

Vocal Behavior of Swinhoe's Storm-Petrel (*Oceanodroma monorhis*)MIKI TAOKA, PYONG-OH WON,¹ AND HIROSHI OKUMURA²*Department of Biology, Japan Women's University, Mejirodai Bunkyo-ku, Tokyo 112, Japan*

Swinhoe's Storm-Petrel (*Oceanodroma monorhis*) is a nocturnal seabird related closely to Leach's Storm-Petrel (*Oceanodroma leucorhoa*). Swinhoe's Storm-Petrel breeds in the northwestern Pacific Ocean on small islands around the Japan Sea or off Korea (Palmer 1962, Cramp and Simmons 1977, Won and Lee 1986). A few distinctive call types have been described (James and Robertson 1985a, Won and Lee 1986), but little is known about their importance in communication.

We studied Swinhoe's Storm-Petrel on Ch'ilbal Islet (125°48'E, 34°47'N) off the southwest coast of Korea from 27 June to 26 July 1987. Approximately 7,900 pairs breed on this islet from mid-May to October, and the egg-laying period is early July (Won unpubl. data). We recorded spontaneous vocalizations of birds inside burrows with a Sony TC-D5PRO cassette recorder and Sony F-115 dynamic microphone. After each recording, we examined the burrows for the presence or absence of eggs and the number of adults. Chicks were not present during the study period. The sex of the birds was determined by examining their gonads or by their Flight Calls (see below).

We conducted playback experiments to birds inside burrows to clarify sex recognition by Flight Call. Two pairs of Flight Calls of both sexes were played back with a Sony TCM-17 cassette recorder placed at the entrance of the burrow. The birds' responses were recorded on a cassette tape. First, the male call was played back five times at the rate of once every 5 s, followed by a playback of the female call in the same way. This was performed in reverse order on another day. We selected randomly 70 burrows for the experiments and all were used to test both pairs of calls. The same burrow was used only once on any day. To avoid the possibility that birds abandon their burrows because of this procedure, the burrows were not inspected after each trial. Therefore, it was unknown whether the birds were silent or merely absent from their burrows when no vocalizations were heard.

The colonies on the slopes around the islet were roughly divided into five parts and a study site was located near the top of each part. At each study site, we counted the Flight Calls given by birds in flight (FFC), and on the ground or inside burrows (GFC), for 10 min at 0100 and 0300. These counts were conducted on two nights in early and late July at each site. We counted FFCs directly. We recorded GFCs with a cassette recorder using a microphone and parabolic reflector pointed downwards at a height of 1

m. Afterwards, the recorded Flight Calls were counted.

Vocal activity was scarce in the daytime but increased 1 or 2 h after sunset. We recognized three main calls: the Flight Call, Burrow Call, and Aggressive Call (Fig. 1). Rarely, calls of "ku, ku," or "chu, chu," were also recorded.

Flight Calls showed a characteristic rhythm with >12 syllables (Figs. 1-1, 1-2). The rhythm of the early part of the call was similar to that of the Chatter-call of Leach's Storm-Petrel (Cramp and Simmons 1977, Taoka et al. 1988). This call was given in flight, on the ground, and inside the burrows. We heard only Flight Calls in the daytime. The Flight Calls were divided according to the differences in frequency components. One type consisted of broad-band syllables (FC-A, Fig. 1-1). The other consisted of the fundamental frequency bands and their harmonics (FC-B, Fig. 1-2). Laparotomies were performed on birds giving Flight Calls. All FC-As were male calls ($n = 10$), and all FC-Bs were female calls ($n = 7$). Hence, we could determine the sex of the birds by the sound of their Flight Calls because the two types were easily distinguished by ear.

