Call Mimicry by Eastern Towhees and Its Significance in Relation to Auditory Learning

Jon S. Greenlaw, 1.4 Clifford E. Shackelford, 2.3 and Raymond E. Brown'

ABSTRACT-We document cases of Eastern Towhees (Pipilo erythrophthalmus) using mimicked alarm calls from three presumptive mode is [Blue Jay (Cvanocitta cristata), Brown Thrasher (Toxostoma rufum), and American Robin (Turdus migratorius)]. In four instances, male towhees employed heterospecific calls without substitution in their own call repertoires. Three birds (New Jersey. New York) used jay-like calls mixed with "Chewink" calls in the same bouts of calling. One bird (New York) increased the frequency of its mimicked call during intense reactions to disturbance (high rate of calling). A Texas towhee employed jay-like and Chewink calls separately in different contexts. In another case, sequences of robin-like alarm calls were used by a towhee to form unusual, distinctive song-types during bouts of singing. These observations suggest that some aspects of towhee alarm call repertoires may be influenced by auditory learning. and that mimicked alarm calls also can be incorporated into song repertoires. Received 22 Jan. 1998. accepted 21 April 1998.

Although avian vocal mimicry has attracted interest for centuries (Witchell 1896, Armstrong 1975), most of what is known about development of species-typical vocal repertoires, including mimicry, is based on recent studies of sound imitation and its role in song development in songbirds (e.g., Marler and Mundinger 1971, Marler 1991). Mimicry of heterospecific and inanimate sounds can be a facultative response to sound experience, or a regular imitation of songs or calls that may be adaptive (e.g., Baylis 1982). Yet, the role of mimicry in the development of call repertoires rather than as elements of song remains poorly understood (Baylis 1982).

Eastern Towhees (Pipilo erythrophthalmus) rarely mimic other species. Previous

cases of vocal mimicry in this species involved the use of mimicked songs or song phrases from two heterospecific models to form distinctive song types (Borror 1977, Richards 1979). Here, we report instances in which towhees mimicked the calls of several other species and used these calls in their call or song repertoires. The use of mimicked calls in call repertoires is rarely reported in songbirds. Its occurrence in towhees may indicate at least limited flexibility in the development of the call repertoire in this species.

STUDY AREAS AND METHODS

The term "vocal mimicry" is **used** here in a purely descriptive sense, and does not carry any functional connotation. It describes a vocalization of one species that resembles the sounds of another species (Baylis 1982). In this case, we address the specific issue of "call mimicry."

Observations of presumptive call mimicries by towhees were obtained at: (1) W. L. Hutcheson Memorial Forest (HMF), near East Millstone, Somerset Co., New Jersey (1968); (2) Kalbfleisch Field Research Station (KFRS), Dix Hills, Suffolk Co., New York (1970-1972); (3) Fire Island National Seashore (FINS), near Fire Island Lighthouse, Suffolk Co., New York (1970); (4) Muttontown Nature Preserve (MNP), Muttontown, Nassau Co., New York (1972); and (5) Big Thicket National Preserve, Tyler Co., Texas (1995). With the possible exception of the Muttontown NP towhee, all birds were territorial males. Visits to the territories of two northeastern males spanned periods from late spring to mid- (HMF) or late summer (KFRS). Multiple visits to two other males' territories extended from mid-June to July (Texas male) or to August (FINS). The Muttontown NP male was observed only once (21 March 1972). and its breeding status was unknown. A Kalbfleisch FRS male (color-banded as a hatch-year bird in August 1969) was present from 1969-1 976. and we noted it using robin-like calls in his primary songs from 26 April 1970 to 10 August 1972. The Texas male was unmated, and was observed from 14 June to 2 July 1995.

