SOUNDS OF LAYSAN AND BLACK-FOOTED ALBATROSSES

DONALD W. SPARLING, JR.

ABSTRACT.—Both albatross species have diverse acoustical repertoires ranging from simple bill sounds to stereotyped vocalizations. Most of the vocalizations have basic frequencies around 3 kHz but frequencies range from below 85 Hz to 25 kHz. Evidence suggests that many of the sounds are important in communication and as potential isolating mechanisms. Calls used in epigamic displays are interspecifically dissimilar while agonistic calls are similar between species.—*Department of Zoology, Southern Illinois University, Carbondale, Illinois. Present address: Department of Biology, University of North Dakota, Grand Forks, North Dakota 58202.* Accepted 9 October 1975.

LAYSAN and Black-footed Albatrosses (*Diomedea immutabilis* and *D. nigripes*) are sympatric throughout their ranges and are known to interbreed (H. Fisher 1972). Their tameness on the breeding grounds makes them excellent subjects for the study of communication in general and isolating mechanisms in particular.

Most early papers on their behavior (cf. W. Fisher 1903, 1904a, 1904b; Hadden 1941; Yocum 1947; Bailey 1952) were primarily qualitative. Later papers developed a display terminology (Richdale 1950, 1952), attempted to homologize certain calls (Rice and Kenyon 1962), and described the Laysan's courtship dance in detail (Meseth 1968). H. Fisher (1971, 1972) carried out in-depth studies of the Laysan's nesting behavior and its sympatry with the Black-foot.

H. Fisher (1972) concluded that several differences in the two species' coloration, nesting and egg-laying times, and behavior could help maintain species integrity. He also listed differences in their vocalizations including intonation, pitch, intensity, and duration. The purposes of my paper are to describe quantitatively acoustical displays of the two species, and to determine if these displays may serve as species-isolating mechanisms.

MATERIALS AND METHODS

This study was conducted on Midway Atoll between 8 November 1972 and 2 January 1973 during the species' egg-laying and incubation periods. Because the birds tolerated close approach without noticeably changing their behavior, microphones were usually placed near the birds. The observer and tape recorder were generally 15 m from them. Some birds were removed from their nests to record nest approach vocalizations while others were prodded with a foot or stick to elicit aggressive calls.

Recordings were made at 15 inches per sec with a Nagra IV-L tape recorder, an AKG D900 microphone, and Scotch 202 recording tape. More than 400 sounds from 90 Laysans and 200 from 40 Black-foots were analyzed with a Kay Electric Co. 6061B Sound Spectrum Analyzer and a Textronix 549 storage oscilloscope. Precise frequency information was obtained from narrow band spectrograms and sections while temporal parameters were determined from the oscilloscope and wide band spectrograms.

Display terminology follows Richdale (1950) and Meseth (1975). Additional discussion of sounds is in Sparling (1975).

MECHANICAL BILL SOUNDS

Bill sounds are made by a bird snapping its mandibles together or by two birds striking the sides of their bills together. The first method results in single or serial snaps and clicks, the second produces raps.

