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Male Song Repertoire Size and Syllable Sharing of Oriental Great Reed Warblers, *Acrocephalus orientalis*

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Abstract: The size of song repertoires mainly provides evidence for explaining sexual selection for female choice as well as male-male competition. We investigated the role of oriental great reed warbler songs (*Acrocephalus orientalis*) of breeding territorial males. Early arrived males possessed larger song repertoires, paired earlier, and tended to become polygynous. No correlation was found between arrival date and territory size, but polygynous males significantly occupied larger territories than non polygynous males. Song sharing was low among males and the degree of similarity did not relate with spatial distance. Our results suggest that song repertoire of the oriental great reed warbler males play a role in female choice, where territory quality may affect male pairing success.

Key words: song repertoire, sexual selection, female choice, syllable sharing, *Acrocephalus orientalis*

INTRODUCTION

Bird song diversity has been explained with various selective forces and their constraints in the process of avian communication, where two evolutionary forces of inter-(female choice) and intrasexual selection (male-male competition) have helped to explain the diversity of song structure and its usage (Catchpole and Slater, 1995; Falls, 1988; McGregor, 1991). In particular, larger song repertoires are favored by these two evolutionary forces because the exaggerated number or complexity of song and syllable types are more efficient in attracting females and in excluding intruders from the territory (Searcy and Andersson, 1986; Read and Weary, 1992; Catchpole and Slater, 1995). The males with larger repertoires or more complex songs increased mating success by attracting females earlier in the season or by extra-pair copulation (Howard, 1974; Catchpole, 1980, 1986; Temrin, 1986; Björkund, 1990; Buchanan and Catchpole, 1997), which suggest that female choice has played an important role in using song repertoires.

Song may serve as a reliable indicator of male quality (Catchpole and Slater, 1995). Female songbirds may select older males using repertoire size because the older males being able to increase the number of song repertoire may indicate survival ability as well as offspring viability (Hasselquist et al., 1996; Kokko, 1998). However, when the repertoire size itself is considered to be a key target for selection, the effect of female preference for larger repertoire size disappeared after territory quality, which was confounded with repertoire size, was controlled in some species (for example, great tit *Parus major*: Krebs et al., 1978; McGregor et al., 1981; red-winged blackbird *Agelaius phoeniceus*: Yasukawa, 1981; and pied flycatcher *Ficedula hypoleuca*: Alatalo et al., 1986). This is also seen in the great reed warbler (*Acrocephalus arundinaceus*; Catchpole, 1986; Forstmeier and Leisler, 2004).

The oriental great reed warbler, *Acrocephalus orientalis*, is a common summer visitor in East Asia and commonly breeds in wetlands with reed-beds (Lee et al., 2000). It was once recognized as the same species with Europe great reed warblers, *Acrocephalus arundinaceus* (Won and Gore, 1971; Dyrcz and Nagata, 2002). A clear taxonomic status is needed. As for the great reed warblers living in Europe, it is well studied on the aspects of song characters and behaviors: its song plays a role in the sexual attraction of females (Catchpole, 1980, 1983) as well as in the reproductive success (Catchpole, 1986). However, to date, few studies have been conducted on the oriental great reed warbler songs in terms of mate choice and sexual selection.

Our research goal was to investigate the relative importance

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of male song characteristics as measured by the repertoire size and territory quality by territory size on female choice. In addition, as the various sizes of repertoires in songbirds may be consequences of song learning by a process of social interaction, the song learning may ultimately increase the repertoire sizes. Thus, we examined the degree of song sharing among males within a population to infer the song learning and interaction through male-male competition.

METHODS

The study was conducted from 1 March to 30 July 2006 at Yangsuri, Yangpyung-gun, Kyoungki-do, Korea (37°33'N, 127°19'E). The study area is an island located in the confluence of Bukhan and Namhan rivers, and the great reed warbler population annually breeds in a natural reed-bed along the rivers. A total 14 males were observed. We regularly visited the study site from 04:30-09:00 and 17:00-20:00 and noted males' nuptial status, territory boundaries, and singing behavior. To identify territorial boundaries among males, 8 sticks of 2 m height were arrayed at 10 m intervals. Individual territories were numbered and mapped on a diagram through daily observation except for raining or heavy windy days. As the territory boundaries varied with progress of breeding season, territory size (m^2) was estimated by the time of pairing. Pairing date was defined as the date on which the female was first seen on the territory and continued to be present on the next observation date.

