

We wish to thank Terry Anthony for having provided Nunn with a Beauliere R-16 16-mm movie camera, by which a useful record of the slaughter was obtained.—WILLIAM G. GEORGE AND TIMOTHY KIMMEL, Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901. Accepted 2 Aug. 76.

**Vocal virtuosity in the Brown Thrasher.**—Ethograms, or catalogues of behavioral acts, in a variety of animal species have typically revealed a relatively limited and finite number of behaviors (e.g. Kaufman and Rosenblum 1966, Wilson and Fagen 1974). This is also true for vocal behaviors in songbirds: some species may have only a single song (Marler and Tamura 1964), several wren species may sing approximately 100 songs (Verner 1975), and 'type-token' analyses for Mockingbirds (*Mimus polyglottos*) have yielded estimates of 66–244 song types for four males (Wildenthal 1965). Our recent studies reveal a vocal behavior in the Brown Thrasher (*Toxostoma rufum*) where song types of an individual number in the thousands and may even be improvised during display.

On 14 May 1973 we recorded 113 minutes of singing from an adult male Brown Thrasher in full song at the Rockefeller University Field Research Center near Millbrook, New York. The bird sang nearly continuously from a single perch, but pauses of up to 11 min in length became more frequent during the last half of the recording session. Tapes were analyzed on a continuous spectrum analyzer (Hopkins, Rossetto, and Lutjen 1974). Although Brown Thrashers sing in a "continuous" fashion, the field biologist recognizes temporally distinct song units that often (approximately one-third of the time) consist of twice-repeated syllables (see Fig. 1). These song units were considered distinct units in this study if separated from other units by at least one-fourth sec (same method used by Borror 1964), though occasional exceptions were made when it was obvious that the same pattern of notes was continued after a longer pause. Using this method a total of 4,654 song units was distinguished in the 113 min of recordings from the one male.

In order to estimate the number of different song units occurring in this sample of 4,654, every hundredth song unit was examined for its occurrence elsewhere in the sample. Two song units were considered the same if they consisted of the same sequence of notes, although the number of repetitions of the specific note sequence (syllable) might vary. Song units 1,800 and 3,600 were considered to be the same, leaving a total of 45 song units that were studied systematically.

Many of the song units (20 of 45) did not recur in the entire singing record, but two occurred as many as seven times (Fig. 2). While some song units were distributed throughout the sample (e.g. unit 200 recurred at 3,269 and 4,416), others seemed to recur several times within a few minutes time (see Fig. 1).

These 45 song units accounted for 116 of the 4,654 song units. The average number of occurrences (116/45 = 2.6) divided into 4,654 yields an estimate of 1,805 different song units in the sample (95% confidence limits of 1,483 and 2,307; median number of occurrences was 2, yielding an estimate of 2,327 different song units, with confidence limits of 1,722 and 3,585).

Estimating the zero class, i.e. the number of song units the male was capable of singing but did not actually sing in the sample of 4,654, cannot be done with much statistical confidence from the distribution of Fig. 2. Preparing the customary 'type-token' curves would require literally millions of sonogram comparisons (5.4 million if each song type occurs twice in the sample), but would allow no more sophisticated a

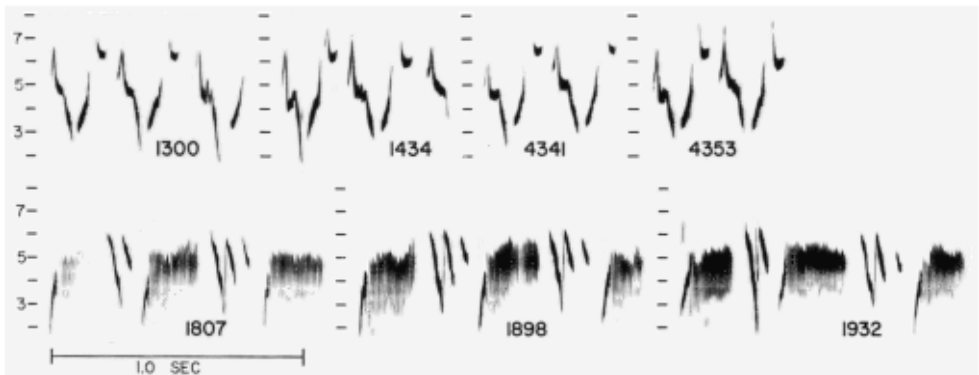


Fig. 1. Examples of recurrences of song units 1300 and 1807 in the sample of 4654. Timing mark is 1.0 sec, while vertical axis is kHz. (See reference (4) for additional sonograms.)

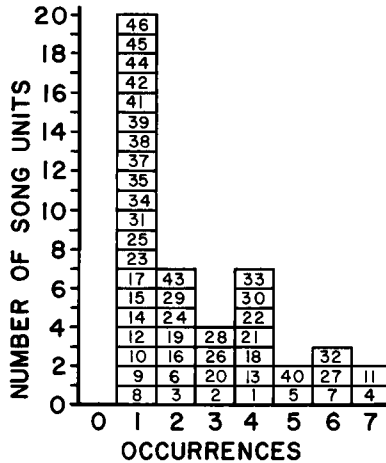


Fig. 2. Histogram of the number of occurrences of every hundredth song unit (excepting no. 3,600—see text).

conclusion than that derived from the present analysis, namely, that a male Brown Thrasher sings a tremendous variety of different song units. Males may repeat a song unit after an hour of intervening singing, but whether the repertoire is constant or whether males continually improvise or learn new songs is at present unknown.

