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Relationships of Settlement Date and Body Size with Reproductive Success in Male Oriental Great Reed Warbler *Acrocephalus orientalis*

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Yu-Seong Choi, Yun-Kyoung Lee, and Jeong-Chil Yoo (2010) Relationships of settlement date and body size with reproductive success in male Oriental Great Reed Warbler *Acrocephalus orientalis*. *Zoological Studies* **49**(3): 398-404. Relationships of the settlement date and body size with the reproductive success of Oriental Great Reed Warbler *Acrocephalus orientalis* males was studied at Yangsu-ri, Yangpyeong-gun, and Gyeonggi-do, Korea during 4 breeding seasons (1998-2001). Although most males were monogamous (50.6%), some were polygynous (25.9%), and others were unmated (23.5%). Males that settled earlier were more likely to mate with females earlier, were likely to be polygynous, and consequently had higher reproductive success. Early-settling males had longer wings and tails, and greater mass than later-settling ones. However, although body size was an important factor affecting the settlement date in males, it did not directly affect reproductive success. This study showed that the settlement date is an important factor predicting reproductive success in males. http://zoolstud.sinica.edu.tw/Journals/49.3/398.pdf

Key words: *Acrocephalus orientalis*, Body size, Breeding status, Reproductive success, Settlement date.

In migratory birds, males that arrive earlier at the breeding grounds often occupy better territories and consequently have higher reproductive success (Arvidsson and Neergaard 1991, Wiggins et al. 1994, Aebischer et al. 1996, Lozano et al. 1996, Potti 1998, Currie et al. 2000). It is widely accepted that the timing of arrival at breeding sites by migratory birds is correlated with the condition of the birds, which leads to individuals of higher quality occupying better breeding territories (Møller 1990 2001, Kokko 1999, Morbey and Ydenberg, 2001, Lampe and Espmark 2003). For some species, there is evidence that males with the highest phenotypic quality (e.g., longer tail or wings) are the first to arrive (e.g., Lundberg and Alatalo 1992, Nyström 1997, Møller 2001, Regosin and Pruett-Jones 2001, Møller et al. 2003, Ninni et al. 2004). Some authors argued that arrival time generally reflects male quality, because the costs of advancing arrival time is always greater for individuals in a poorer condition (Møller 1994, Kokko 1999, Forstmeier 2002, Ninni et al. 2004). Competition for early arrival is most intense in polygynous mating species, in which some males mate with several females, while others remain unmated (e.g., Hasselquist 1998, Forstmeier 2002).

When choosing a mate, females can seek direct and/or indirect benefits. In several studies, the reproductive success of males depended on individual quality and territory quality (Searcy 1979a b, Alatalo et al. 1984, Ezaki 1990, Leisler et al. 1995, Hasselquist 1998, Lampe and Espmark 2003, Miyazaki and Waas 2003). However, a male's condition does not always correspond to high reproductive success. Because reproductive success of males is mainly limited by the availability of unmated females (Hasselquist 1998),

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males often compete among each other for mating opportunities (Emlen and Oring 1977, Urano 1985, Davies 1991). Thus, in territorial migratory birds with asynchronous arrival times among males, the availability of females will partly depend on the male's settlement date.

The Oriental Great Reed Warbler *Acrocephalus orientalis*, a summer visitor to Korea, is a marsh-nesting passerine bird with a polygynous mating system. It was formerly classified as a subspecies of the European Great Reed Warbler *A. arundinaceus* of western Eurasia (Dyrcz and Nagata 2002). Most males arrive earlier on the breeding grounds than females (Lee 2002, Park et al. 2009). Males that are already mated can acquire a new mate after a short (approximately 1 wk) period of pair-formation and nest-building (e.g., Urano 1985, Ezaki 1990). Thus, unmated males must compete with already-mated males for late-arriving females.

