

enough to produce mimicry. It was. What the outcome of explicit training procedures would be with starlings remains to be explored. We offer these data as an incentive for others to pursue the study of these talented and companionable birds.

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Vocalizations of the Black-throated Gray Warbler.—Vocalizations of birds range from simple notes to complex repertoires that vary in structure and function (e.g., Thorpe, *Bird-song*, Cambridge Univ. Press, London, England, 1961; Lemon, *Condor* 77:385–406, 1975; Catchpole, *Vocal Communication in Birds*, Univ. Park Press, Baltimore, Maryland, 1979). The study of avian vocalization adds to knowledge of pair formation and breeding behavior, territory establishment and defense, and ultimately to aspects of competition and the formation of assemblages of species. In this study we analyze vocalizations of the Black-throated Gray Warbler (*Dendroica nigrescens*), and through playback experiments, describe the information content of these songs. The singing behavior of other *Dendroica* warblers has been described (e.g., Morse, *Wilson Bull.* 78:444–455, 1966, *Wilson Bull.* 79:64–74, 1967; Ficken and Ficken, *Auk* 87:296–304, 1970; Lein, *Nature* 237:48–49, 1972, *Can. J. Zool.* 56:1266–1283, 1978; Kroodsma, *Auk* 98:743–751, 1981), but controversy surrounds the meanings of different song types (Lein 1972, 1978; Krebs, *Anim. Behav.* 25:475–478, 1977, *Anim. Behav.* 26:304–305, 1978; Slater, *Anim. Behav.* 26:304, 1978). Although songs of the black-throated gray have been compared with closely related congeners (Stein, *Living Bird* 1:61–71, 1962), we know of no other study that gives details on the singing behavior of this species.

Study area and methods.—Songs of breeding Black-throated Gray Warblers were recorded during April and May of 1981 and 1982 near the west entrance of the Finley National Wildlife Refuge (FINLEY), Benton Co., Oregon, using a Nagra III recorder and Gibson parabolic microphone, model P-200. The study area (about 30 ha) was characterized by a mixture of mature Oregon white oak (*Quercus garryana*) and Douglas-fir (*Pseudotsuga menziesii*). A more complete description of the study area, including a description of the habitat use and foraging behavior of black-throated grays at FINLEY, was given by Morrison (*Auk* 99:503–513, 1982). About eight male black-throated grays were located in the study area each year. The songs of at least five different individuals were recorded in 1981; we do not know if songs recorded in 1982 were of the same or different individuals as those in 1981. Songs recorded in the wild were analyzed on a Kay Elemetrics Sona-Graph Model 7029A using the 300 Hz wide band filter and the 80–8000 Hz frequency spectrum. The resulting sonagrams were studied to compare song types recorded at FINLEY. All tape recordings made in this study were deposited in the Florida State Museum Bioacoustic Archives as FSM master tape numbers 560, 563, and 577. About 50 h on 20 days for the 2 years of study was spent recording and observing the singing behavior of the black-throated gray. About 70% of the observations were conducted within 3 h of sunrise; 15% were conducted during late morning and 15% during afternoon. About 80% of the fieldwork was conducted in 1981.

Tapes used for playback experiments were made by transferring the original recordings to cassette tapes; experiments were also conducted using the Nagra and the original tapes.