Snapping type.—Snapping sounds resemble sounds made by striking two pieces of

The Auk 94: 256–269. April 1977

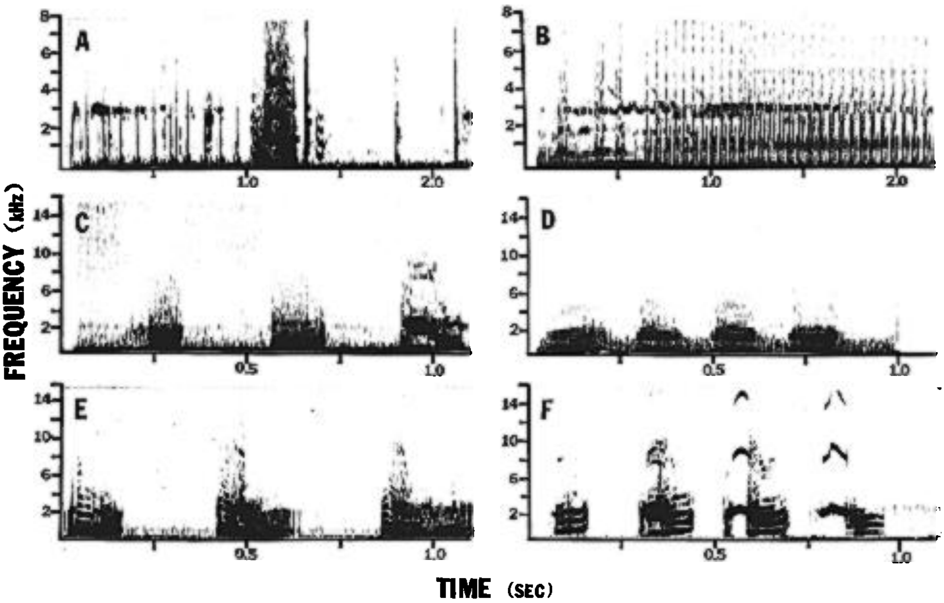

Fig. 1. Spectrograms of Laysan and Black-footed Albatross sounds : A, Laysan bill-under-wing; B, Laysan head-up clacker; C, Laysan noiselike "eh"; D, Black-foot noiselike "eh"; E, Laysan "eh" call while bending over egg; F, Laysan squeak.

seasoned wood together (H. Fisher 1971) and comprise the majority of bill sounds. These sounds may occur as a single strike (termed bill snap), a series of strikes separated by noticeable and varied intervals (bill clap), or a series of rapid, regularly spaced strikes (bill clacker or clapper) (Sparling 1975).

A bill snap lasts 8 to 10 msec and accompanies courtship and agonistic displays, displacement activities, and comfort movements (Meseth 1975). During agonistic behavior bill snaps may grade into bill clapping. Sounds separated by intervals of 0.7 sec or more are termed bill snaps while claps have shorter intervals.

TABLE 1

BILL CLAPPING IN LAYSAN AND BLACK-FOOTED ALBATROSSES: BEHAVIORAL ANALYSIS

	Behavior			
	Enticement	Dance	Agonistic	Displacement
Number of snaps				
Laysan	11 ± 1[1] (7)[2]	7 ± 2 (6)	13 ± 16 (12)	10 ± 4 (9)
Black-foot	16 ± 5 (4)	13 ± 4 (6)	8 ± 2 (8)	10 ± 6 (6)
Intervals (sec)				
Laysan	0.28 ± 0.03 (7)	0.20 ± 0.11 (6)	0.24 ± 0.10 (12)	0.25 ± 0.05 (9)
Black-foot	0.11 ± 0.08 (4)	0.14 ± 0.04 (6)	0.18 ± 0.04 (8)	0.17 ± 0.05 (6)
Duration (sec)				
Laysan	2.90 ± 0.50 (5)	1.40 ± 0.40 (5)	2.40 ± 2.60 (12)	2.30 ± 1.20 (9)
Black-foot	1.90 ± 0.70 (4)	1.80 ± 0.60 (6)	1.30 ± 0.30 (8)	1.50 ± 1.20 (6)

[1] Values are means ± SD.
[2] Numbers in parentheses are the number of birds recorded.

TABLE 2

ALBATROSS STEREOTYPED BILL CLAPPING SOUNDS

	Display			
	Bill under wing	Scapular action	Head-up clacker	Bow clacker
Number of snaps				
Laysan	17 ± 4[1] (7)[2]	17 ± 2 (3)	27 ± 0.8 (18)	4 ± 0.02 (27)
Black-foot	16 ± 5 (6)	21 ± 11 (6)	17 ± 1.29 (7)	11 ± 0.23 (13)
Intervals (sec)				
Laysan	0.09 ± 0.03 (6)	0.10 ± 0.02 (3)	0.05 ± 0.01 (20)	0.04 ± 0.002 (23)
Black-foot	0.10 ± 0.04 (6)	0.12 ± 0.02 (6)	0.05 ± 0.001 (8)	0.05 ± 0.001 (13)
Duration (sec)				
Laysan	1.30 ± 0.40 (6)	1.70 ± 0.20 (3)	1.36 ± 0.04 (19)	0.14 ± 0.01 (25)
Black-foot	1.60 ± 0.70 (6)	2.30 ± 1.20 (6)	0.50 ± 0.08 (6)	0.51 ± 0.02 (13)

[1] Values are mean ± SD.
[2] Numbers in parentheses are the number of birds recorded.