In this study, factors affecting male reproductive success in Oriental Great Reed Warblers, especially the effect of settlement time on reproductive success, were investigated. Male reproductive parameters and body characteristics which could affect male settlement time and female mate choice were measured. The ecological significance of settlement timing and body size on male reproductive success is discussed.

MATERIALS AND METHODS

This study was carried out during 4 consecutive breeding seasons from late Apr. to late July of 1998-2001 at Yangsu-ri, Yangpyeong, Gyeonggi, Korea (37°31'-37°33'N, 127°18'-127°20'E). The study area consisted of reed beds along a river, and was surrounded by rice fields and lotus ponds.

Daily visits were made to territories throughout the breeding season, from late Apr. to late July, and the settlement date, breeding behavior, and mating status were recorded. When a male frequently sang in an area not shared with other males for at least 3 d, he was regarded as a territorial male. Males normally settled in a territory within a few days after arriving at the breeding site, because they sought a proper site and had to compete with other males (Ezaki 1995). We could not determine the exact arrival dates of males, and hence we used the settlement date as the 1st observation day of a male in a territory. In most cases, once a male established a territory, it maintained it until the end of the breeding season. Territorial males were caught with mist-nets within 3 d from the 1st observation day for a newly settled male in each territory and marked with unique combinations of 3 colored bands and 1 aluminum band. The birds were released as soon as they were banded and measured. Adult birds were sexed by brood patch (females) or cloacal protuberance (males) and by differences in behavior (Urano 1985, Hesselquist 1998). Captured males were weighed with a portable digital balance (accurate to 0.1 g, Ohaus, USA). Body characteristics such as bill, tarsus, wing (outer primary feather), and tail lengths were measured with a pair of calipers (accurate to 0.01 mm, Mitutoyo, Japan) and a ruler (accurate to 0.1 mm).

It was also difficult to confirm the arrival dates of females as they were very quiet and cryptic, in contrast to males, and they moved within dense reedbeds and bushes. Females visited a number of males before settling in a territory (Bensch and Hasselquist 1992). Recently mated males began to sing short songs and guard their mate, and this period is regarded as the pairing time (Ezaki 1987, Hasselquist and Bensch 1991, Bensch and Hasselquist 1992, Hasselquist 1998). However, since it was difficult to know the exact date of pairing, the laying date of the 1st egg in the 1st clutch was used as a reference point for the pairing date of males (Urano 1985). To estimate the reproductive success rate of males, we determined the total number of females and young (as nestlings still alive on day 9 or 10 after hatching) in each territory (Urano 1985, Ezaki 1990, Bensch 1996, Hasselquist 1998). The mating status of males was defined as the number of females with which a given male was simultaneously mating. That is, polygynous males mated with at least 2 females simultaneously, monogamous males mated with only 1 female, and bachelors formed no pair during the breeding season.

In a statistical analyses of variables related to the settlement date, data were standardized as *Z* scores to remove variations among years; data were standardized by subtracting the mean for the year and dividing the result by the standard deviation for the year. As some males yielded data for more than 1 consecutive breeding record across the 4 yr of the study, we used only 1 season's data for the analysis (the 1st yr when they were observed) for each male to avoid pseudoreplication. We used a linear regression to analyze relationships between the settlement date and parameters which possibly affected male

reproductive success (pairing date, and numbers of mates and fledglings). We also used linear regressions to look at relationships of settlement date with body mass and size. Residuals from all tests were tested for normality. To examine the effect of body size on male reproductive success, body size was defined as the main parameter from a principal component analysis (PCA) with varimax rotation (Rising and Somers 1989). Linear regressions were then conducted to examine relationships between body size in the PC1 and PC2 scores and reproductive success. To examine differences in the settlement date and body size in relation to male mating status, non-parametric Kruskal-Wallis tests were used, and multiple pairwise comparisons were made with Dunn's test. We used SPSS 11.5 (SPSS 2002, Chicago, IL, USA) and methods described by Zar (1999). Two-tailed tests were used for all analyses.