Mimicked vocalizations were taped in New York and Texas using a Uher 4000L recorder. a Uher microphone in a 61 cm (24-inch) parabolic reflector (HMF), and a Dan Gibson 46 cm (18-inch) electronic parabolic microphone (KFRS, FINS), or a Uher 4000 Report IC recorder and a Dan Gibson EPM Model P-200 parabolic reflector (46 cm shield: Texas). Sound

¹ 2813 SW 43 Lane, Cape Coral, FL 33914; E-mail: jsg@iline.com.

² Wildlife Habitat and Silviculture Laboratory, Southern Research Station, PO. Box SFA Station, Nacogdoches, TX 75962.

³ Present address: Texas Partners in Flight, Texas Parks and Wildlife Dept.. 4200 Smith School Rd., Austin, TX 78744.

⁴ Corresponding author.

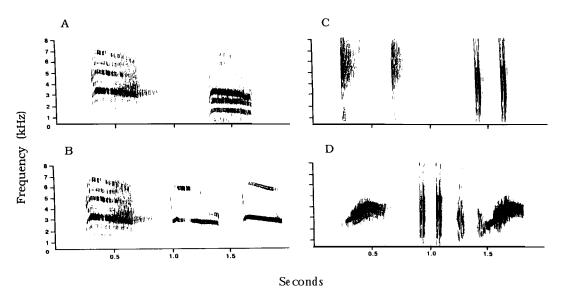


FIG. 1. Sound spectrograms of mimicked calls in the call repertoires of Eastern Towhees compared with corresponding calls in the repertoires of presumptive model species. A, right, mimicry of Jay call of towhee in New York (KFRS male), left, Jay call of Blue Jay (New York); B, right, two Jay-like mimicries of towhee in Texas, left, Jay call of Blue Jay (New York); C, right, thrasher-like calls of towhee in New York (FINS male), left, corresponding calls of Brown Thrasher (New York); D, Chewink calls and thrasher-like mimicries of FINS male in a representative portion of a mixed-call sequence. All recordings by the authors.

spectrograms were prepared on a Kay Elemetrics Sona-graph 7029A 5-16 kHz Spectrum Analyzer with a Krohn-Hite Model 3550 filter. Most calls from presumptive models were recorded in New York by the authors using the same equipment. Robin calls were obtained from the archives of the Borror Laboratory of Bioacoustics.

RESULTS

We documented call mimicry during the breeding season in six male towhees in three states. Presumptive heterospecific sound models of these birds were Blue Lay (Cyanocitta cristata), Brown Thrasher (Toxostoma rufum), and American Robin (Turdus migratorius).

Among these call mimickers, the Blue Jay's characteristic "Jay" call (Fig. 1A, B, left) was rendered in 4 of 7 cases. Three of these individuals (HMF, KFRS, and Texas) incorporated this call into their call repertoires without substitution. Another bird (FINS) used the alarm call of the Brown Thrasher (Fig. 1C, left) in the same manner. A male at Muttontown NP employed a Jay call in a prolonged, muted soliloquy that contained primary song elements and some species-typical calls. Comparisons of these calls from most of the birds

mentioned with corresponding calls From the putative models are shown in Figure 1.

Three males (New Jersey, New York) mixed heterospecific and "Chewink" calls in the same bouts of alarm calling when disturbed. No bouts consisted of just one or the other call types. Heterospecific calls were uttered 1-3 times between "Chewink" calls or call sequences. The Kalbfleisch FRS male also exhibited a tendency to utter more jay-like calls during periods of intense (high calling rate) calling than during more "relaxed" periods (low calling rate). Another variation occurred during a bout of rapid calling near an active nest. The Kalbfleisch FRS male began by coupling the jay-like and "Chewink" calls into a single compound vocalization ("jeahchwee ...") in which a longer pause occurred between the jeah-chwee couplets than within them. Later in the same calling bout, as the rate of calling slowed, jeah and chwee calls were separated into single notes. In one period (165 s) of mixed calling, the Fire Island NS male uttered 54 mimicries (41.2%) and 77 Chewink calls. This towhee often rendered its mimicry in single or doubled versions ("tchap-tchap") in thrasher-like fashion.

