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SEXUAL DIFFERENCES IN FLIGHT CALLS AND THE CUE FOR VOCAL SEX RECOGNITION OF SWINHOE'S STORM-PETRELS[1]

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Abstract. Previous studies have shown that the Flight Calls of Swinhoe's Storm-Petrels (*Oceanodroma monorhis*) differ clearly between the sexes in their frequency component and that birds can discriminate the calls of either sex with few errors (Taoka et al. 1989b). But the cue for sex recognition has not yet been identified. In this study, we quantitatively analyzed the calls of both sexes for call length, number of syllables, and duration and interval of syllables. We found some sexual differences in rhythmic components, but mean ± standard deviation overlapped in all syllables. In order to make synthetic calls for playback experiments, frequency and rhythmic components were systematically manipulated. Birds recognized the synthetic calls having the same harmonic structure as female calls but those without harmonic structure were recognized as male calls regardless of whether the rhythm was that of the female or the male. Therefore, we concluded that harmonic structure is the cue for sex recognition. The mechanism of vocal sex recognition was compared with that of the closely related species, the Leach's Storm-Petrel (*O. leucorhoa*).

Key words: Vocalization; flight call; sexual difference; sex recognition; synthetic call; Swinhoe's Storm-Petrel, nocturnal seabird.

INTRODUCTION

There have been several studies on sexual dimorphism in the vocalizations and vocal sex recognition of nocturnal seabirds (James 1984, Taoka et al. 1989c). The birds' sexually monomorphic appearance and the limited visual information available at night increase the importance of vocal signals for communication.

Recently, we studied the vocal behavior of the nocturnal seabirds, Swinhoe's Storm-Petrels (*Oceanodroma monorhis,* Taoka et al. 1989b). We found that the Flight Call was sexually different in frequency component (Fig. 1) and birds inside burrows responded only to the playback Flight Calls of the same sex. However, sexual differences in parameters other than the frequency component have not yet been investigated. In the present study, recorded Flight Calls were analyzed for sexual differences in the rhythmic component of the calls. Four synthetic calls were used for playback experiments to evaluate which acoustic components are involved in sex recognition.

METHODS

The study was carried out on Chi'lbal Islet (125°48′E, 34°47′N) off the southwestern coast of Korea from 27 June to 26 July 1987. About 7,900 pairs of Swinhoe's Storm-Petrels breed on this islet and the egg-laying period is in early July (Won, unpubl. data). Flight Calls spontaneously given by birds inside nesting burrows were recorded with a cassette recorder (TC-D5PRO, Sony) and dynamic microphone (F-115, Sony). The rhythmic component of the recorded Flight Calls of 50 males and 50 females was analyzed with a digital sonagraph (model 7800, Kay) using a 300-Hz filter for the following parameters: call length, number of syllables, interval between onset of adjacent syllables, and duration of syllable. Sexual differences within these parameters were tested according to the t-test. When the variances differed significantly between the sexes (F-test, $P < 0.05$), the Cochran-Cox method was used.

Four synthetic calls were made for playback experiments by an FM sound generator (YM-2203, Yamaha) which was controlled by a sound board (PC-9801-26K, NEC) and microcomputer (PC-9801M, NEC). They were combinations of male or female types of frequency components and rhythmic components (Table 1). The sexual difference in the frequency component of Flight Calls has been described already (Taoka et al. 1989b): male calls are broad band sounds consisting of various frequencies, while female calls have harmonic structure (Fig. 1). Frequency components of the synthetic calls were made to reveal whether or not harmonic structure is re-

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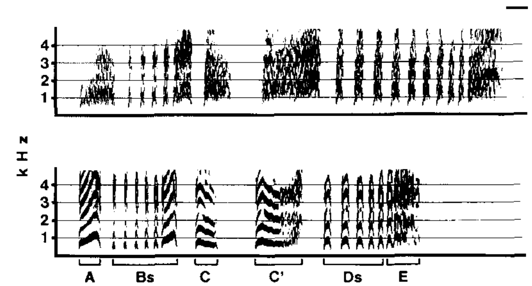