To count repertoire size of the great reed warbler songs, we used an Orbitor parabolic microphone (OR 308X) connected to laptop computer, where songs were recorded and analyzed through Raven 1.2 software (Cornell Lab. of Ornithology, Ithaca, NY) with sampling rate 44.1 kHz. We did not band any territorial male, but we could confirm the identification of each individual by checking the song syllables while recording the warbler songs through the laptop computer on the spot. Then, we printed out all songs in order to identify and compare the repertoire sizes among males.

"Syllable" was used as a unit of song composition to measure the repertoire sizes as Catchpole (1986) did. The number of syllable types obtained from the each subject male tended to increase till pairing date and then become asymptotic (Fig. 1). Thus we measured the asymptotic value as the repertoire sizes. In addition, to infer the degree of similarity between songs of neighboring males, we used adjusted Jaccard's coefficient, Sj (adj), as suggested by Tracy and Baker (1999), that is:

$$Sj\ (adj)=a/(a+b+c)-s,$$

Where a is the number of syllables shared between any two songs, b is the number of syllables unique in one song, c is the number of syllables unique in the other song and s is the difference of the number of syllables between the two songs. By adding the 's' term to the original JC, Sj (adj) can produce pair-wise simailarity among non-matched syllable sets more precisely. Mantel tests (Mantel, 1967) were performed to examine the effects of geographc distance on syllable similarity among male songs within a population. Two symmetric matrixes were produced with 10,000 permutations for randomization distributions.

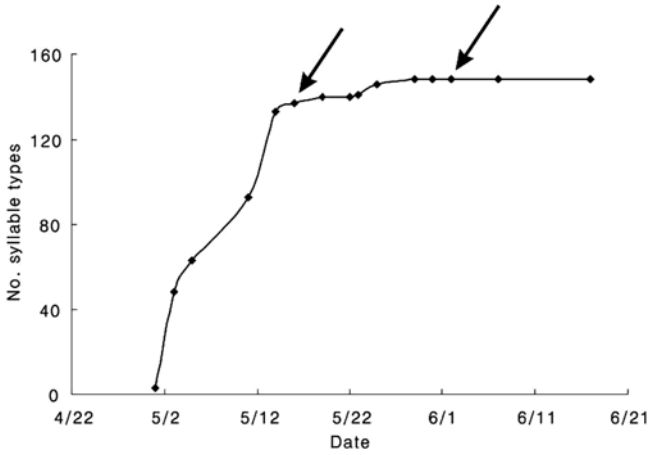

Fig. 1. Cumulative numbers of new syllable types across the breeding periods of polygynous Male A of oriental great reed warblers. Arrows indicate the pairing dates. After first pairing, the graph became asymptotic, where repertoire size is determined.

We tested the data for deviation from the normality (One-sample Kolmogorov-Smirnov Test $P<0.05$) prior to the use of parametric statistical tests. We used one-way ANOVAs to compare the repertoire sizes between polygynous and non-polygynous male songs. Non-parametric Spearman's rank tests (Zar, 1999) were used to evaluate the relationship among measurements of male reproductive performance, pairing success, and territory size. In particular, a partial correlation was used to describe the relationship between repertoire size and arrival date while controlling for the effect of territory size. Numerical data are presented as mean±SD. Data were analyzed using SPSS statistical software (v.11.5; SPSS, 2002).