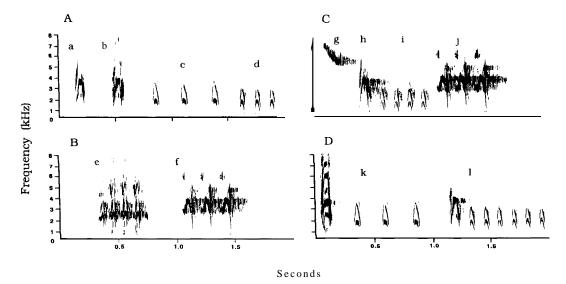


FIG. 2. Sound spectrograms of robin-like calls in the song repertoire of an Eastern Towhee in New York, compared with corresponding calls of American Robins. A, a, Stip! call of robin (BLB 13688), b, Stip! call of towhee (see text), c, Pup-chatter of robin (BLB 13688), d, Pup-chatter of towhee; B, e, Chee-whinny by robin (BLB 16350), f, Chee-whinny by towhee; C, towhee mimicry of robin call combination, used in song repertoire as a song-type [see stip! pup pup pup cheechee(g, h, i, j)]; and D k, Stip! pup pup pup combination of robin (BLB 13688). 1, Stip! pup pup pup combination of towhee.

The towhee observed in Texas exhibited still another mimetic variation. Its jay-like and Chewink calls were employed separately in different contexts. The jay-like call was the sole vocalization used in mobbing observers (CES, REB), while only the Chewink call was given after the towhee ceased mobbing and began foraging.

A color-banded (XR-GG) male present at Kalbfleisch FRS from 1965 (at least) to 1972 sang two distinctive song-types that incorporated sequences of three or four different robin-like calls as song elements. These calls are characterized as follows: (1) See-scream, a high-pitched squeal, seee (perhaps "sss" of Bent 1949; Fig. 2g), (2) Pup-chatter, a lowpitched, soft pup, repeated in a series (phrase) as pup-pup-pup. ("tut-tut..." syllables of Bent 1949; Fig. 2c, d), and (3) Chee-whinny, an insistent, loud chitter, performed as a short series of notes, e.g., "chee-chee-chee" ("eacheach-each" of Bent 1949; Fig. 2e, f). A fourth call type, transliterated as "stee" ("stip"), is probably convergent on a robin-like call and is discussed below.

DISCUSSIO N

Our observations suggest that learning may play a role in the acquisition and use of certain calls by the Eastern Towhee. Some individuals expand their call repertoires by adding a mimicked sound, and others may employ sequences of mimicked calls as distinctive song types. Among individuals that employ such sounds in their call repertoires, variation in the temporal and contextual characteristics of novel call use in relation to the Chewink call is also noteworthy.

Several types of evidence support the view that mimicry of sounds from heterospecific models best explains most of our observations. (1) Hundreds of hours of observations yielded no evidence that unusual "nonmimicked" sounds (atypical calls that could not be matched to likely models) occur even rarely in towhee call repertoires. Rather, in each of the cases reported here, an unexpected call was rendered by towhees in widely separated geographic settings that corresponded to a distinctive sound employed otherwise only by another species. (2) These unusual and unlikely sounds were remarkably similar in sound "quality" to their heterospecific analogues. Also, there are no sounds in the normal call repertoire of the Eastern Towhee that even closely resemble in sound structure the

jay-like or thrasher-like sounds uttered by the call mimics (Greenlaw, unpubl. data). (3) The presumptive models were characteristic faunal neighbors of the towhees. Consequently, we regard these uncharacteristic towhee sounds as evidence of call mimicries. As such, they represent distinctive "markers" that implicate some learning in the development of call use in call and song repertoires in Eastern Towhees.