FIGURE 1. Sonograms of Flight Calls of a male (upper) and a female (lower). Letters under the sonograms are the names of syllables. Bs indicates a series of syllables between A and C, and Ds between C' and E. Syllables in Bs are numbered from the right and named B1, B2, . . . Syllables in Ds are numbered from the left and named D1, D2, . . . Time scale = 100 msec.

lated to vocal sex recognition. The male type consisted of 625 Hz and 726.5 Hz pure tones and the female type consisted of 625 Hz and 1,250 Hz pure tones (Fig. 2). Two types of rhythmic component imitated the durations and intervals of syllables of a male Flight Call and those of a female (Fig. 2).

The method used for the playback experiment of synthetic calls was the same as one used previously in a study for sex recognition of natural Flight Calls (Taoka et al. 1989b). So, we were able to compare the results of the synthetic calls with those of natural Flight Calls. In the previous study, Flight Calls of either sex were paired and played to birds inside burrows in the following way: a call of one sex was played five times followed by five playbacks of the other sex call. Birds inside usually responded with Flight Calls and/or aggressive calls, but some birds remained silent. Flight Calls were almost always emitted when the same sex calls were played. When the synthetic calls were tested in the same way, the synthetic call which evoked Flight Calls of males was determined to be recognized as a male call and the synthetic call evoking female Flight Calls was a female call.

The experiments were done at night from 17 to 26 July with a cassette recorder (TCM-17, Sony) placed at the entrance of the burrow. The four synthetic calls were divided into two groups (Table 1). One group consisted of the frequency and rhythmic components of the same sex and those of the second group consisted of the frequency and rhythmic components of the opposite sex. Two kinds of experimental tapes were

TABLE 1. Explanation of the four synthetic calls.

Synthetic call	Components of Frequency	Components of Rhythm
1st group		
MM	Male	Male
FF	Female	Female
2nd group		
MF	Male	Female
FM	Female	Male

made for each group (MM-FF and FF-MM for the first group, MF-FM and FM-MF for the second group). Each tape contained two synthetic calls which were tape-recorded to be played five times at the rate of once every 5 sec, respectively. In the first group MM-FF test, playbacks of MM were followed by playbacks of FF and the order was reversed in the FF-MM test. In the MF-FM and FM-MF tests of the second group, MF and FM were tested in the same way as in the first group tests.

A total of 131 burrows was used for the experiments. Each of the four kinds of tests was made only once for the same burrow. The order of the four tests for one burrow was randomly determined and tests were made at ≥2-day intervals. Vocalized responses to playback synthetic calls were recorded on cassette tape. For a test, the bird giving Flight Calls even once during five playbacks of the synthetic call was counted as a response but cases of more than one bird giving Flight Calls were eliminated. Burrows from which no vocalization was heard during a test were also eliminated. Birds giving vocalizations other than Flight Calls were counted as nonresponses. So the numbers of subject birds varied between the four tests. The sex of responding birds was determined by their Flight Calls (Taoka et al. 1989b).

RESULTS

No sexual differences were found in call length and number of syllables. Within the interval of a syllable, the only sexual difference was between the syllables B2 and B1; however, many sexual differences were evident in syllable duration (Fig. 3). Mean ± SD overlapped between the sexes in all syllables. The changing patterns between syllables in the rhythmic components were very similar between the sexes.

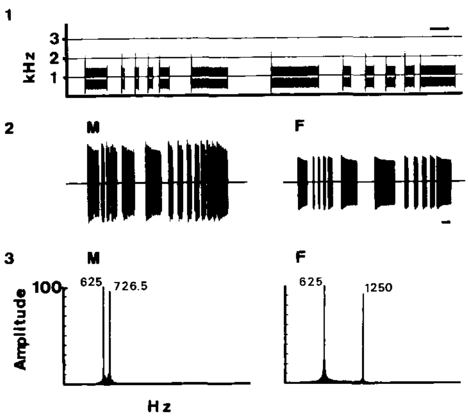

FIGURE 2. Explanation of the synthetic calls. (1) The sonogram of synthetic call, FF. (2) Wave forms of the rhythmic components of the male type (M) and the female type (F). (3) Power spectrograms of the frequency components of the male type (M) and the female type (F). M and F indicate the male type and the female type of the frequency or rhythmic component. Time scale = 100 msec.

