Sexual Dimorphism of Chatter-calls and Vocal Sex Recognition in Leach's Storm-Petrels (*Oceanodroma leucorhoa*)

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Sex specific signals of various sensory modalities have been reported in many animals (Sebeok 1977), but visual information is of little use to nocturnal animals. For example, vocal signals are important for sex advertisement in nocturnal seabirds (Brooke 1978, James 1984, Storey 1984). The Leach's Storm-Petrel (*Oceanodroma leucorhoa*) has only a few calls (Ainslie and Atkinson 1937, Hall-Craggs and Sellar 1976, Cramp and Simmons 1977, Ainley 1980). Three distinctive calls which are given by both males and females, namely the Chatter-call, Purr-call, and Screech-call (Taoka and Okumura 1988). The Chatter-call has a characteristic rhythm with ca. 10 syllables (Fig. 1) and is given by birds in flight, on the ground, and inside nesting burrows. We analyzed quantitatively the Chatter-calls of Leach's Storm-Petrel and performed playback experiments to clarify whether or not Chatter-calls are used for sex recognition in Leach's Storm-Petrels.

Daikoku Island (42°52′N, 144°52′E), located in the easternmost part of Hokkaido, is the only known colony of Leach's Storm-Petrels in Japan. A detailed description of the breeding biology of Leach's Storm-Petrels on this island is given by Watanuki (1985, 1986). The breeding season is from early May to late September. We conducted playback experiments on this island from June to August, 1984, and from May to July, 1985. We recorded Chatter-calls given in the nesting burrows with a cassette recorder (TC-D5PRO, Sony) and a dynamic microphone (F-115, Sony). The sex of vocalizing birds was determined by laparotomy (Taoka et al. 1988). The recorded Chatter-calls were analyzed by a sonograph (7029A, Kay) with a 150 Hz filter. We analyzed three Chatter-calls from each bird for the number of syllables, the interval between the onset of adjacent syllables, the duration, and the frequency of each syllable (Fig. 1). The mean of the three calls from the same birds was used to analyze sexual differences. We measured the frequencies at the part with the highest value within the fundamental frequency band of each syllable (abbreviated as HF). Calls of 16 birds were also analyzed by the power spectrograms obtained from the FFT analyzing system composed of a 12-bit A/D converter board (I/O Data) and a 16-bit microcomputer (PC-9801M, NEC). The sampling rate for digitizing is 20 kHz. Each HF was almost identical with the frequency at the peak on the power spectrogram (Taoka et al. 1989). Chatter-calls of two males and two females were used for playback experiments to birds inside burrows. The test call was played back 10 times (once every 5 s) with a cassette recorder (TCM-17, Sony) placed at the entrance of each burrow. The responses of birds inside burrows were recorded on a cassette tape. Afterwards, the burrows were inspected to count the birds. Each burrow was tested only once. We eliminated cases where more than one adult was found in the same burrow.

We analyzed Chatter-calls for 14 males, 12 females, and 63 birds of unknown sex. Standard deviations (SD) of calls from the same birds were small. The values of CV (CV = SD/$\bar{x}$) were <5% in most of the birds. Chatter-calls given by the same birds were almost identical.

We found a clear sexual difference in HF of syllable-C (HFC, Fig. 2). Chatter-calls were separated into two groups. HFCs of all known males had a frequency of >800 Hz. HFCs of all known females made up a group of <750 Hz. Consequently, we considered the calls in the higher frequency group to be those of males, and those in the lower frequency group to be females. Five pairs of calls were recorded from burrows where a male-female pair was present. Calls of each pair were also separated into these two groups (Fig. 2). In other call parameters, the ranges of known males overlapped those of known females, and the calls of sex-unknown birds were not separated in the two distinct groups. Only HFC analysis was reliable for sexing.

We sexed 89 birds by HFC analysis of Chatter-calls: there were 48 males and 41 females. HFC ($\bar{x}$ ± SD) of the 48 males was 990 Hz ± 95; that of the 41 females was 650 Hz ± 61. The distributions of male and female calls were not significantly different from the normal distribution (Kolmorgorov-Smirnov test, $P > 0.200$). The probability that the HFC of a male call would be <750 Hz was <0.006. The probability that the HFC of a female call would be >800 Hz was <0.006. We believe the sex of the birds can be determined reliably by the HFC. To date, only cloacal inspection (Serventy 1956) and laparotomy (Taoka et al. 1988) have been used for sexing Leach's Storm-Petrels.

