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Song Type for Intrasexual Interaction in the Bush Warbler

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In many species of passerines, males sing more than one song type (Kroodsma and Baylis 1982). Recent studies have shown that the use of different song types can vary depending on the sex of the receiver (Kroodsma 1981, Catchpole 1983, Groschupf 1985, Smith and Smith 1992, Wiley et al. 1994, Luschi and Seppia 1996), the level of intrasexual aggression (Lein 1972, 1978; Trainer 1987), and whether the song is used for long-range or short-range communication (Lein 1978, Catchpole and Leisler 1989, Titus 1998).

Bush Warblers (*Cettia diphone*) are small passerines that breed from April to October throughout most of Korea. Their songs consist of an introductory "whistle" portion and an ending "syllable" portion (see Fig. 1). The whistle portion is composed of 1 to 15 notes, and the syllable portion has 2 to 6 syllables. Bush Warblers give two distinctive song types that are easily recognized in the field. In the first half of the song, one type has an intensive and continuous whistle, whereas the other type has a weak and discontinuous whistle.

Yoon et al. (1995) analyzed singing rate, syllable composition, and physical characteristics of the two song types from three local populations of Bush Warblers. They found that the number of notes in the whistle portion was the most distinctive feature to define the song types. The alpha song has only one or two notes in the whistle portion and seems to have one long, continuous introductory note (Fig. 1). In contrast, the beta song has more than two notes in the whistle portion (Fig. 1), which sounds like a stuttered whistle. Compared with beta songs, alpha songs have fewer notes and a higher dominant frequency in the whistle portion, a higher maximum frequency in the syllable portion, and are of longer overall duration (Table 1). Alpha songs also have more syllables in the syllable portion than do beta songs, and the duration of the syllable portion is longer (Table 1, Fig. 1).

During spontaneous singing, species such as Cetti's Warblers (*Cettia cetti*) and Eastern Kingbirds (*Tyrannus tyrannus*) sing only one song type or an extremely high proportion of one song type (Smith and Smith 1992, Luschi and Seppia 1996). In contrast, individual Bush Warblers mix two song types during a single bout of singing (Yoon 1995) such that alpha and beta song types normally are given every second or third song, with about 10-s intervals between songs (e.g. ABABABAABA; Fig. 2). One song type is not usually repeated more than two times in succession (Yoon 1995). Although the function of altering the presentation of different song types during spontaneous singing is not clear, it has been suggested that such behavior varies with the level of aggression (Catchpole and Leisler 1989).

The characteristics of alpha and beta songs in Bush Warblers are comparable to song types of other species. For example, the length and complexity of the two songs are similar to those of Great Reed-Warblers (*Acrocephalus arundinaceus*; Catchpole 1983) and Five-striped Sparrows (*Aimophila quinquestriata*; Groschupf 1985), and the different notes in the whistle portion are comparable to the different structural phrases in the songs of Blue-winged Warblers (*Vermivora pinus*; Kroodsma 1988). That is, the beta song of Bush Warblers is shorter in duration and has fewer syllables than the alpha song. These similarities in song structure imply that the two song types of Bush Warblers might have similar functions to the song types of other species.

Studies of Bush Warblers have assessed song recognition (Park et al. 1995) and geographic variation in song (Yoon 1995, Park et al. 1996), but no comprehensive study has examined the function of alpha and beta songs. Here, we present results of playback experiments that we conducted to investigate whether the use of alpha and beta song types by Bush Warblers varies with simulated territorial intrusions.