The use of robin-like calls in two songtypes sung by XR-GG deserves special comment. The "stee!" or "stip!" element was widely represented in the song repertoires of Long Island towhees (Ewert 1978: fig. 11V, appendix 2). Thus, this element was probably copied from other towhees, or improvised, and is convergent on the similar robin's call (Fig. 2, a vs b). The other robin-like elements were unique to XR-GG. Yet, regardless of origin, both mimicked and convergent notes were uttered by XR-GG as components of songs in the same sequences commonly heard in nonsong contexts in American Robins (JSG, pers. obs.; Fig. 2D). This may mean that the unit of mimicry was a call complex, not individual calls that were later assembled into a robin-like sequence.

Little is known about vocal development in Eastern Towhees. Song sharing is well known among immediate neighbors in towhee populations (Green law 1996). Also, nestling towhees that were isolated from wild populations failed to develop the familiar Chewink call. Rather, they use abrupt, atypical notes that bear little resemblance to this call (Ewert 1979; R. E. Ball, pers. comm.). Our observations suggest that call mimicries may express themselves in adulthood either in call repertoires (simple call mimicry) or in song repertoires (mimicry of heterospecific call complex, or a sound "template" that allows assembling mimicked call units into a complex sequence).

This report of call mimicry in Eastern Towhees suggests that sound or social experience may play some role in the development of call repertoires in this species, and in the specific use of mimicked calls in generalized "alarm" contexts. The hypothesis that calls in songbirds are "genetically fixed" (strictly maturational; e.g., Lanyon 1960) needs to be ex-

amined using isolation and tutoring experiments on a case by case basis.

ACKNOW LEDGMENTS

We are grateful to J. B. Falls who supplied reprints of critical references and suggeated other citations. We thank the Southern Research Station. U.S. Forest Service, for its support. We also thank Sandra L. L. Gaunt for providing recordings of robin calls from archives of the Borror Laboratory of Bioacoustics (BLB), Dept. of Zoology, Ohio State Univ., Columbus, Ohio (all rights reserved by BLB on materials provided). We are grateful for the help of anonymous referees and the editor, whose advice greatly improved the manuscript.

LITERATURE CITED

- Armstrong, E. A. 1975. The life and lore of the bird in nature, art, myth, and literature. Crown Publ., Inc.. New York.
- BAYLIS, J. R. 1982. Avian vocal mimicry: its function and evolution. Pp. 51–83 in Acoustic communication in birds, vol. 2 (D. E. Kroodsma and E. H. Miller, Eds.). Academic Press, Inc., New York.
- **Bent**, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. Bull. U.S. Nat. Mus. 196: 1-452.
- BORROR. D. J. 1977. Rufous-sided Towhee mimicking Carolina Wren and Field Sparrow. Wilson Bull. 89:477-480.
- EWERT, D. N. 1978. Song of the Rufous-sided Towhee (*Pipilo erythrophthalmus*) on Long Island, New York. Ph.D. diss., City Univ. of New York, New York.
- EWERT, D. N. 1979. Development of song of a Rufoussided Towhee raised in acoustic isolation. Condor 81:313-316.
- GREENLAW, J. S. 1996. Eastern Towhee (*Pipilo ery-throphthalmus*). *In* The birds of North America, no. 262 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania: The American Ornithologists' Union, Washington, D.C.
- LANYON, W. E. 1960. The ontogeny of vocalizations in birds. Pp. 321-347, in Animal sounds and communication (W. E. Lanyon and W. N. Tavolga, Eds.). American Institute of Biological Sciences, Washington, D.C.
- MARLER, P. 1991. Song-learning behavior: the interface with neuroethology. Trends Neurosci. 14: 199–206.
- MARLER, F? AND P. MUNDINGER. 1971. Vocal learning in birds. Pp. 389-450, in The ontogeny of vertebrate behavior (H. Moltz, Ed.). Academic Press, New York
- RICHARDS, D. G. 1979. Recognition of neighbors by associative learning in Rufous-sided Towhees. Auk 96:688-693.
- WITCHELL, C. A. 1896. The evolution of bird-song. Adam and Charles Black, London, U.K.