Table 1 presents some characteristics of bill clapping. Although not obvious from the table, Black-foot clapping is often characterized by interstrike intervals of 0.10 to 0.12 sec. The pattern accounts for 89%, 100%, 60%, and 22% of the recorded sequences in greeting, dance, postdance, and agonistic behavior, respectively.

Claps also occur while birds make nibbling motions at their feathers during bill-under-wing and scapular action displays (Meseth 1975). Although they cannot be distinguished temporally from other clapping sequences (Table 2), they are softer. A typical bill-under-wing display including grunts, snaps, and clapping is shown in Fig. 1A.

Bill clackers are of two types, distinguished by motor patterns and temporal characteristics. Head-up clacker is associated with a horizontal head and bill posture while bow clacker occurs with head bowing or scoop (Meseth 1968). Both clackers are in the dance.

The Laysan's head-up (Fig. 1B, Table 2) and bow clackers differ from each other and from bill clapping in the number of strikes, intervals between strikes, and durations of sequences ($P < 0.05$, Mann-Whitney U-test). Females appear to give the head-up clacker less frequently than males. Of 14 Laysans that gave the call and whose sex was known, only two were females.

Black-foot clackers are significantly different from each other in the number of strikes and duration of sequences ($P < 0.05$, Table 2).

The two species' head-up clackers differ only in interval length ($P < 0.001$) while bow clackers differ in all three characteristics with no overlap in the number of strikes or duration.

Clicking type.—Clicks are soft, rapid bill sounds repeated at intervals of 10 to 40 msec. Although they have been described only for Laysans, they may be given by Black-foots before the head-up clacker. Meseth (1968) thought that the sound is made when the edges of the mandibles slide laterally across each other.

The Laysan head flick display (Meseth 1975) (first part, Fig. 1B) consists of four sets of three or four clicks with intervals of 0.08 to 0.20 sec between sets. Head flick is

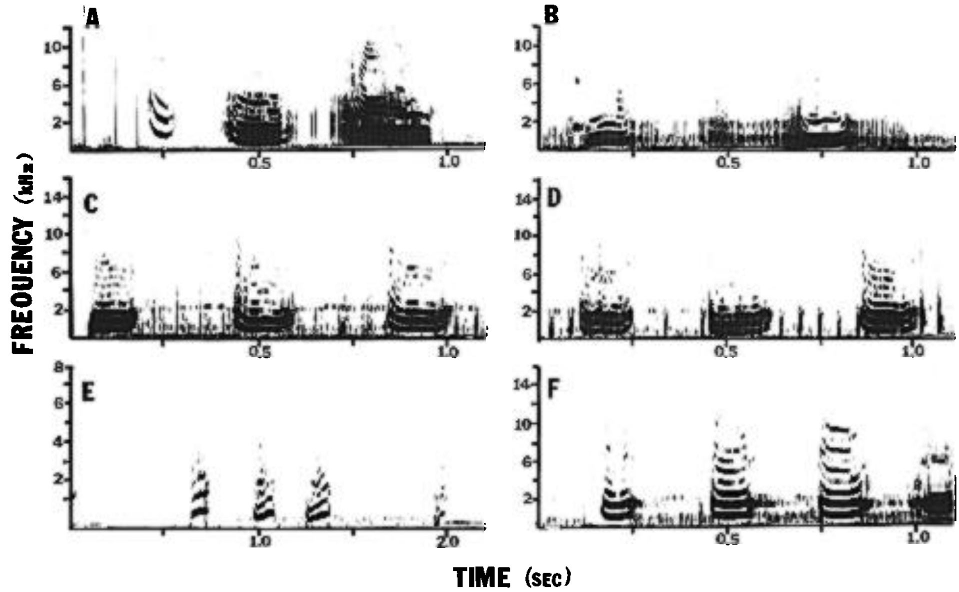

Fig. 2. Spectrograms of Laysan Eh Calls: A, Female 11-1 3 noted call; B, Male 11-1 noisy call; C, Male 13-4; D, Male 14-2; E, Male 9-1; F, Male 9-8. C,D,E, and F show individual distinctiveness.

always followed by an interval of 0.19 to 0.40 sec and head-up clacker, although only half of the head-up clackers are preceded by head flick.