Methods.—The study area was located on Wando Island (34°30′N, 126°80′E) about 1 km from the Korean peninsula. Spontaneous songs of three individual Bush Warblers that did not have adjoining territories were recorded as stimulus songs on Jeju Island about 120 km from the study area. We used a Uher

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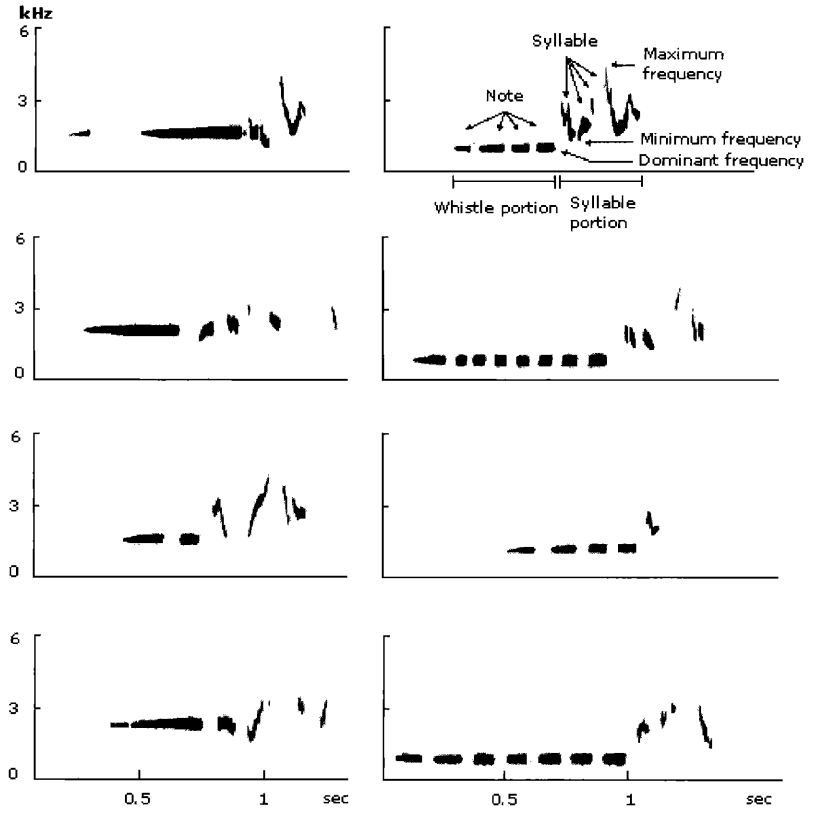

FIG. 1. Comparison of alpha (left) and beta (right) song types of four individual Bush Warblers.

4000 Report IC tape recorder with an AKG c1000s microphone mounted in a 54-cm parabolic reflector for the recording. Recorded individuals on Jeju Island have typical alpha and beta song types and similar repertoire sequences to Wando individuals, although they use several different syllables (Yoon et al. 1995). Each stimulus recording was 3 min in duration. The proportion of songs and the song interval were not manipulated in the playback tapes. Each playback tape consisted of 18 (9 alpha and 9 beta), 19 (9 alpha and 10 beta), and 19 (10 alpha and 9 beta) songs.

Territorial boundaries of 13 subject males were determined by observation before the playback experiments. All playback experiments were carried out between 0630 and 1100 from 10 to 13 May 1995 and from 22 to 27 April 1996. We recorded about 50 spontaneous songs from subject males immediately before starting playback experiments. The playback commenced only when the bird was singing. One of the three playback tapes was selected at random, and each male was tested only once. The stimulus song was broadcasted from a JBL-ProIII speaker placed approximately at the center of the subject male's territory. The speaker was connected to a Sony TCM-5000EV cassette recorder using 20 m of electrical chord and was attached to a tree 1.5 m above the ground. Using a precision integrating sound-level meter (Larson Davis Laboratories Model 800B), we adjusted the volume level of the playback song to about 90 dB at a distance of 1 m from the speaker. The songs of each subject were recorded during the 3-min playback experiments and for 3 min after the playback. Recordings of responses were made 20 to 30 m from the playback speaker at a tape speed of 190 mm/s using the same equipment that was used for recording spontaneous singing.