From the calls of 89 birds, we selected calls of 50 birds (33 males and 17 females) for further analysis. The number of D-syllables in series was greater in female than in male calls (Mann-Whitney *U*-test, $P < 0.01$). However, the $\bar{x}$ ± SD of both sexes overlapped. Only a few syllables were sexually different in duration and interval (Mann-Whitney *U*-test, *P* <

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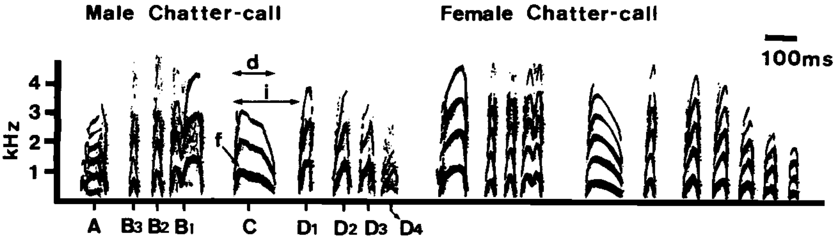

Fig. 1. Sonograms of Chatter-calls. The syllables (A, B3, B2 . . .) are shown under the sonograms of male call. Parameters for each syllable are interval between adjacent syllables (i), duration (d), and HF which was measured at the point (f) of the highest frequency within the fundamental frequency band.

0.01), and the means of both sexes also overlapped. Hence, the rhythms of the calls were common to both sexes. The ranges of HFC frequency of both sexes overlapped except for syllable-C (Fig. 3). Means of male HF, however, were higher than in females in all syllables and the mean of the sexes did not overlap in syllables B2, B1 and C (Fig. 3). In general, male calls are higher than female calls. To analyze the frequency changes between syllables, we calculated the differences in HFs between adjacent syllables. The changing frequency pattern is essentially identical between the sexes (Mann-Whitney *U*-test, $P > 0.10$). Similarities in call rhythm and changing frequency pattern make it difficult for the human ear to discriminate between the calls of the sexes.

In playback experiments, birds inside burrows gave Screech-calls, wheeze parts of Purr-calls and Chatter-calls in response. Only Chatter-calls were different between the sexes. The birds giving Chatter-calls were sexed by HFC analysis. Birds inside the burrows responded only to the playback calls of the same sex (Table 1). We sexed birds which did not give Chatter-calls by laparotomy. All the birds that did not respond to the playback of male calls were female ($n = 27$) and only two females did not respond to the playback of female calls ($n = 23$). Birds inside burrows almost always responded to playback Chatter-calls of the same sex but never responded to those of the opposite sex.

Recently, the sexual differences in the vocalizations of nocturnal seabirds have been reported (Brooke 1978, 1986; Ristow and Wink 1980; Simons 1981; James 1984; James and Robertson 1985a, b, c; Taoka et al. 1989). Sexual differences in calls of these species seem to be detectable by the human ear, but no quantitative analyses have been conducted except in the case of the Bulwer's Petrel (James et al. 1985c). We demonstrated sexual dimorphism in Chatter-calls of Leach's Storm-Petrels by quantitative analyses. Sexual dimorphism in calls of other species considered to be sexually monomorphic might be detected through a similar quantitative analysis.

Leach's Storm-Petrels recognize conspecifics by vocal signals. To function in sexual recognition, the difference in Chatter-calls should be very clear. We found that HFs in other syllables were also associated with sex recognition. The call rhythm is an essential factor to elicit responses from birds in the playbacks of synthetic calls (Taoka and Okumura 1988, in prep).

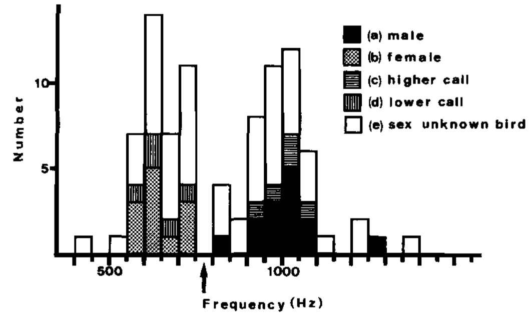

Fig. 2. Histogram of sexual difference in HFCs of 89 birds. The arrow separates the two groups; (a) and (b) are calls of birds sexed by laparotomy; (c) and (d) are calls of both members of a pair; (c) is the higher frequency call of a pair and (d) is the lower; (e) is the bird not sexed by laparotomy.

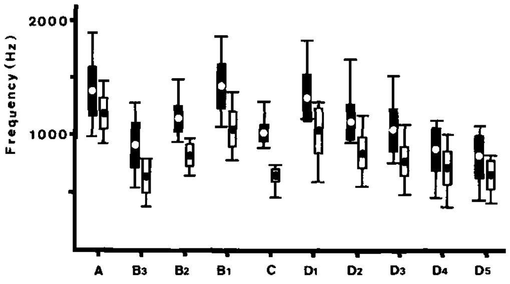

Fig. 3. Frequencies of syllables of calls of both sexes. Syllable names as in Fig. 1. Open circles, in dark boxes represent the $\bar{x} \pm$ SD of 33 male calls. Dark circles and clear boxes represent calls of 17 females. Vertical lines indicate ranges. Only the mean for syllable-C was significantly different between sexes (Mann-Whitney *U*-test, $P < 0.01$).

TABLE 1. Discrimination of Chatter-calls by birds inside burrows.