Clicks may also occur with head shaking when birds clear their mouths of debris. These are very soft clicks of low frequency and amplitude that are repeated seven to eight times. Head shaking clicks have not been previously described although H. Fisher (1971) mentioned a clicking sound produced by sleeping birds. Both are too soft for analysis.

Rapping type.—Rapping sounds are produced during the dance. They are usually very soft in the Laysan, somewhat louder in the Black-foot. They are easily covered by background noise and are not analyzed.

VOCALIZATIONS

Eh-eh call.—The "eh-eh" call (Meseth 1975) or double call (Rice and Kenyon 1962) is a series of distinct, moderately long notes. The call is found in many different behaviors and is the vocalization both species give most often.

There are two forms of "eh" ("eh" refers to a note, "eh-eh", or more simply, "eh" call, refers to the call). The noiselike "eh" has a condensed harmonic structure (Fig. 1C, 1D) while the harmonic "eh" has fewer frequency bands spaced farther apart (Figs. 2, 3). The Laysan's notes sound onomatopoeically like "eh" while the Black-foot's noiselike "eh" is a more nasal and louder "haw" and its harmonic "eh" has a whistled quality.

Within either species the two types of notes have the same durations and may occur within the same sequence, hence temporal data are pooled (Table 3). The duration of intervals exceeds that of notes within both species ($P < 0.01$, Student's *t*-test).

Interspecifically compared, the harmonic "ehs" differ in the number of frequency

TABLE 3

CHARACTERISTICS OF REPETITIVE NOTE CALLS

		"Eh" call					
		Harmonic		Noiselike		Whinny	
		Lays.	Blkft.	Lays.	Blkft.	Lays.	Blkft.
Number of notes	X̄	4.16	9.52	[1]	[1]	[2]	[2]
	SD	1.27	6.68				
	n	52	28				
Duration (sec)							
Notes	X̄	0.13	0.14			0.08	0.13
	SD	0.003	0.002			0.001	0.002
	n	54	28			35	6
Intervals	X̄	0.22	0.21			0.04	0.05
	SD	0.007	0.01			0.001	0.001
	n	51	28			26	7
Syllables	X̄	[3]	[3]			0.11	0.18
	SD					0.002	0.002
	n					26	7
Sequence	X̄	1.35	3.23			1.25	1.40
	SD	0.95	2.53			0.32	0.26
	n	53	28			35	6
Number of harmonics	X̄	11.31	3.57	25+	25+	3.91	2.95
	SD	3.42	1.28			1.68	0.69
	n	38	24	28	16	35	10
Frequency (kHz)							
Basic	X̄	2.21	2.33	2.61	0.70	3.26	2.90
	SD	0.72	0.62	1.07	0.44	0.23	0.28
	n	43	24	27	16	34	10
Fundamental	X̄	0.91	2.33	0.64	0.62	3.26	2.90
	SD	0.25	0.62	0.21	0.18	0.23	0.28
	n	49	24	28	16	34	10
High	X̄	11.04	11.81	10.04	12.18	15.14	15.49
	SD	3.16	2.96	3.24	3.77	0.96	0.64
	n	37	24	22	16	31	10
Modulation	X̄	0.38	0.50	[2]	[2]	0.42	0.75
	SD	0.18	0.28			0.17	0.36
	n	44	24			34	10

[1] Temporal characteristics pooled with harmonic notes.
[2] Was not determined.
[3] Syllables do not occur in the "eh" call.

bands, frequency intervals, and basic frequency ($P < 0.05$, Lohrding's t for unequal variances, equal coefficients of variation). The Black-foot sequences are longer ($P < 0.025$, Student's t-test) and have more notes ($P < 0.05$, Welch's approximate t for unequal variances and coefficients of variation) than Laysan sequences.

An interspecific analysis of the "eh" call in different contexts (Table 4) reveals significant differences in the number of notes per sequence (agonistic, post dance, and nest approach, $P < 0.05$; enticement, $P < 0.025$, Duncan Multiple Range Test, DMRT) and mean duration of sequences (agonistic and nest approach, $P < 0.05$; post dance and enticement, $P < 0.01$).