We analyzed spontaneous and response songs of the 13 subject males using a Kay 5500 Sonagraph with the following settings: frequency range, DC-8 kHz; input shaping, Hi-Shape; buffer size, 4.0 s; dynamic range, 43 dB; and analysis attenuation, 20 dB. During the analysis, we individually measured the number of the alpha and beta songs before, during, and after the playback experiments.

We used angular transformations of the data to create a normal distribution (Sokal and Rohlf 1981). We used a group *t*-test to assess whether responding males used the song types differently during spontaneous singing and playback experiments in 1995

TABLE 1. Characteristics ($\bar{x} \pm$ SD) of alpha and beta songs of male Bush Warblers in Korea (adapted from Yoon et al. 1995: table 3).

Whistle portion			Syllable portion				
No. of notes	Dominant frequency (Hz)	Duration (s)	No. of syllables	Maximum frequency (Hz)	Minimum frequency (Hz)	Duration (s)	Song duration (s)
Alpha songs (n = 134)							
1.4 ± 0.34*	1,591.1 ± 152.25*	0.82 ± 0.20	3.6 ± 0.66	4,629.5 ± 574.45*	1,066.0 ± 157.60	0.38 ± 0.11*	1.32 ± 0.21*
Beta songs (n = 130)							
4.4 ± 0.61	945.2 ± 30.56	0.72 ± 0.12	2.3 ± 0.89	3,755.2 ± 731.54	1,047.4 ± 141.17	0.22 ± 0.10	0.98 ± 0.16

* $P < 0.05$ (one-way ANOVA between alpha and beta song types).

versus 1996 and a paired t-test to determine whether one song type was used more frequently during and after playback compared with spontaneous singing.

Results.—The 686 spontaneous songs that we recorded (range 24 to 79 songs per individual) consisted of 373 alpha songs (range 30.8 to 73.2%) and 313 beta songs (range 26.8 to 69.2%). Bush Warblers did not use one song type more than the other during spontaneous singing (Fig. 3), and the proportional use of the two song types during spontaneous singing and during response to playbacks did not differ between 1995 and 1996.

During playback, four males sang only beta songs, and nine males sang both song types. The 119 response songs recorded ($\bar{x}$ = 9.2 ± SD of 5.03 songs, range 4 to 20) consisted of 23 alpha songs (range 0 to 40.0%) and 96 beta songs (range 60.9 to 100%). The 187 songs recorded after playback ($\bar{x}$ = 15.6 ± 5.12 songs, range 4 to 23) consisted of 78 alpha songs (range 0 to 76%) and 109 beta songs (range 24 to 100%). Bush Warblers sang a significantly higher proportion of beta songs during the playback experiment than during spontaneous singing (t = 7.50, P < 0.0001), but differences between spontaneous singing and singing after the playback experiment were not significant (Fig. 3). The proportion of beta song in response to playback increased during the initial 2 min of playback, and then gradually decreased.

Discussion.—We found that male Bush Warblers responded to playback stimuli on their territories by changing the proportion of song types given during a song bout. In our previous experiments, Bush Warblers generally approached the playback speaker within a few minutes of hearing the stimulus and then searched for intruding males. When they did not find an intruder, they started singing (Yoon 1995, Park and Park 1996). During the experiments conducted for this paper, all subject males approached the speaker and then sang.

During playbacks, Bush Warblers used more beta songs than alpha songs, indicating that the relatively short, simple beta song functions in territorial interactions. Great Reed-Warblers and Aquatic Warblers (*Acrocephalus paludicola*) also use a shorter song type when challenged by rival males (Catchpole 1983, Catchpole and Leisler 1989), and Five-striped Sparrows use their short song in intrasexual interactions (Groschupf 1985). Our results provide another example of the use of relatively short songs during interactions between males. We do not know why short songs are used in these situations, but it has been suggested that the use of short songs enhances communication in a rapidly changing situation (Highsmith 1989).

