wild Northern Mockingbirds. *Condor* 108:953–957.
- FLETCHER, L. E. AND D. G. SMITH. 1978. Some parameters of song important in conspecific recognition by Gray Catbirds. *Auk* 95:338–347.
- HITCHNER, S. 1996. Brown Thrasher. Pages 298–299 in *Atlas of the breeding birds of Maryland and the District of Columbia* (C. S. Robbins, Editor). University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.
- HOWARD, R. D. 1974. The influence of sexual selection and interspecific competition on Mockingbird song (*Mimus polyglottos*). *Evolution* 28:428–438.
- KROODSMA, D. E. 2005. The singing life of birds: the art and science of listening to birdsong. Houghton Mifflin Company, Boston, Massachusetts, USA.
- KROODSMA, D. E. AND L. D. PARKER. 1977. Vocal virtuosity in the Brown Thrasher. *Auk* 94:783–785.
- LOGAN, C. A. AND K. R. FULK. 1984. Differential responding to spring and fall song in Mockingbirds (*Mimus polyglottos*). *Journal of Comparative Psychology* 98:3–9.
- MARLER, P. 2004. Science and birdsong: the good old days. Pages 11–18 in *Nature's music* (P. Marler and H. Slabbekoorn, Editors). Elsevier Academic Press, New York, USA.
- MAZZONI, D., M. BRUBECK, J. CROOK, V. JOHNSON, L. LUCIUS, AND M. MEYER. 2000. Audacity, Version 1.2.4. SourceForge.net, Fremont, California, USA.
- MERRIT, P. G. 1985. Song function and the evolution of song repertoires in the Northern Mockingbird (*Mimus polyglottos*). Dissertation. University of Miami, Coral Gables, USA.
- PETERSON, R. T. 1990. A field guide to bird songs: eastern and central North America. Third Edition. Houghton Mifflin Company, Boston, Massachusetts, USA.
- PRICE, J. J., S. M. EARNSHAW, AND M. S. WEBSTER. 2006. Montezuma Oropendolas modify a component of song constrained by body size during vocal contests. *Animal Behaviour* 71:799–807.
- THOMPSON, N. S., E. ABBY, J. WAPNER, C. LOGAN, P. G. MERRITT, AND A. POOTH. 2000. Variation in the bout structure of Northern Mockingbird (*Mimus polyglottos*) singing. *Bird Behavior* 13:93–98.
- WALTON, R. K., R. W. LAWSON, AND R. T. PETERSON. 2002. *Birding by ear: eastern and central North America*. Houghton Mifflin Company, Boston, Massachusetts, USA.
- WILDENTHAL, J. L. 1965. Structure in primary song of the Mockingbird (*Mimus polyglottos*). *Auk* 82:161–189.
- ZOLLINGER, S. A. AND R. A. SUTHERS. 2004. Motor mechanisms of a vocal mimic: implications for birdsong production. *Proceedings of the Royal Society of London Series B Biological Sciences* 271:483–491.