RESULTS

Male mating status

From 1998 to 2001, 85 males occupied territories in the study area (average, 21.2; range, 17-26 males/yr). Most males were monogamous (50.6%); 25.9% were polygynous, and the rest were unmated (23.5%). The frequency of males in relation to the breeding status did not differ among years (Chi-square test, $\chi^2_6 = 4.816$, $p = 0.568$; Fig. 1). The sex ratio (females/males) did not differ for the 4 breeding seasons (mean ± SD = 1.09 ± 0.06, range, 1.00-1.12; Chi-square test, $\chi^2_3 = 0.097$, $p = 0.992$).

Settlement date

Most early-arriving males successfully mated while late-arriving ones did not. The mean settlement date differed according to the males' breeding status (Kruskal-Wallis test, $H_2 = 19.69$, $p < 0.001$; Fig. 2). Polygynous males arrived first, followed by monogamous males and bachelors (post-hoc Dunn's test, $p < 0.05$ in all cases). There were significant relationships between the settlement date and reproductive parameters among males (Fig. 3). Males that established a breeding territory earlier tended to have higher reproductive success. Earlier-settling males tended to pair earlier (linear regression, $F_{1,41} = 33.375$, $p < 0.001$; Fig. 3A), have more mates ($F_{1,57} = 26.807$, $p < 0.001$; Fig. 3B), and produce more fledglings ($F_{1,57} = 19.675$, $p < 0.001$; Fig. 3C).

Body size

Early-settling males had longer wings ($F_{1,40} = 5.945$, $p < 0.05$) and tails ($F_{1,40} = 12.042$, $p < 0.001$) than late-arriving males. Bill length ($F_{1,40} = 2.787$, $p = 0.103$) and tarsus length ($F_{1,40} = 0.800$, $p = 0.376$), however, were not related to the settlement date. Two components (PC1 and PC2) of body size variations estimated from the PCA results of 4 body characters (wing length, tail length, bill length, and tarsus length)

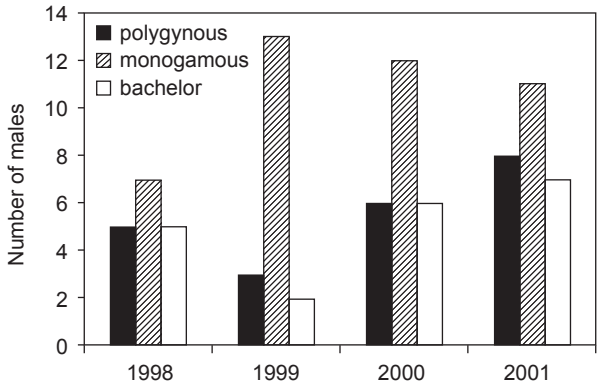

Fig. 1. Frequencies of the mating status of Oriental Great Reed Warbler males during 1998-2001 at Yangsu-ri, Yangpyeong, Korea.

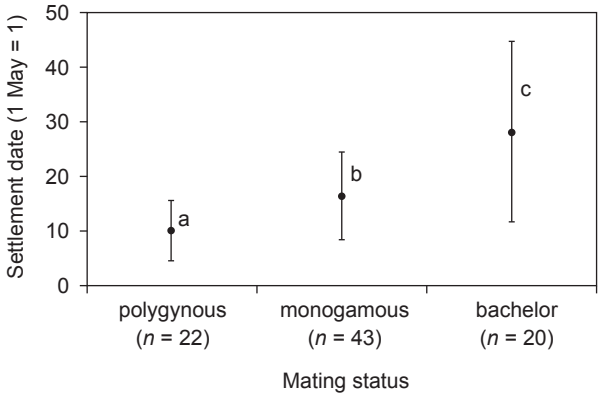

Fig. 2. Settlement dates (mean ± SD) of Oriental Great Reed Warbler males according to the mating status (1 May = 1) during 1998-2001 at Yangsu-ri, Yangpyeong, Korea. Numbers in parentheses are sample sizes. Different letters next to the mean circles denote a significant difference based on Dunn's multiple-comparison test ($p < 0.05$).

