

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-

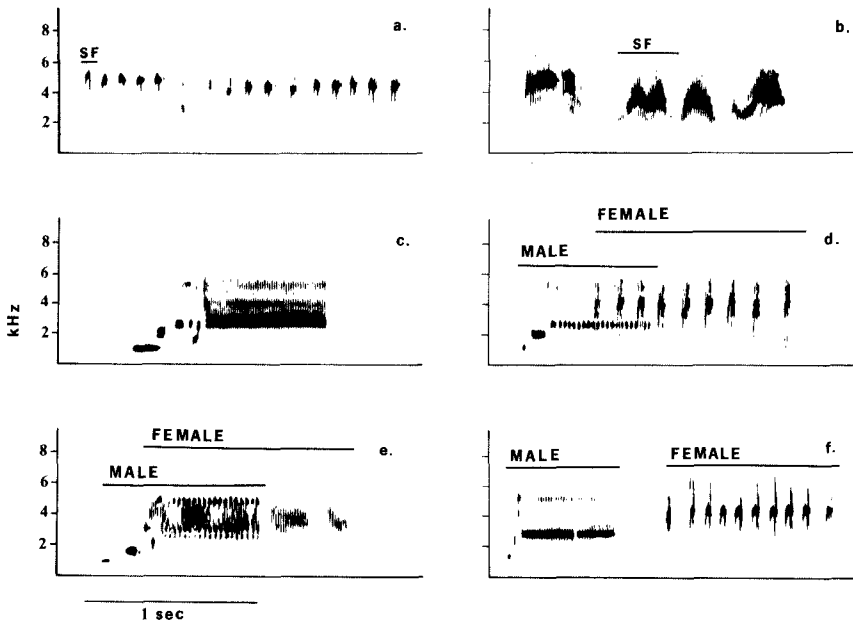


FIG. 1. Sonograms of red-wing songs: a. type 1 female song; b. type 2 female song; c. typical male song; d. type 1 song overlapping male song; e. type 2 song overlapping male song; f. type 1 female song following male song. (SF = song figure)

wings with the objective of determining if this male-female vocal interaction was temporally and biologically significant.

Methods.—Observations were conducted on a field in Old Field, Long Island, New York. Male red-wings, polygynous breeders, arrive in spring several weeks before females. Females arrived in mid-April in 1978 and subdivided the larger male territories into smaller, female “sub-territories” (Nero, *Wilson Bull.* 68:129–150, 1956; pers. obs.), which were defended from conspecific females. Males in the present study had one to three females nesting on their territories. The boundaries of the male territories and female sub-territories were determined by noting song perches and then connecting the outermost of these points. Birds were not marked, but spectrographic analysis of male song recordings made throughout the breeding season showed that all four males observed on the field maintained the same territories for the duration of the study (Smith et al., *Condor* 82:259–266, 1980). In addition, several banding studies have shown that female red-wings tend to maintain territorial position during the breeding season (Nero, *Wilson Bull.* 68:5–37, 1956; Lenington, *Anim. Behav.* 28:347–361, 1980; three of four females banded by M. Hayes at the University of Michigan/Dearborn Biological Field Station in 1981 remained on their territories).

Female red-wings sing two distinct song types (Fig. 1a, b). At times the two song types are combined into a single song, usually consisting of type 1 song figures followed by type 2 figures. Type 1 song appears to function in pair-bond maintenance, while type 2 appears to be an aggressive vocalization, sung chiefly in the presence of territorial intruders (Beletsky,