RESULTS

Male arrival and pair formation

A total of 14 male great reed warblers arrived at breeding sites from 1 May till 29 May and females started to settle on from 16 May. Five of the six males that already settled before females arrived at the breeding site became polygynous and the other male became a bachelor while five of eight males settled after females arrived became monogamous, two male bachelors, and one male polygynous. Early arrived males paired earlier ($r_s=0.89$, $n=14$, $P<$

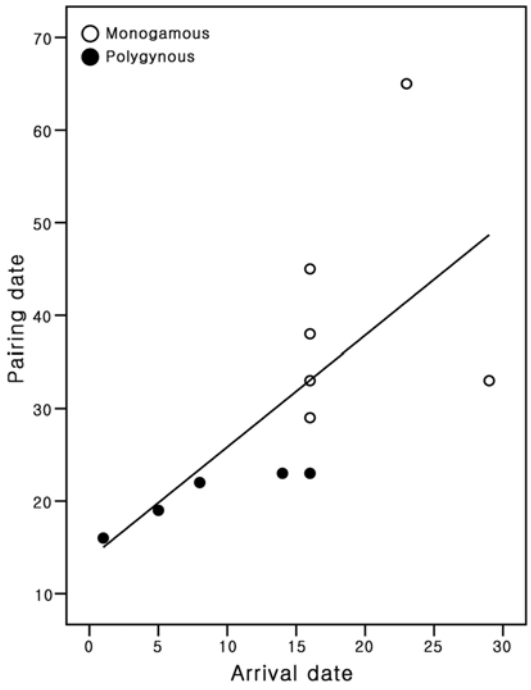

Fig. 2. The positive relationship between arrival date and pairing date. The ticks of X-axis refer from 30 April to 30 May, and Y-axis from 10 May to 9 July.

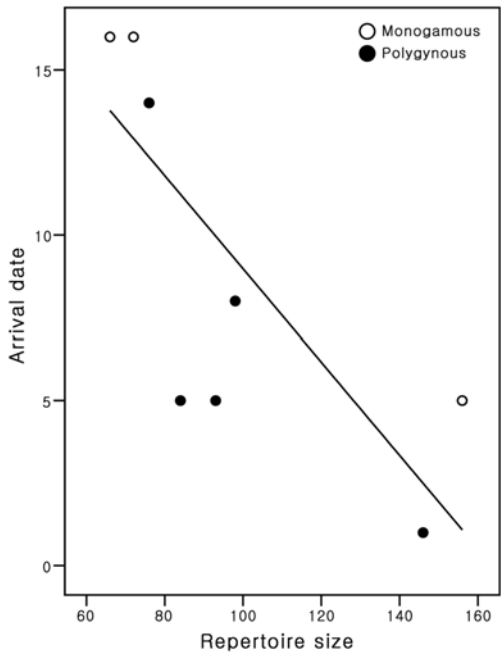

Fig. 3. The negative relationship between arrival date and repertoire size. The ticks of Y-axis refer to the date from 30 April to 15 May.

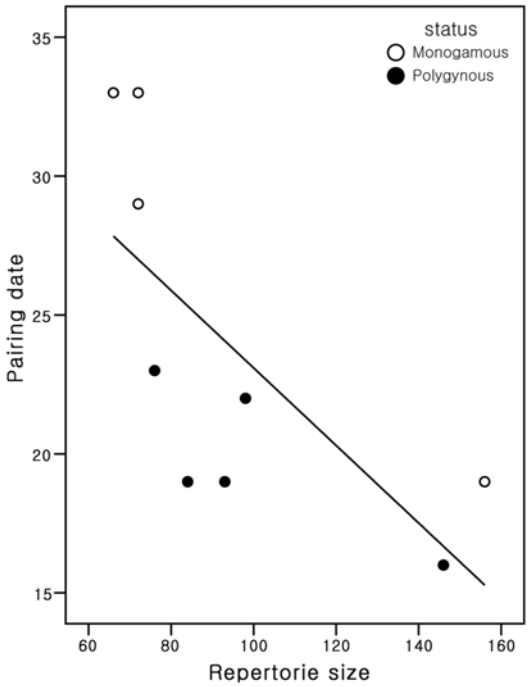

Fig. 4. The negative relationship between pairing date and repertoire size. The ticks of Y-axis refer to the date from 15 May to 4 June.