Playback	With response		Without responses
	Male	Female	
Male call			
(A)	52	0	31
(B)	12	0	9
Female call			
(A)	0	37	45
(B)	0	11	19

According to Catchpole (1982), diurnal seabirds are usually in close proximity in breeding colonies, so emphasis is on visual signals. Sounds are more likely related to sexual behavior and mate recognition than to territorial defense. In the Manx Shearwater (*Puffinus puffinus*), a nocturnal seabird, vocalizations play important roles in mate recognition and attraction of potential mates, and also in territorial defense and competition for mates (Brooke 1978, Storey 1984, James 1985). Vocalizations related to territorial defense in nocturnal seabirds are reported in other species (Brooke 1986). In Leach's Storm-Petrel, calls played loudly from a speaker attracted birds of the opposite sex (Taoka et al. 1989), which may be related to pair formation. The vocalizations of Leach's Storm-Petrels appear to have increased functions when compared with other diurnal seabirds because visual signals are not available (Brooke 1978, James 1984, Storey 1984, Taoka et al. 1988).

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Orientation of Trans-Saharan Passerine Migrants in Southwestern Spain

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Radar observations in the southwestern Iberian Peninsula revealed south-southwesterly directions for trans-Saharan passerine migrants (Hilgerloh 1985a, 1988, 1989). If an individual species was oriented to the southeast (Zink 1977, Gwinner and Wiltschko 1978), one would not realize it on the radar screen. Orientation tests are necessary to determine the orientation direction of different species. The questions arise, whether mean directions of species differ significantly from one another and whether they correspond to the mean directions observed by radar.

Test birds were captured in the "Algaida" pine forest near Sanlucar de Barrameda (36°48'N, 06°17'W) at the mouth of the river Guadalquivir (southwestern Spain) during August, September, and October in 1985 and 1987. I tested the most numerous species (Hilgerloh 1985b) on 52 nights. These included Pied Flycatcher (*Ficedula hypoleuca*), European Willow Warbler (*Phylloscopus trochilus*), Garden Warbler (*Sylvia borin*), European Nightingale (*Luscinia megarhynchos*), Greater Whitethroat (*Sylvia communis*), Spotted Flycatcher (*Muscicapa striata*), and European Reed-Warbler (*Acrocephalus scirpaceus*). Sample sizes varied according to the number of birds captured. I tested each bird on the night after the day on which it was captured; subsequently, I released it. Orientation tests were performed outdoors at the location of capture. I used funnel-shaped orientation cages (Emlen and Emlen 1966) to record the birds' activity; typewriter correction paper was the recording medium (Beck and Wiltschko 1981). Tests commenced shortly after sunset and lasted 90 min. The tests were performed on moonless nights with less than 3/8 overcast and with a natural magnetic field.

The data were analyzed by quantifying footprint densities in each of twenty-four 15° sectors. Nightly mean directions relative to true north were calculated by vector analysis (Batschelet 1981) and pooled for analysis of individual species. Birds with <20 scratches total activity were excluded. A mean direction of orientation was calculated for each species with >15 tested individuals. The Rayleigh test was used to test for nonuniformity of the distributions. For compar-

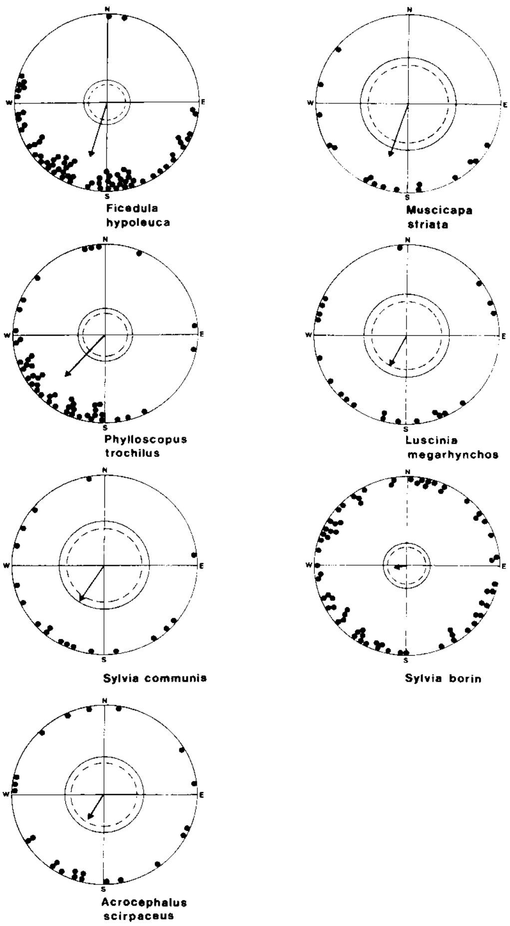

Fig. 1. Orientation of long-distance passerine migrants. Each dot represents one night's average for an individual. The arrow represents the mean vector; the two inner circles are the 5% (dotted) and the 1% significance border for the length of the mean vector (Rayleigh Test).