respectively accounted for 38.8% and 35.2% of the body size variation (Table 1). Tail length (0.891) was the most important PC1 parameter followed by wing length (0.869), while bill length (0.844) was the most important PC2 parameter followed by tarsus length (0.754). Finally, there was a significant relationship between the PC1 parameter and settlement date (linear regression, $F_{1,40} = 6.008$, $p < 0.05$; Fig. 4A), while the PC2 parameter was not related to the settlement date ($F_{1,40} = 4.016$, $p = 0.052$; Fig. 4B): males with larger wings and tails arrived earlier than males with smaller ones. However, there were no significant relationships between the PC1 parameter and reproductive success (no. of mates, $F_{1,40} = 1.996$, $p = 0.165$; no. of fledglings, $F_{1,40} = 3.054$, $p = 0.088$). There were also no significant differences between males' breeding status and body size measurements (Table 2).

DISCUSSION

In many territorial migratory bird species, early breeding results in higher reproductive success (Price et al. 1988, Møller 1994, Aebischer et al. 1996, Kokko 1999, Vergara et al. 2007). This implies a selective advantage for males that arrive early on the breeding grounds because they can occupy a territory of high quality (von Haartman 1968, Alerstam and Högstedt 1981, Alatalo et al. 1984 1986, Francis and Cooke 1986, Lundgerg and Alatalo 1992, Lozano et al. 1996, Lampe and Espmark 2003). In studies of the European (*A. arundinaceus*) and Oriental Great Reed Warblers (Urano 1985, Dyrcz 1986, Ezaki 1990, Bensch et al. 1998, Hasselquist 1998, Hansson et al. 2000), territorial occupation order in males was an important factor predicting male reproductive success and was positively correlated with pairing success and the number of fledglings. In our study, males that settled early in the season more

Table 1. Principal component (PC) analysis of 4 body characteristics of 41 male Oriental Great Reed Warblers during 1998-2001 at Yangsu-ri, Yangpyeong, Korea. The percentage of explained variance is also shown

Variable	PC1	PC2
Bill length	-0.037	0.844
Wing length	0.869	0.272
Tarsus length	0.051	0.754
Tail length	0.891	-0.236
Percent of total variance	38.83%	35.25%