0.0001; Fig. 2). In addition, early arrived males tended to establish a larger territory but the territory size decreased with arrivals of later males. Thus, the territory size was not significantly related with male arrival date (r_s=–0.37, n=14, P=0.198), nor with pairing date (r_s=–0.36, n=14, P=0.213).

The mean repertoire size of nine male songs was 95.9 (±33.0), and the male repertoire size strongly negatively correlated with male arrival date (r_s=–0.87, P=0.003; Fig. 3) and male pairing date (r_s=–0.87, P=0.002; Fig. 4), and not with territory size (r_s=0.24, P=0.527). In addition, repertoire size strongly negatively correlated with arrival date even when territory size is held constant (r=–0.897, P=0.003). In terms of male pairing success (measured as harem size), polygynous males occupied larger territories ($F_{1, 12}$=9.490, P=0.010), arrived earlier ($F_{1, 12}$=6.661, P=0.024), and paired earlier ($F_{1, 12}$=8.502, P=0.013) than non-polygynous males. However, there was no difference in male repertoire sizes between polygynous and non-polygynous males ($F_{1, 7}$=0.113, P=0.746).

Repertoire size and syllable similarity

A total of 226 syllable types were identified from nine male songs and a syllable catalog for 95 types was prepared (Park, 2007). The mean ratio of the number of shared syllable types among male songs to repertoire size of each male was 0.10±0.03 (n=9, range=0.06~0.13). Syllable similarity coefficients (Sj(adj)) within a population were calculated from six male songs based on the degree of sharing syllables (Table 1). The degree of syllable similarity between songs of A and F was highest (0.55) while between songs of C and F was lowest (0.18). There was no relationship between syllable similarity based on pair-wise comparisons of male songs and geographic distance (Mantel test: r=–0.314, p=0.1827; Fig. 5).

Table 1. Syllable similarity coefficients (Sj(adj)) obtained by pair-wise comparisons between total syllable types of each individual within a population in the oriental great reed warblers

	A	B	C	D	E
A	1.00				
B	0.53	1.00			
C	0.49	0.41	1.00		
D	0.45	0.24	0.28	1.00	
E	0.43	0.25	0.43	0.24	1.00
F	0.55	0.34	0.18	0.19	0.34

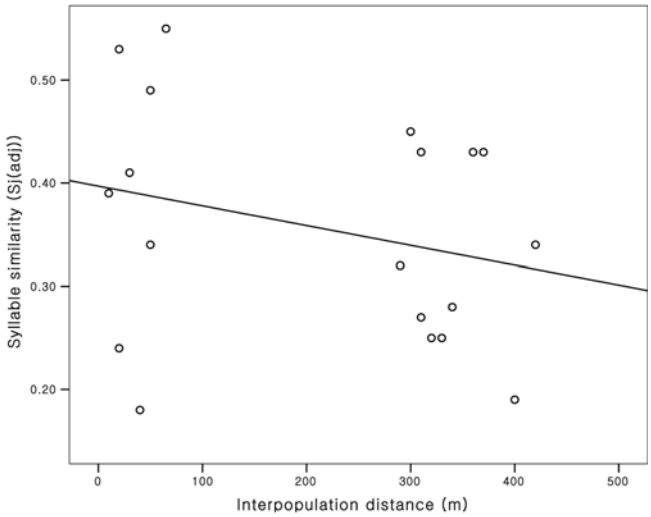

Fig. 5. Syllable similarity among male songs based on the pair-wise coefficients (Sj(adj)) in relation to spatial distance.

DISCUSSION

Female choice for larger repertoire size of warbler songs

The present results demonstrate that song repertoire of the oriental great reed warbler males plays a role in female choice, where territory quality may affect male pairing success. The warbler males that arrived at breeding site earlier possessed more song repertoires and paired earlier without occupying larger territories than the later arrived males. The males with larger repertoire sizes tended to become polygynous, but the polygynous males did not possess larger repertoires; rather the territory size plays a role in some way in male pairing success because polygynous males significantly occupied larger territories than non-polygynous males. For the same population studied in 2000 and 2001 by Lee (2002), similar results were reported, but the females mated earlier with males with larger territory sizes.