Male Brown Thrashers are very vocal in early spring and, during intense vocal duelling, neighboring territorial males may countersing with very similar songs (heard several times by Kroodsma), but the birds sing very little after pairing and nesting begin. Such a brief song season suggests that this complex vocal behavior of the Brown Thrasher functions primarily in the acquisition of territory and/or mate (Catchpole 1973), and plays a lesser role in either maintaining territorial boundaries or strengthening the pair bond after nesting has begun.

Nevertheless, the nagging question persists: Why such a complex behavior in the Brown Thrasher when far simpler behaviors suffice for the majority of oscines? Under intense sexual selection in polygynous mating systems or in very dense populations, one might expect elaboration of a display involved in appropriating resources in short supply (Kroodsma 1976, in press); yet Brown Thrashers are monogamous and territories are often widely dispersed. Possibly comparative work with other Mimids and closely related species could reveal selective forces involved in elaboration of male song, but at present the evolution of the Thrasher vocabulary remains an enigma.

Research was supported by NIH Grants GM 01789 and MH 14651 in Behavioral Sciences at Rockefeller University. Copies of tape recordings used in this study have been deposited with the Cornell University Library of Natural Sounds.

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**Lower jaw action during prey capture by pelicans.**—Schreiber et al. (1975) gave a detailed account of the technique of prey capture by the Brown Pelican (*Pelecanus occidentalis*) based on photography of individuals diving into a marina. Their excellent illustrations show clearly the remarkable extent to which the rami of the lower jaw bow outwards during the capture of a fish. Although they do not comment on the mechanics involved in mandible bowing, Schreiber (in litt.) has suggested interaction with the water as the means by which this is brought about. Obviously, this possibility must be considered carefully.

Forces acting on the lower jaw under water can be considered under two heads: those acting directly on the jaw, and those acting via the gular pouch. As the lower jaw moves forward during the bird's entry into the water, pressure against the water will inevitably exert some backwardly directed force upon it. This would tend to compress the jaw along its long axis, and thus to bow the rami outward. However the force can be only a small one, as the lower jaw presents a very small area to the water from its anterior aspect; moreover, as the jaws bowed outwards, continuing motion in the same direction would increasingly produce forces acting against the lateral surface of the rami, and tending to counteract bowing. It seems unlikely, therefore, that direct interaction between lower jaw and water would produce the bowing effect.

Mandible bowing could be produced by the gular pouch only while it is relaxed and distended. In this condition, as the photographs show, it assumes a rounded cross section as it is filled by water, bulging out either side of the lower jaw rami to which it is attached. In this condition an outward force component would act on each ramus; with a contained weight of water of 5-8 kg, this force component may be of substantial magnitude. However this does not explain how it is possible for the rami to bow while the pouch is contracted, as shown clearly in Figures 2A and 2B of Schreiber et al. (1975). Contraction of muscles in the pouch (presumably *M. mylohyoideus* anterior though this has not been checked by dissection) would inevitably exert a medially directed force on the rami, tending to pull them together. Moreover, as the photographs show (Figs. 3B, 3C) the rami can move together again while the pouch is fully distended.

It seems, therefore, that interactions between jaw and water are insufficient to explain how bowing is brought about. Confirming this view, some photographs of pelicans show considerable mandible bowing out of water, e.g. those of *P. onocrotalus* (Nicolai 1974: 132). Extensive bowing out of water is also shown during the Bill Throw performance of *P. occidentalis* (Schreiber 1977, Fig. 6).

An alternative mechanism is that provided by *M. pterygoideus*, the large and complex jaw muscle linking the lower jaw with the palatine and pterygoid. Part of this muscle (*M. pterygoideus ventralis medialis*) originates on the ventral surface of the palatine and inserts on the internal process of the lower jaw. When the internal process is pulled forward, the lower jaw ramus is pivoted on its articulation with the quadrate, swinging its lateral surface outwards. This action, which can be modified by means of the other jaw muscles, has been fully described and discussed in various other groups of birds, (notably the Charadriiformes and Procellariiformes) by Judin (1961), Zusi (1962), and Burton (1974). Pending further research, I would suggest that this is also the main mechanism of mandible bowing in *Pelecanus*. An illustrated description of *M. pterygoideus* in *Pelecanus* is given by Hofer (1950), and further dissection of this genus and other Pelecaniformes may shed more light on the structural basis of this action. Nevertheless it is clear that *M. pterygoideus ventralis medialis* is indeed well developed in pelicans, with its area of origin enlarged by means of a deep ventral keel along the midline between the ankylosed right and left palatines. It is interesting to see from the photographs of Schreiber et al. that the upper jaw is able to perform extensive movements independently of the lower, even while the latter is fully bowed. Schreiber (in litt.) has pointed out that during the Bill Throw, throwing the head high stretches the pouch taut, producing forces that will tend to cause bowing. The precise contributions of the pouch and pterygoideus musculature in this situation are impossible to assess without experiments involving stimulation of surgically isolated muscles; but it may be noted that the photographs of *P. onocrotalus* in Nicolai (1974) show birds bowing the mandibles in a roughly horizontal position, when the pouch would be making no contribution to the action.