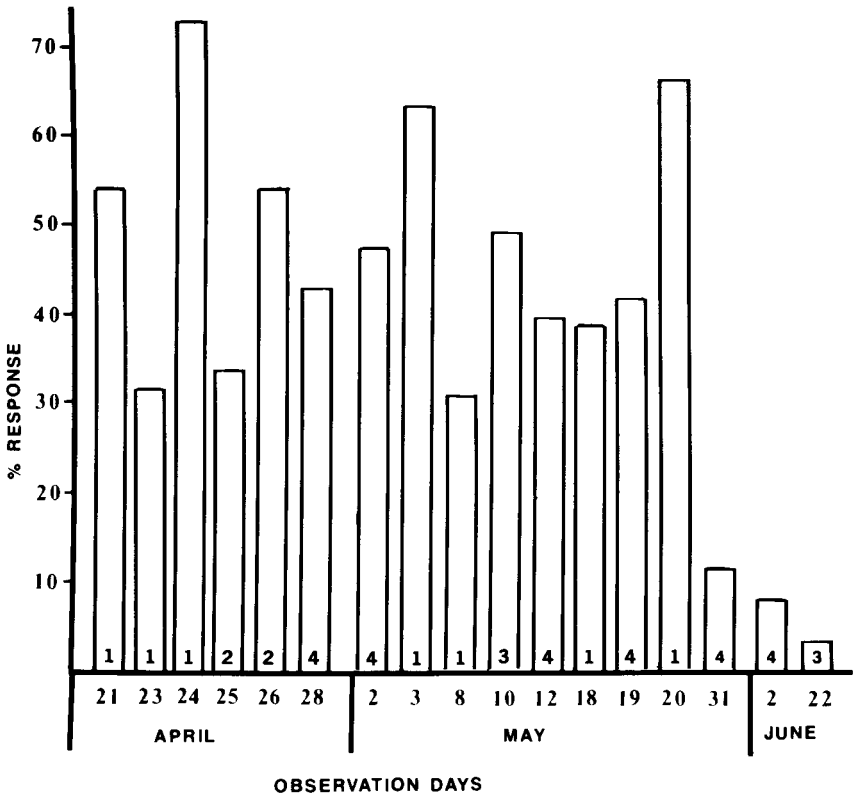


FIG. 2. The average percent response of female song to male song during the breeding season. Percent response = no. of female responses/no. of male songs given. The numbers inside the histogram bars are the number of pairs of red-wings, out of the possible seven, observed on each day.

Z. Tierpsychol. 62:47-54, 1983). The differential use of the two song types was not documented in 1978, but it was obvious that, although type 2 song occasionally followed male song, type 1 was sung by the females in the great majority of these situations. For a description of male red-wing song, see Orians and Christman (Univ. Calif. Publ. Zool. 84, 1968) or Smith et al. (1980).

Observations took place between 06:00 and 08:00 EST on the dates appearing in Fig. 2. The frequency and time of occurrence of male and female songs were recorded verbally into a cassette recorder, yielding a real-time record of the acoustic activities of the birds. Observations were begun when mated individuals were within 5 m of each other and ended when one of the birds flew out of sight (usually 5-10 min). Though only a fraction of the red-wing pairs were observed on any one day, over the 17 observation days all pair combinations were observed (two males had one female each on their territories, one had two females, and one had three females = seven possible pair combinations). From field observations and

playback experiments of male song to resident females performed in 1977, it was determined that a 1-sec-response criterion would closely reflect the natural timing of female songs to male song, i.e., a female was considered to have responded to a specific male song if her song followed the termination of that song within 1 sec. The percent response of a female to mate song was determined by dividing the number of female song responses by the total number of male songs sung during the observation period.

Recordings were made with a Nagra IV-L tape recorder through a Sennheiser 211 microphone mounted on a 46 cm parabolic reflector. Sonagrams were prepared using a Kay Electronics Vibralyzer model 7030A using the 300 Hz filter.

Results.—The first females arrived on the male territories on 17 April. On 21 April, when observations were initiated, all seven females were present on the territories. The data presented in Fig. 2 indicate that females consistently sang over 30% of their songs in response to male song within days of their arrival on territories of males; this high rate, averaging over 65% during some observation days, was maintained by the females under observation through most of May. As male and female red-wings typically sing at rates of four to five songs/min (Smith, Behaviour 56:136–156, 1976) and three songs/min (Beletsky, Anim. Behav. 31:355–362, 1983), respectively, and mean song durations for both sexes routinely fall between 1.0 and 1.5 sec (Smith et al. 1980; Beletsky 1983), the high percentages of male songs responded to vocally by females clearly depart from percentages that would be expected if chance alone was temporally connecting the songs. After 20 May, percent response to male song declined; this decrease coincided with an increase in the occurrence of copulatory and nest-building behaviors.

Discussion.—Data presented in Fig. 2 support the idea that female red-wings often respond immediately to their mates' songs with their own songs. The females of several other icterine species have been observed to answer their mates' songs with their own vocalizations, including Common Grackles (*Quiscalus quiscula*) (Wiley, Z. Tierpsychol. 40:244–264, 1976), Western Meadowlarks (*Sturnella neglecta*) (Falls, pp. 61–89 in *Advances in the Study of Communication*, Krames, Pliner and Alloway, eds., Plenum, New York, 1978), Northern Orioles (*Icterus galbula*) (Beletsky, Condor 84:445–447, 1982) and Brown-headed Cowbirds (*Molothrus ater*) (Dufty, Anim. Behav. 30:1043–1052, 1982).