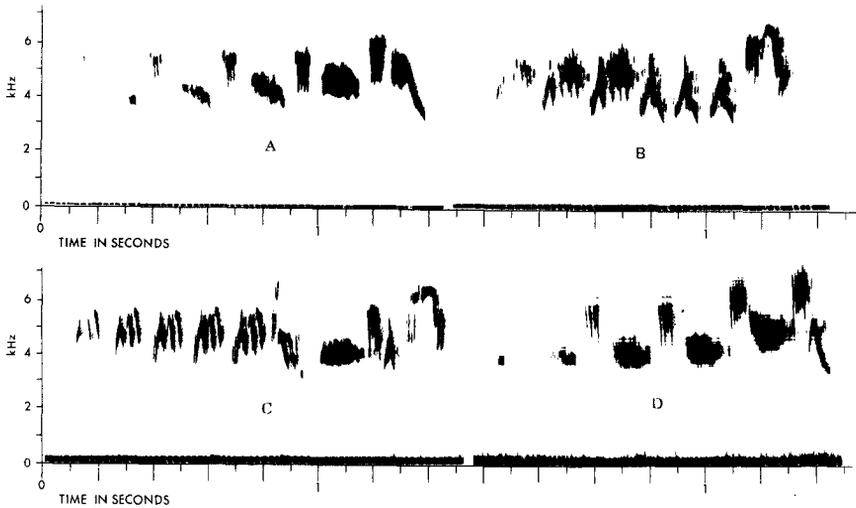


FIG. 1. Sonograms of male Black-throated Gray Warblers from vocalizations recorded at Finley National Wildlife Refuge, Benton Co., Oregon. A. Type-II. MLM tape 1. FSM 560, cut 1, song 2. B. Type-I (simpler type). MLM tape 8, FSM 577, first song. C. Type-I (more complex). MLM tape 19. FSM (not yet catalogued), song 4. D. Soft song—type II. MLM tape 4. FSM 563, cut 2, song 2.

Experiments were conducted by placing a speaker within 30 m of a singing, and thus likely territorial, male black-throated gray; a description of these experiments is presented elsewhere (Morrison 1982).

Terminology used to describe the function of song types herein conforms to that presented elsewhere: our type-I song corresponds to the “accented ending song” and type-I song, and our type-II song corresponds to the “unaccented ending song” and type-II song as summarized by Kroodsma (1981).

Results.—Two distinct types of songs, plus a modification of one song type, were identified during this study. Type-II songs are 1.3–1.5 sec long, begin softly, and with each figure increase in amplitude, forming a crescendo (Fig. 1A). Each motif up to the last one consists of two rapid frequency modulated figures. The first of these figures is the lower pitched, centering in the first four motifs at 3.9–4.2 kHz, and in the fifth one at about 4.8 kHz. To the ear and eye it is a buzzy, only slightly tonal sound. (Its tonal character is evident when the sound is played at half speed, and it then may be described as a guttural warble.) The second figure of each motif is the higher pitched one, ranging from about 4.2–5.8 kHz in the first four motifs to 4.5–6.3 kHz in the fifth, which is the penultimate figure of the entire song phrase. These second figures of the motif are less rapidly modulated. They still sound buzzy, but the rising and falling tonality can be heard and seen. The final motif of the song is composed of a single lower-pitched stroke-glissando figure that is a purely tonal whistle, rising abruptly from 4.8–5.5 kHz and then falling to 3.0 kHz. A phonetic rendering of the complete song phrase might be: *buzz see buzz see buzz see buzz see buzz see wueeo*.

Type-I songs are more complex and difficult to describe or render phonetically. The simpler type-I's are about 1.3 sec long and consist of three guttural warbles in which the warble

motifs have several up-down glissandos so rapidly uttered that they run together (Fig. 1B). These are followed by a series of three less guttural and discretely separated up-down glissando warble figures and a terminal figure composed of a buzz leading into a short stroke steep glissando ending. The frequency span of the song is mostly from 3.0–5.2 kHz until the last motif, which rises to 4.0–6.8 kHz. Phonetically it might be rendered: *wurtelee wurtelee wurtelee wurlee wurlee wurlee buzzeoz*.

The more complex type-I's are about 1.5 sec long (Fig. 1C). They have an opening motif of five or six rapid guttural warbles in which three stroke-glissandos form a vibrato at 3.0–5.8 kHz. This is followed by a broad buzz centered at 4.0 kHz, then a higher guttural buzz, an up-down glissando, and a buzzy rising-then-falling whistle. Phonetically it might be written: *wurtelee wurtelee wurtelee wurtelee wurtelee buzz bree weeo bruzeoo*; but phonetics are not applied easily or aptly to such a complicated utterance.

The final song, the “soft song,” is apparently not a distinct song type. Soft songs were given by males closely attending females and are type-II songs uttered at low amplitude (Fig. 1D). This difference in amplitude is not a factor that can be shown readily in a sonogram. At least in the one shown (Fig. 1D) the pitch starts out at the same frequency as normal type-II songs, but ends at 6.5–7.0 kHz.