Burrow Calls were usually long-lasting and consisted of repeated short notes with a terminal wheeze part (Fig. 1-3). This call was given mainly from burrows, but sometimes we heard it from birds on the ground. We examined 16 burrows where Burrow Calls were emitted. We found male-female pairs in 14 of 16 burrows and only 2 had an egg. From 28 June to 12 July, we inspected randomly the burrows without Burrow Calls and compared the results with those with Burrow Calls (Table 1). The Burrow Call was given in situations where a male-female pair was in the burrow before egg-laying (Table 1). Burrow Calls decreased remarkably in late July. This decrease was due to the end of the egg-laying period.

Burrow Calls were given generally by just one bird; the partner remained silent. Occasionally, the partner gave Flight Calls or wheeze parts of Burrow Calls. These Flight Calls interrupted the Burrow Call and elicited the Flight Calls from the caller of the Burrow Calls. We determined the sex of the callers by their Flight Calls in nine cases. Most callers were male ($n = 7$), and the female callers ($n = 2$) had eggs in both of their burrows (Table 1). Females gave the Burrow Calls much less frequently than males. We frequently observed that the caller was at the inner part of the burrow and the partner was at the entrance as if it had just entered the burrow. These observations correlate Burrow Calls with courtship or mating behavior.

Aggressive Calls were broad-band unstructured

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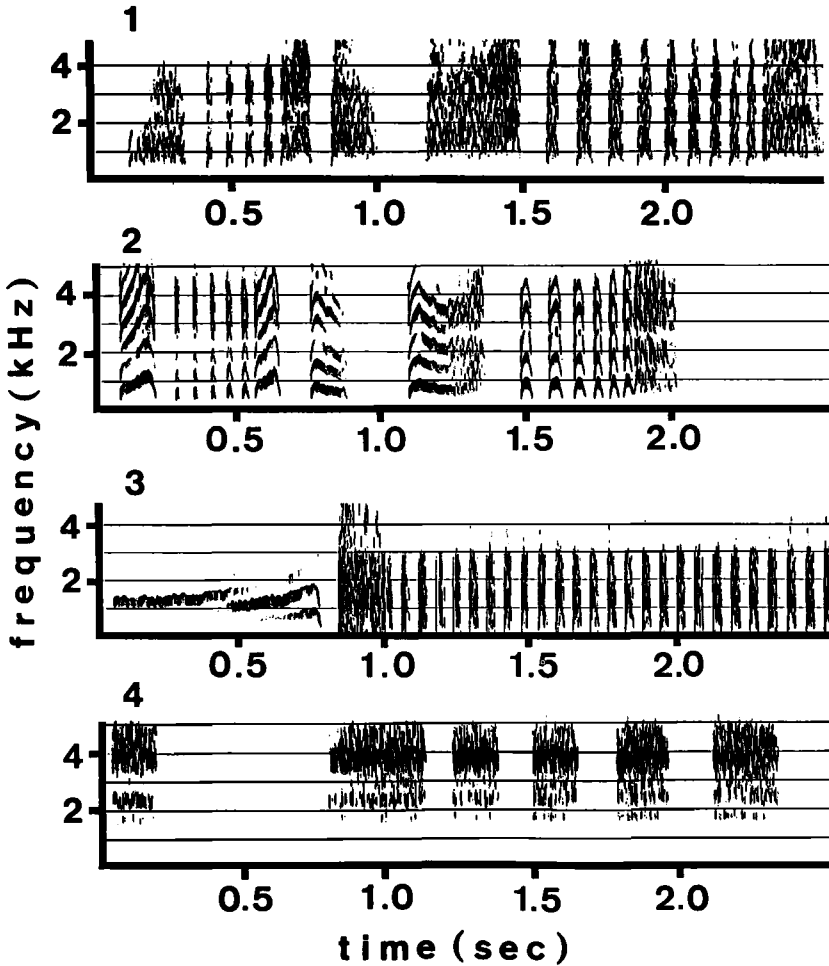


Fig. 1. Sonograms of Swinhoe's Storm-Petrels: (1) male Flight Call (FC-A); (2) female Flight Call (FC-B); (3) Burrow Call; (4) Aggressive Call.

sounds (Fig. 1-4). They were given only in aggressive encounters. Birds of both sexes within the nesting burrows gave this call when we approached. We often heard Aggressive Calls with Flight Calls when two birds on the ground nipped at each other aggressively. These bill-fighting birds were males, as judged by their Flight Calls.