Corral noted that females did not appear to sing in response to non-mate (neighbor and intruder males) song. However, playback experiments reported on elsewhere (Beletsky and Corral, J. Field Ornithol. 54:200–202, 1983) indicated that female red-wings responded with song to playback of both mate and non-mate male song. It was concluded that females responded vocally to any male occupying the territory; in the natural course of events, the male occupying the territory is the mate.

It is possible that one function of female song and its timing to male song is to convey pair-bond status information to the mate. Thorpe (Nature 197:774–776, 1963) suggested that songbird duets, precisely timed mutual singing between mates, may maintain or strengthen the pair-bond, facilitate the synchronization of reproductive physiologies, and keep mates aware of each other's locations. Evidence that red-wings use temporal information in their vocal communication system is given by Smith and Norman (Condor 81:83–84, 1979) who report "leader-follower" singing in male red-wings. They found that resident males sang their songs immediately following intruder songs at a relatively invariant time interval. It was proposed that this acoustic interaction served to inform the intruding males that the resident male was responding directly to the intruder. Likewise, it is possible that the female, by timing her song to that of the male, is conveying to her mate information such as her individual identity, physiological state and/or other pair-bond information. Since the response of females to male song is seemingly restricted to the pre-nesting phase of the breeding cycle, some aspect of the female song response could indicate to the male the female's readiness

to breed. Two advantages that might accrue to the female by singing in this relationship to her mate are: (1) most of the information is likely to be received by the male at a time when he is silent; and (2) constant repetition of the message at a fixed time interval would more clearly inform the male that the female is responding directly to him.

The results of this preliminary study indicate that at times the female red-wing is timing her song to follow her mate's song. Although more work is needed to describe the content of the information being exchanged, the mode of information exchange described now in inter- and intra-sexual social contexts for Red-winged Blackbirds might present a common, but usually overlooked form of animal communication.

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Selection of song perches by sagebrush-grassland birds.—Although song perches have been recognized as important components of avian habitat (Hilden, *Ann. Zool. Fenn.* 2: 53–75, 1965; Wiens, *Ornithol. Monogr.* 8, 1969), few studies have examined selection and characterization of perches in detail. Harrison (*Wilson Bull.* 89:486–487, 1977) tried, but was unable to show selection of higher artificial perches by five of six grassland species studied. A minimum number of suitable perches is considered a necessary habitat feature for several species of grassland and shrubland birds (Lack, *J. Anim. Ecol.* 2:239–262, 1933; Lack and Vanables, *J. Anim. Ecol.* 8:39–71, 1939; Kendeigh, *Condor* 43:165–174, 1941; Kendeigh, *Condor* 62:418–436, 1945; Zimmerman, *Auk* 88:591–612, 1971). Harrison and Brewer (*Jack-Pine Warbler* 57:179–183, 1979) and Knodel-Montz (*Wilson Bull.* 93:547–548, 1981) concluded, however, that population densities of grassland birds were not increased by providing additional perches in their studies.

The purpose of this study was to examine in detail characteristics of song perches used by four species of passerines that breed in sagebrush-grassland habitats: Brewer's Sparrow (*Spizella breweri*), Vesper Sparrow (*Pooecetes gramineus*), Western Meadowlark (*Sturnella neglecta*), and Horned Lark (*Eremophila alpestris*). My objectives were: (1) to describe vegetational features of song perches used by each species; (2) to make interspecific comparisons; and (3) to determine if there were preferences in use of perches compared to what was available. Several questions were addressed. Do individuals tend to select relatively large and conspicuous perches from which to sing? Do individuals that occupy the same local area show species-specific patterns of use? How do perches differ among vegetationally different sites? Are available perches limiting to shrubland and grassland birds?

Study area and methods.—The study was conducted 20 April–18 June 1980 on three 16-ha sites on the Vernon Division of the Wasatch National Forest, 10 km S of Vernon, Tooele Co., Utah. This cold desert area is located at 1800 m elev. in the southern end of Rush Valley. Big sagebrush (*Artemisia tridentata*) dominated two sites: one that had been plowed and seeded to grasses in 1963 (NONMAN) and one that had been chained and seeded in 1976 (CHAIN). The remaining site (BURN) was dominated by grasses, but sagebrush islands missed by a controlled burn in 1976 comprised 8% of the site. The most common grasses were bluebunch wheatgrass (*Agropyron spicatum*), crested wheatgrass (*A. cristatum*), cheatgrass (*Bromus tectorum*), and Sandberg bluegrass (*Poa sandbergii*). More detailed site de-