The relative frequency of occurrences of noiselike and harmonic "ehs" differs with context within a species. For example of those Laysans recorded in courtship (dance and enticement) and nest exchange, most (18 of 20 and 7 of 8, respectively) gave mostly (51% to 100%) harmonic "ehs" while most of those in agonistic behavior (7 of 10) gave more noiselike than harmonic "ehs". Similarly the total number of recorded harmonic "ehs" outnumbers noiselike "ehs" in courtship and nest exchange contexts

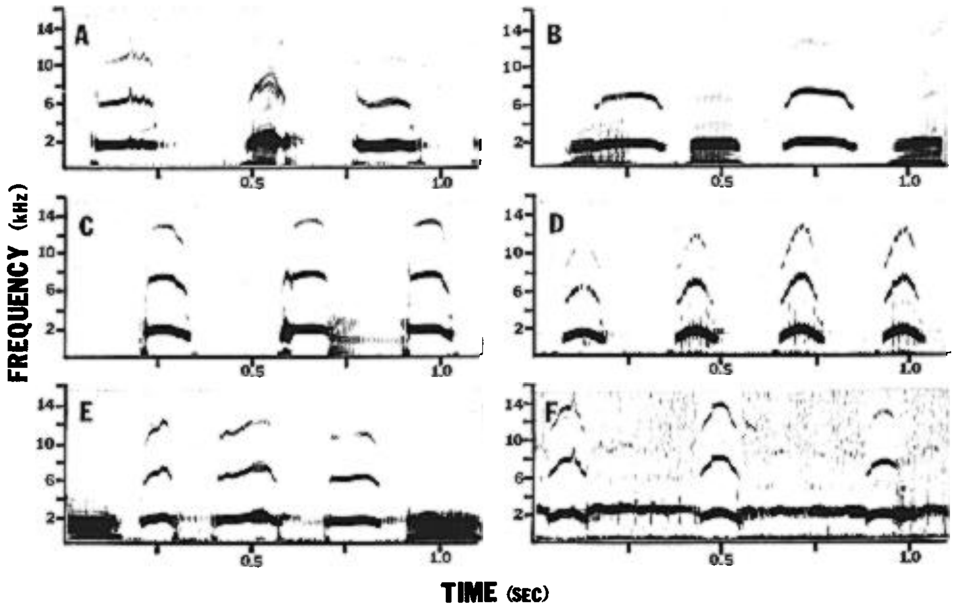

Fig. 3. Spectrograms of Black-foot "eh" calls showing individual distinctiveness: A, Male 16-2; B, Male 18-4; C, Male 16-3; D, Male 16-6; E, Female 12-2; F, Male 4-1.

(113 to 54) and noiselike "ehs" are nine times more numerous than harmonic "ehs" in agonistic behavior.

The same relationship exists in the Black-foot where all (12) of the courting individuals have more harmonic "ehs" than noiselike "ehs" and all (8) of the Black-foots in aggressive behavior have mostly noiselike "ehs" (actual count: courting behavior,