The results of playback experiments of synthetic calls are summarized in Table 2. Among birds responding to only one out of the two synthetic calls in each test of the first group (MM and FF), MM always elicited responses from males and FF elicited responses from females with one exception. These birds discriminated between MM and FF, and recognized MM as a male call and FF as a female call. There were some birds that responded to both synthetic calls during a test; however, most of the male responses were given when MM was played first and most of the female responses were given when FF was played first. This is due to the fact that birds inside burrows have a tendency to give Flight Calls in response to playback Flight Calls of the opposite sex after responding to Flight Calls of the same sex (Taoka et al. 1989b). In the tests of the second group (MF and FM), the responses to MF were almost identical to MM and the responses to FM were almost identical to FF. Both MM and MF were recognized as male calls despite differences in rhythmic components. Similarly, FF and FM were recognized as female calls. This implies that the sexual differences in the rhythmic components of calls are not important but the presence or absence of harmonic structure within the frequency component is essential for sex recognition.

The numbers of birds correctly responding to

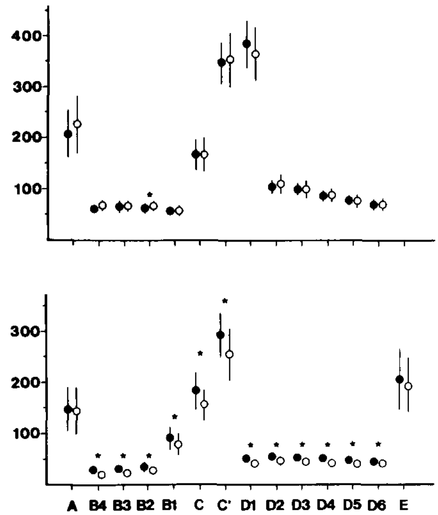

FIGURE 3. Sexual differences in interval (1) and duration (2) of syllables of the male calls (n = 50) and the female calls (n = 50). Circle with vertical line indicates $\bar{x} \pm$ SD. Closed circles indicate means of male calls and open circles indicate those of female calls. Names of syllables are shown under trace. Numbers of syllables in Bs and Ds varied between calls; $\bar{x} \pm$ SD of Bs is 4.5 ± 1.0 for males and 4.2 ± 1.1 for females, and that of Ds is 6.0 ± 1.7 for males and 6.2 ± 1.8 for females. There were no significant differences between the sexes (t-test, $P > 0.1$). Intervals were always measured between adjacent syllables and intervals to the followed syllables are shown. Stars indicate the syllables which are significantly different between the sexes (t-test, $P < 0.05$).

the synthetic calls (Table 1, values with stars) in the tests of the first group were significantly more than those in the tests of the second group (χ^2 = 4.38, $P < 0.05$). Sexual differences in the rhythm of a call have a certain relation to the cue for sex recognition.

DISCUSSION

Flight Calls of Swinhoe's Storm-Petrels can elicit responses from birds of the opposite sex as well as the same sex. When Flight Calls of either sex are played from a speaker on the ground, birds in flight are attracted above and emit Flight Calls in response to playbacks of calls of the opposite sex (Taoka et al., unpubl.), so vocal sex recognition of Flight Calls plays a role in pair formation as well as intrasexual territoriality (Taoka et al. 1989b). The ability to discriminate calls of either sex seems to be well developed because errors in sex recognition occur very rarely when the calls are played to birds inside burrows (Tao-

TABLE 2. Responses to synthetic calls (calls defined in Table 1). n = total number of birds. R = percentage that responded correctly to synthetic calls.