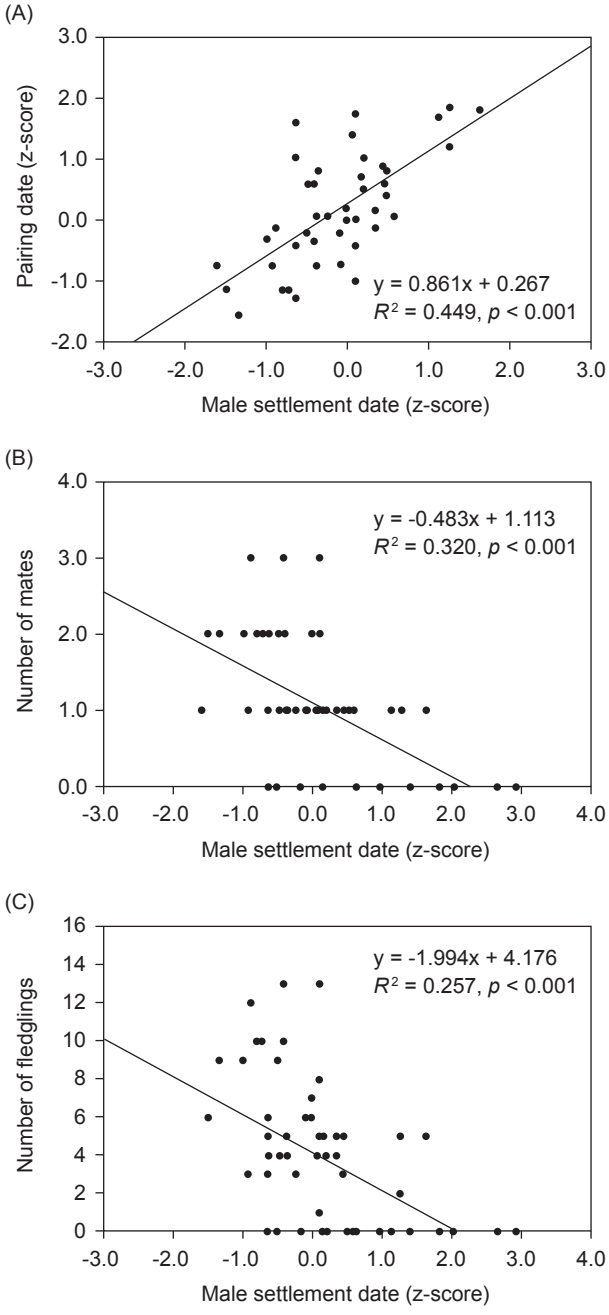

Fig. 3. Relationships between settlement date and reproductive success of male Oriental Great Reed Warblers during 1998-2001 at Yangsu-ri, Yangpyeong, Korea: (A) pairing date, (B) number of mates, and (C) number of fledglings. The settlement and pairing dates were transformed to Z-scores (see "MATERIALS AND METHODS"). The lines are fitted regression lines.

often became polygynous (Fig. 2), and thus the settlement date of males affected their breeding success (Fig. 3). These results show that early arrival on the breeding grounds is advantageous to males in terms of breeding success.

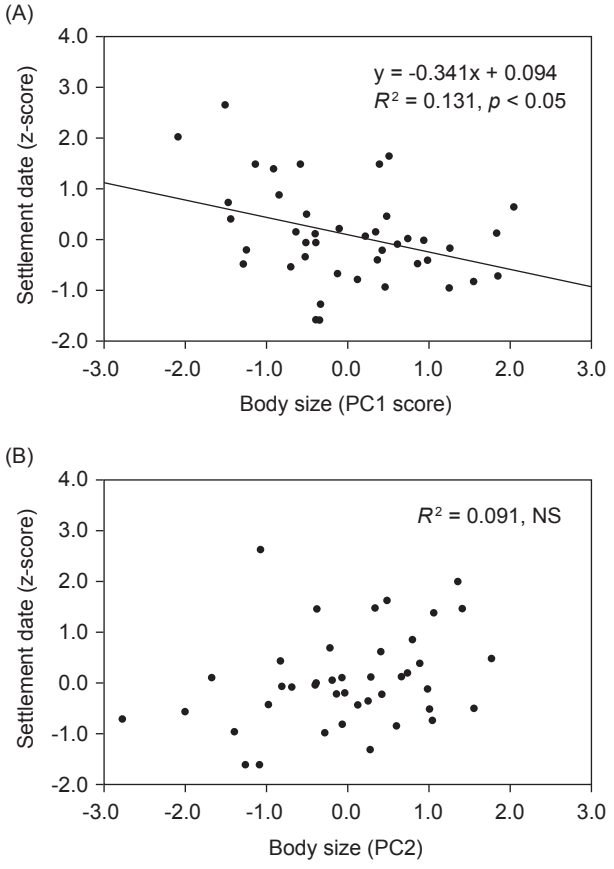

Fig. 4. Relationships between body size and settlement date in Oriental Great Reed Warbler males (n = 41) during 1998-2001 at Yangsu-ri, Yangpyeong, Korea: (A) principle component (PC)1 and (B) PC2 parameters. Body size variation scores were extracted from the PC analysis (PCA) of 4 body measurements (see "MATERIALS AND METHODS"). The lines are fitted regression lines.