In case of the well studied songs of European great reed warblers, once recognized as the same species with oriental great reed warblers, the role of song repertoire size for harem size is less emphasized due to territory quality and male age (Hasselquist, 1998; Forstmeier and Leisler, 2004). A recent research by Forstmeier and Leisler (2004) showed positive correlation between repertoire size and harem size from a German population in 1981-1982, and not in 1994-2000. The former was probably caused by covariation with territory quality while the latter was caused by a declined population size that in turn changed the role of territory quality. In addition, Hasselquist (1994, 1998) showed repertoire size of male songs was positively correlated with harem size, which was confounded by the factor of male age so that female preference may not obvious. In our study, several possibilities remain: first, the previous study on the same population showed territory quality played an important role in female choice (Lee, 2002). Second, we did not capture the territorial males to reveal the age effect, so that we could not tell at present whether it is the case by age effect. To be en effect, song repertoire sizes should increase with age like the Swedish population (Hasselquist 1994, 1998) or syllable switching (a measure of immediate versatility and strophe length) increased with age like the German population (Forstmeier et al., 2006).

The fact that males with larger repertoire sizes settled and attracted females earlier indicate that song may serve as a reliable indicator of male quality (Catchpole and Slater, 1995; Nowicki et al., 2000). In migratory birds, early arrived males should face to early harsh conditions, such as weathers and food, to overcome. Only males with good body condition can afford to the costs of early arrival and they may be the males of highest phenotypic quality (Marra and Holberton, 1998; Møller and de Lope, 1999). Females in this population tended to mate with heavier males with longer wings (Lee, 2002). In general, early arrived males occupy and defend high-quality territories. At present, we do not know whether female choice is directly based on the larger repertoire size of oriental great reed warbler songs or on the territory quality, or on both. We do not role out the possibility of female preference for the larger song repertoires, and we need more detailed study on this subject.

Syllable sharing among territorial males within a population

Syllable sharing is common in many other species of songbirds because song learning is extensive (Kroodsma, 1974; Payne, 1981; Mundinger, 1982; Sung and Handford, 2006). The learning procedure in particular between territorial neighbors may include a process of social interaction, such as by copying a male that matched one of the memorized song types stored from a hatching year or the following spring (Marler, 1990; Nelson and Marler, 1994). A frequently observed phenomenon of male-male interaction for territory establishment and maintenance is song matching, by which they may increase song similarity

between them as well as they may finalize repertoire size (Nicholson et al., 2007).

In addition, males with high song similarity were better to keep their territory longer or to increase their reproductive success (Beecher et al., 2000; Beecher and Brenowitz, 2005). Thus, high intensity of male-male competition between neighboring males may increase syllable similarity, which in turn the males may efficiently maintain territorial boundaries by matching songs.

In this population, song sharing between neighboring males was low and syllable similarity did not related with spatial distance. The results may happen if oriental great reed warbler males show low breeding site fidelity and if song learning is limited within very short period time (e.g. between the first and second years of age). On the other hand, if repertoire size increases with age through song learning, new songs will be added ultimately through male-male competition. Furthermore, if the song is used for male-male competition, the song similarity will be increased and the increased repertoires, in turn, may help to occupy and maintain territories more efficiently (Yasukawa, 1981; Krebs et al., 1978). From the several years of studies on two different populations of the great reed warblers, Forstmeier and Leisler (2004) suggested that song repertoire is related to more male-male completion rather than female choice. The main reasons were the strong correlation between repertoire size and territory quality and no clear female preference to song repertoire size. At present, we do not know the age effect on song repertoire size. However, there was no relationship between territory size and repertoire size and the bachelors in this population kept producing new syllable types (Park, 2007) regardless of neighboring males' song repertoire till pairing. In other words, the repertoire size produced by them might be related to male quality of memorizing and using songs (Nowicki et al., 1998; Buchanan, 2000) directed for female choice.

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