Sexual differences occur in frequency components of calls of other nocturnal seabirds (Brooke 1978, James and Robertson 1985b, Taoka et al. 1987, Taoka et al. 1989, Taoka and Okumura 1988). In the Madeiran Storm-Petrels (*O. castro*) and Manx Shearwater (*Puffinus puffinus*), sounds of the males are clearer but those of the females are harsher (James and Robertson 1985b, Brooke 1978). The sexual differences in the calls of both these species are opposite from the Flight Calls of Swinhoe's Storm-Petrels in frequency components. On the other hand, calls of Leach's Storm-Petrels of

TABLE 1. Comparison of burrows with Burrow Calls and without calls, inspected randomly.^a Number of burrows with egg are in parentheses; period of study was until 12 July.

	(A) With calls (n = 14)	(B) Without calls (n = 36)
Male and female	12* (2) ^b	1 (0)
Male only	1* (0)	23 (8)
Female only	0* (0)	12 (10)
2 males and 1 female	1 (0)	0 (0)
Total with egg	2*	18

^a Fisher exact probability: * = $P < 0.01$, significantly different between (A) and (B).

^b Burrow Calls given by females.

TABLE 2. Response to playback of Flight Calls. Response A = male call played first, female second; Response B = female call played first, male second.

Responses	A		B	
	Male (n = 31)	Female (n = 21)	Male (n = 26)	Female (n = 17)
To male call	27	0	24	0
To female call	0	21	1	14
To both calls	4	0	1	3

both sexes are clear. The male calls are higher in frequency than the female calls (Taoka and Okumura 1988, Taoka et al. 1989).

In the Flight Call playback experiments of both sexes, the birds inside burrows gave Aggressive Calls and wheeze parts of Burrow Calls as well as Flight Calls in response. Some birds were completely silent during playbacks. We found no clear differences in the responses between the sexes apart from Flight Call vocalizations. Only the Flight Call was considered in analyzing the responses. We counted a response as positive when a bird gave a Flight Call at least once during the five playbacks of the same call within a trial. We excluded cases where more than one bird responded. When birds responded only to the calls of one sex, they almost always replied to the playback calls of the same sex (Table 2). These birds could distinguish the calls of males and females. Some birds responded to the calls of both sexes. But these responses were restricted to the cases where the calls of the same sex were played first (Table 2). These birds tended to respond to the calls of both sexes after responding to the calls of the same sex. Recognition of sex by Flight Call may play an important role in breeding behavior because there are no sexual differences in plumage and visual signals are not available in nocturnal birds.

Nocturnal seabirds inside burrows reportedly respond to calls of the same sex (Brooke 1978, Storey 1984, James 1984, Brooke 1986, Taoka et al. 1987, Taoka and Okumura 1988). In the Manx Shearwater, this was correlated with territorial defense or competition for mates (Brooke 1978, James 1985, Storey 1984). Vocal sex recognition also plays a part in the interaction between the birds of opposite sexes. In Manx Shear-

water, calls act as mate attraction or territorial defense under different conditions (Brooke 1978, Storey 1984). The Flight Call of Swinhoe's Storm-Petrel was given most commonly. Birds in flight emitted Flight Calls only; and Burrow Calls and Aggressive Calls were usually accompanied by Flight Calls. The Flight Call may act as sex advertisement in various situations. We examined Flight Calls given in flight, on the ground, or inside burrows in relation to sex. The number of female FFCs generally was greater than male FFCs in each period, but the male GFCs were greater than female GFCs in all cases (Table 3). These differences were significant (randomization test for paired samples, $P < 0.01$). The recordings of GFCs might include some FFCs. The difference in sex ratio of GFCs, however, is still significant because female FFCs outnumbered male FFCs.