Species such as Eastern Kingbirds and Aquatic Warblers provide information on their social behavior through the proportional use of two different song types (Catchpole and Leisler 1989, Smith and

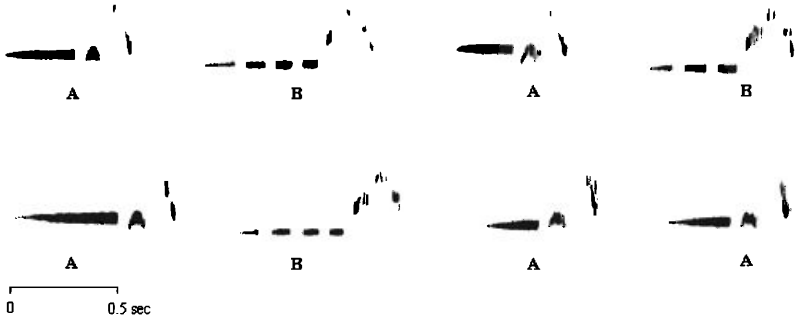

FIG. 2. Example of a series of songs given by a male Bush Warbler (A, alpha song; B, beta song). The intervals among song types are not real time.

Smith 1992). During playback experiments, most male Bush Warblers increased the proportion of beta songs, and 4 out of 13 individuals sang only beta songs. After the playback, however, the proportion of alpha and beta songs returned to that observed during spontaneous singing. These results imply that male Bush Warblers change the proportion of the two song types in response to the presence of a conspecific male intruder.

Unlike the role of beta song in intrasexual interactions, alpha song probably plays a role in intersexual selection. Yoon et al. (1995) suggested that Bush Warblers use the alpha song to effectively advertise to nearby females because the alpha song has a higher dominant frequency in the whistle portion than does the beta song. This interpretation is plausible given the high densities attained by Bush Warblers (up to 170 individuals per km^2; Haneda and Okabe 1970). Catchpole (1980) showed that female European Reed-Warblers prefer males that produce elaborate songs, and long, complex, variable songs frequently are used to attract mates. The alpha songs of Bush Warblers are longer in duration and contain more syllables than the beta songs. These patterns are similar to the long songs that Great Reed-Warblers, Five-striped Sparrows, and Dark-eyed Juncos (*Junco hyemalis*) use to attract mates (Catchpole 1983, Groschupf 1985, Titus 1998), and they suggest that alpha songs play a role in attracting females. In conclusion, our results indicate that alpha and beta songs of Bush Warblers are specialized for mate attraction and territory defense, respectively, and that the use of two songs for intra- and intersexual selection is not mutually exclusive but complementary through control of the proportion of different song types given during a song bout.

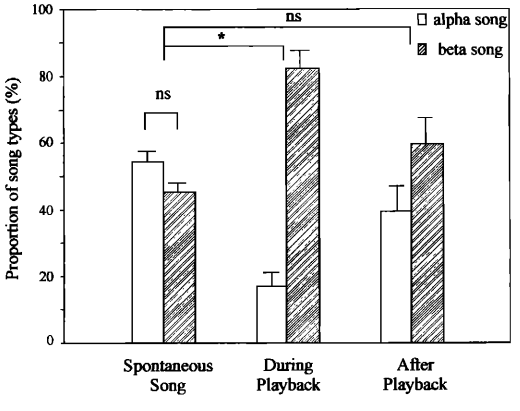

FIG. 3. Proportion of alpha and beta song types ($\bar{x} \pm$ SE) given by male Bush Warblers in spontaneous songs and during and after playback experiments (*, $P < 0.0001$; ns, not significant).

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Use of Blocked Design Increases Efficiency of Data Collection in Field Ornithology Study

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Numerous authors have addressed the need to minimize observer effects in field ornithology studies (Bart and Schoultz 1984, Balph and Romesburg 1986, Verner and Milne 1990). One approach is to train and test observers for song identification ability and hearing range (Kepler and Scott 1981, Hanowski and Niemi 1995). It is also common for ornithologists and ecologists in general to create balanced designs (having equal numbers of known effects per treatment) with observer and other effects in mind. Be-

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