When choosing a mate, females can seek either direct or indirect benefits, or both. In previous studies of the European and Oriental Great Reed Warbler (Ezaki 1990, Bensch and Hasselquist 1991, Bensch et al. 1998, Hasselquist 1998, Hansson et al. 2000), it was pointed out that the quality of a male's territory and/or male quality were important factors for female mate choice. Bensch and Hasselquist (1992) showed that females visited a number of males before settling and tended to choose early-arriving males. The quality of males and that of their territories were closely related to the timing of settlement. That is, earlier settlers could obtain territories of high quality. It is also well documented that individuals in good condition migrate earlier in the season (Francis and Cooke 1986, Alerstam and Lindström 1990, Lampe and Espmark 2003, Battley et al. 2004, Ninni et al. 2004). Earlier settlers had a larger body size than later ones, and body size showed a strong relationship with settlement date in this study (Fig. 4). Therefore, larger males (or those in good condition) arrived earlier than smaller ones (or those in poor condition), and the former might have established territories of higher quality. For instance, Ezaki (1990) showed that territories of early- and late-arriving males significantly differed in size and vegetation density. If females choose their mates on the basis of these qualities, the difference in the chance of acquiring a mate between early- and late-settling males would become even larger (Urano 1985).

A larger body size did not always guarantee higher breeding success, although larger males occupied breeding territories earlier in the season (Fig. 3A). In addition, there were no differences in body size measurements among males of different mating statuses (Table 3). These results suggest that body size did not have a direct influence on male breeding success i.e., females did not prefer

Table 2. Weight and linear measurements of Oriental Great Reed Warbler males in relation to mating status during 1998-2001 at Yangsu-ri, Yangpyeong, Korea. Data are presented as the mean ± SD

Body size characteristic	Polygynous (n = 13)	Monogamous (n = 21)	Bachelor (n = 8)	Kruskal-Wallis test
Body weight (g)	28.9 ± 1.3	28.9 ± 1.6	28.8 ± 1.6	H_2 = 0.012, p = 0.994
Bill length (mm)	24.7 ± 1.5	25.2 ± 0.9	24.7 ± 1.2	H_2 = 1.919, p = 0.383
Wing length (mm)	85.5 ± 2.2	84.7 ± 2.2	85.0 ± 2.4	H_2 = 0.897, p = 0.638
Tarsus length (mm)	28.5 ± 1.0	29.4 ± 1.3	29.1 ± 1.2	H_2 = 4.410, p = 0.110
Tail length (mm)	75.1 ± 2.6	73.9 ± 2.3	72.8 ± 4.4	H_2 = 4.171, p = 0.124

larger males, and also that male-male competition is not settled through body size differences in Oriental Great Reed Warblers. Indubitably, a large body size (more specifically large wing and tail feathers) plays an important role in the ability to fly during the long-distance migration. However, females possibly select their breeding partners by other cues rather than the body size of males. The reproductive success of males is affected by other factors such as age, song repertoire size, and territorial quality (Catchpole 1983, Leisler et al. 1995, Hasselquist 1998). In a study of the same Oriental Great Reed Warbler population in 2000 and 2001, Lee (2002) showed that repertoire size and song length of males as well as territory quality played important roles in female choice. Also, Park et al. (2009) showed that males that arrived at breeding site earlier possessed larger song repertoires and paired earlier without occupying larger territories than later-arriving males. In the European Great Reed Warbler, older males also had a larger song repertoire size and arrived earlier at the breeding site (Hasselquist 1998, Forstmeier et al. 2006). However, our results do not mean that body size is an insignificant factor for reproductive success of males. Although the body size of males is not a direct factor in mate choice by females, it may be an important factor in terms of male breeding opportunities. This is because larger males arrived early at the breeding grounds, allowing them to occupy high-quality territories which in turn resulted in high reproductive success.

In conclusion, early-settling males attracted mates earlier than late-settling ones mainly because late males had not yet settled at the time when females arrived on the breeding grounds. Urano (1985) suggested that early-settling males have a longer time to acquire mates and initially less competition, while late males have a shorter time and experience more competition. As a consequence, later-settling males have fewer opportunities to acquire mates than do earlier-settling males.

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