Female FFCs and male GFCs decreased significantly (randomization test for paired samples, $P < 0.05$) when the data of early July were compared with those of late July at each study site (Table 3). The vocalizations of Swinhoe's Storm-Petrels were rarely heard during or after the incubation period on Kugul Islet, 100 km southwest of Ch'ilbal Islet, where the breeding cycle is almost the same as for Ch'ilbal Islet (Won and Lee 1986). The Flight Calls might decrease throughout incubation and in early July were given largely prior to egg-laying. The opposite biases of the sex ratios between GFCs and FFCs may be related to pair formation. In fact, the cases where only a male was inside an eggless burrow were significantly more common than those of only a female (Fisher exact probability, $P < 0.01$, Table 1). We believe that males on the ground or inside the burrows give Flight Calls to attract mates, and aerial females give Flight Calls to elicit male responses.

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TABLE 3. Calls of birds in flight (FFCs) and on the ground or inside the burrows (GFCs) at 5 sites.^a

Study period	FFCs			GFCs		
	Male	Female	(n)	Male	Female	(n)
Early July	2.7	23.4*	(10)	73.6*	20.9	(10)
Late July	4.4	11.6	(10)	45.9	14.1	(8) ^b

^a Values are the means of calls for 10 min. Both types of calls differed significantly between sexes in each study period (Randomization Test for paired samples, $P < 0.01$); * = significantly different between early and late July (Randomization Test for paired samples, $P < 0.05$).

^b One site not tested in late July due to inclement weather.

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Flight Range Estimates for Shorebirds

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Many models have been proposed to estimate the flight range of migratory birds. They derive either from aerodynamic theory (Pennycuik 1975, Greenewalt 1975), or from a combination of the fat loads of migratory birds and their associated costs of flight (McNeil and Caideux 1972). Aerodynamic models have not gained popularity among ornithologists because they require the input of variables not easy to measure. The other models utilize the cost of flight (i.e. Raveling and Lefebvre's [1967] or variations of the same) and require the input of flight speed, fat load, and body mass.

McNeil and Caideux (1972) used Raveling and Lefebvre's (1967) allometric equation to predict the cost of flight for shorebirds of a given body mass at takeoff. Summers and Waltner (1978) improved this model, and compensated for the effect of the decreased mass as the fat is consumed during flight. Finally Davidson (1984) modified the equation further. In addition to the mass decrease effect, he used the cost of flight for a nonpasserine bird estimated by Kendeigh et al. (1977).

Both the Raveling and Lefebvre (1967) and Ken-

deigh et al. (1977) equations predict that the cost of flight is a simple function of body mass. They assumed no benefits from environmental conditions such as favorable winds. Castro and Myers (1988) developed new equations empirically that allow the calculation of the cost of flight from body mass and morphometric variables related to aerodynamic characteristics, specifically wing length. When compared with flight costs actually measured using doubly labeled water, the estimates of this equation are remarkably more accurate than predictions using any other equation.

We calculated the costs of flight using the equations of Raveling and Lefebvre (1967), Kendeigh et al. (1977), and Castro and Myers (1988), for six species of shorebirds that vary in size from 25 to 428 g (Table 1). When expressed as multiples of basal metabolic rates (BMR), the first two equations predict very similar costs of flight for all the species, while the third equation predicts increasing costs of flight with increasing body mass.

The reason for this fundamental divergence is that the slope of the first two equations is similar to the slope that relates BMR to body mass, and implies that the cost of flight is a simple multiple of BMR. The slope of the third equation is a function of both body mass and aerodynamics. Therefore, the calculated values for the cost of flight are not a simple multiple of

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