Test	Response to MM and FF: Only to MM, Male	Only to MM, Female	Only to FF, Male	Only to FF, Female	To both, Male	To both, Female	Non-response	n	R
MM-FF	13	0	1	19	19	3	33	88	
FF-MM	18	0	0	12	1	7	17	55	
Total	31*	0	1	31*	20	10	50	143	43%

Test	Response to MF and FM: Only to MF, Male	Only to MF, Female	Only to FM, Male	Only to FM, Female	To both, Male	To both, Female	Non-response	n	R
MF-FM	16	3	1	13	26	2	50	111	
FF-MM	19	0	1	10	9	3	28	70	
Total	35*	3	2	23*	35	5	78	181	32%

* Birds that correctly responded to the synthetic calls.

ka et al. 1989b). Since visual signals are less effective in communication between the nocturnal birds, the ability to discriminate Flight Calls of both sexes plays a major role in sex identification of the Swinhoe's Storm-Petrel.

It is considered that there are clear-cut sexual differences in the call structure of Flight Calls because of the few errors in sex recognition. Analyses of call rhythm demonstrated some sexual differences, but considerable overlaps were present between the sexes. On the other hand, the sexual difference in frequency components is so clear that the human ear can easily distinguish the calls of either sex. The cue for sex recognition is more likely to be provided by the frequency components and playback experiments of synthetic calls provided clear evidence for this.

The presence or absence of harmonic structure was sufficient for discrimination. A wide range of frequencies was not necessary for a call to be recognized as a male call. The percentage of responses to the playback synthetic calls was 65% in the MM and FF tests and 57% in the MF and FM tests. These are relatively low in comparison to the percentage of responses to natural Flight Calls which was over 80% (Taoka, unpubl.). When the synthetic calls were played from the speaker on the ground, almost no birds were attracted to the speaker (Taoka, unpubl.). The synthetic calls lacked some features characterizing Flight Calls, though they apparently had the cue for sex recognition. A relatively high-energy band was usually recognized within broad frequency bands of male Flight Calls (Fig. 1). Female Flight Calls have several harmonic bands and frequency changes both within and between syllables. The synthetic calls lacked these more complex frequency components and this may be why synthetic calls elicited fewer responses than natural Flight Calls. This implies Flight Calls may have features which are important for eliciting responses from conspecifics but which are not related to sex recognition.

Sexual dimorphism in vocalizations and vocal sex recognition have been reported in some nocturnal seabirds (Brooke 1978, 1986; Ristow and Wink 1980; Simons 1981; James 1984; James and Robertson 1985a, 1985b, 1985c; Taoka et al. 1989a, 1989b, 1989c). James (1984) divided them into two categories: (1) species where males have a sex-specific call, and (2) where sexual dimorphism exists in call types common to both sexes. Among the species belonging to the latter category, sexual differences of calls of several species exist in frequency components (Brooke 1978; James and Robertson 1985a, 1985b; Taoka et al. 1989b, 1989c). In Leach's Storm-Petrels (*Oceanodroma leucorhoa*) which are closely related to Swinhoe's Storm-Petrels (Cramp and Simmons 1977), the Chatter-call is used for sex recognition (Taoka et al. 1989a, 1989c). Quantitative analyses of Chatter-calls clarified that the rhythm of Chatter-calls has common features to calls of both sexes but the frequency component shows a clear sexual difference (Taoka et al. 1989c). The syllables of male Chatter-calls are significantly fewer than those of females and this sexual difference as well as the difference in frequency component are related to sex recognition (Taoka et al., unpubl.). Further, in the playback experiments of synthetic calls for Leach's Storm-Petrels, correct imitation of the changing frequency patterns between syllables is essential for recognition as a male call but it is not essential for female calls (Taoka and Okumura 1988). The mechanism in vocal sex recognition in Leach's Storm-Petrels seems to be more complex than that of Swinhoe's Storm-Petrels. In the case of Leach's Storm-Petrels, Chatter-calls of both the male and the female have a harmonic structure but male calls are higher in frequency than those of females (Taoka et al. 1989c). The sexual difference in the frequency tonality of Chatter-calls of Leach's Storm-Petrels seems to be more difficult to distinguish than that of Flight Calls of Swinhoe's Storm-Petrels. It is correspondingly difficult for the human ear to distinguish the sex of Chatter-calls (Taoka et al. 1989a, 1989c). So, more marked sexual differences in other parameters have evolved in Leach's Storm-Petrels than in Swinhoe's Storm-Petrels.

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