Black-throated grays are already singing upon arrival at FINLEY in mid-April. Observations of females (e.g., carrying nesting material) indicated that most nest-building was completed by the first week of May. Individual birds were not followed for continuous periods of time; therefore, the exact proportion of time that different song types were sung was difficult to quantify. Prior to 1 May, we estimated that type-II song was given for 95% of 25 h of observation. Beginning about 1 May, the frequency of type-II decreased and the use of type-I increased. As the study area was not visited on consecutive days, the change from type-II to type-I could only be approximated: during 25 h of observation in May and early June, the use of type-I increased until both song types were used equally. Although only short visits were made to the study area during late June and early July, it appeared that type-I was the most frequently used song type during this latter stage of nesting. Although it was difficult to follow individual birds for more than a few minutes, both type-I and type-II songs were given both from exposed perches (e.g., treetops) and while foraging (i.e., within the canopy).

The final song, called the “soft song,” was sung only when males were seen closely following their (apparent) mate while the female was gathering nesting material or foraging. This song could not be heard by the human ear more than about 10 m away from the singer.

When either type-I or type-II songs of the black-throated gray were re-played to a singing conspecific, the bird responded only with type-II song regardless of whether the bird was singing type-I or type-II prior to playback. Birds responded to playback by approaching to within a few meters of the speaker; results for these experiments were presented elsewhere (Morrison 1982).

Males were also observed on at least 10 occasions (undisturbed by playback) to switch from type-I to type-II when one approached to within apparently close (for the black-throated gray) proximity of another male (i.e., 20–30 m). Approaches of under 30 m usually resulted in the chasing of one bird by the other.

Discussion.—Type-II song in the Black-throated Gray Warbler apparently functions in territory establishment and defense and mate attraction, during early stages of the breeding period. This conclusion is supported by results of playback experiments—males always responded with type-II regardless of the song type presented. The frequency of type-II decreased after territory boundaries had become fixed and nesting was well underway.

The “soft song” apparently functions in male and female communication when birds are in close proximity. We do not know if the information content in this song differs from that

of the typical type-II, or if it is simply the result of male nervousness (or anxiety) because of the closeness of the female.

The use of type-I song is more difficult to explain. Morse (1966, 1967) concluded that type-I (his type B) functioned in courtship and pair-bond maintenance with the female in several eastern *Dendroica* warblers; this has been criticized by others (see later). Kroodsmas (1981) also suggested that type-I and type-II songs of the *Dendroica* warblers he studied could be related to mate selection and territorial defense, respectively. We doubt, however, that the specific function of type-I in the black-throated gray is male-female solicitation. Remember that type-I was not given during the early stages of the breeding period; thus it is not likely that type-I is reserved specifically for courtship. An additional hypothesis, concerning the function of multiple song types, was given by Krebs (1977, 1978) (see also McGregor et al., *Am. Nat.* 118:149-151, 1981; Yasukawa, *Anim. Behav.* 29:114-125, 1981). Krebs reasoned (the "Beau Geste" hypothesis) that repertoires allowed a territorial male to create the impression that there were several birds in his territory; new arrivals would thus falsely believe that there was a higher density of conspecifics in the area and thus settle elsewhere. Application of Krebs' hypothesis to our results seems inappropriate. If black-throated grays sought to create a false impression about density at FINLEY, then both type-I and type-II should be used during and shortly after arrival, and not after nesting is initiated.

We believe a more parsimonious explanation for the song types of the black-throated gray has already been given. Using the Black-throated Green Warbler (*D. virens*) studied by Morse (1967) as a model, Lein (1972, see also 1978) suggested that the black-throated green will normally produce type-I. But the addition of various external stimuli during the breeding period, such as the presence of a conspecific male, will cause a "frenzied" response which stimulates type-II (his type A) song. Absence of stimuli for type-II (and the "soft song") will automatically result in the production of type-I. Singing behavior of the black-throated gray can thus be viewed as a variation of a continuum. Both type-I and type-II song thus carry the same general information; that is, proclamation of identity.

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Song response by female Red-winged Blackbirds to male song.—Several studies have demonstrated that information may be transmitted within the temporal components of songs of birds (Falls, *Proc. XII Int. Ornithol. Congr.* 259-271, 1963; Emlen, *Behaviour* 41: 130-171, 1972; Thorpe, *Behaviour Suppl.* 18, 1972). While investigating the role of female vocalizations in the Red-winged Blackbird (*Agelaius phoeniceus*) social system, Corral noticed that, during the early part of their breeding season, female red-wings often gave their songs immediately following the songs of their mates. Whenever this response occurred, the females either initiated their songs within approximately 1 sec of male song, or midway through the song of the male. Examples of these timing relationships are presented in Fig. 1d-f. During the spring of 1978 Corral observed the singing behavior of mated pairs of red-