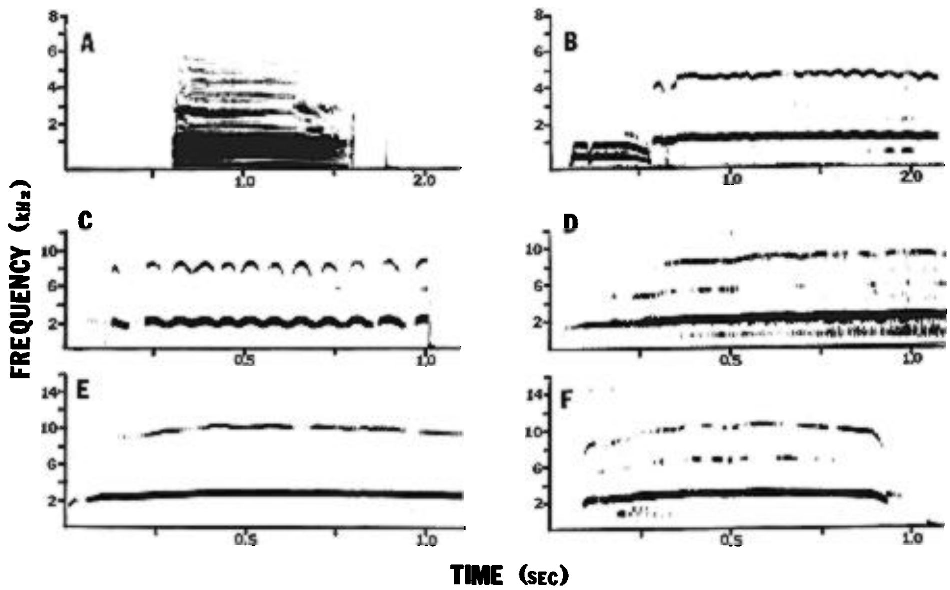

Fig. 4. Albatross vocalizations: A, Black-foot sky call; B, Laysan "ahh"; C, Laysan whinny; D, Laysan victory scream; E, Black-foot victory scream; F, Laysan distress scream.

TABLE 4
BEHAVIORAL ANALYSIS OF "EH" CALLS

		Nest approach		Agonistic		Nest exchange		Dance		Postdance		Enticement	
		Laysan	Blkft.	Laysan	Blkft.	Laysan	Blkft.	Laysan	Blkft.	Laysan	Blkft.	Laysan	Blkft.
No. of notes	$\overline{X}$	4.82	13.10	3.62	7.92	4.04	10.50	3.50	5.55	4.10	5.50	4.82	15.37
	SD	0.96	8.75	1.19	3.92	0.63	0.71	1.18	2.50	1.05	3.43	2.07	9.21
	n	9	5	5	6	8	2	8	5	9	5	8	5
Duration (sec)													
Notes	$\overline{X}$	0.14	0.13	0.14	0.14	0.14	0.13	0.11	0.21	0.12	0.15	0.12	0.16
	SD	0.01	0.02	0.10	0.001	0.11	0.002	0.01	0.14	0.01	0.004	0.01	0.002
	n	9	5	8	6	7	2	9	7	9	6	9	5
Interval	$\overline{X}$	0.22	0.20	0.22	0.25	0.26		0.24	0.08	0.19	0.25	0.19	0.21
	SD	0.18	0.002	0.18	0.01	0.18	na	0.16	0.01	0.12	0.01	0.14	0.003
	n	9	5	8	4	8		9	4	9	3	9	5
Sequence	$\overline{X}$	1.61	3.84	1.15	2.81	2.13	3.81	0.88	1.11	1.02	1.82	1.25	5.57
	SD	0.66	3.20	0.61	1.23	1.99	0.65	0.33	0.89	0.28	1.45	0.53	3.96
	n	9	5	8	6	8	2	9	5	9	6	9	5
Frequency													
No. of bands	$\overline{X}$	18.7	3.8	12.1	3.5	10.9	3.9	10.5	2.8	11.6	4.0	9.2	3.4
	SD	3.7	0.3	4.4	1.0	3.2	1.2	2.8	0.4	2.1	2.0	3.4	0.4
	n	6	8	6	3	8	2	7	5	5	8	6	4
Interval (kHz)	$\overline{X}$	0.73	3.21	0.90	4.27	0.90	3.71	1.14	3.98	0.82	2.87	0.87	4.32
	SD	0.20	1.45	0.14	2.15	0.15	2.55	0.42	0.78	0.01	1.47	0.10	0.32
	n	8	2	7	3	9	2	8	5	8	8	9	4
Basic (kHz)	$\overline{X}$	3.03	3.05	2.77	2.95	2.20	2.75	2.18	2.87	1.85	2.63	1.80	2.77
	SD	0.61	0.21	0.46	0.66	0.69	0.36	0.61	0.18	0.22	0.39	0.18	0.22
	n	5	2	5	3	9	2	7	5	9	8	8	4
Fundamental (kHz)	$\overline{X}$	0.80	1.92	0.96	2.79	0.96	2.11	1.08	2.51	0.84	2.30	0.79	2.60
	SD	0.19	1.30	0.24	0.60	0.30	0.48	0.33	0.01	0.24	0.32	0.16	0.24
	n	8	2	7	3	9	2	8	5	8	7	9	4
High (kHz)	$\overline{X}$	13.18	12.80	12.19	12.64	11.66	11.62	10.81	11.76	10.88	10.83	7.86	14.64
	SD	3.79	1.40	2.60	2.93	3.47	4.32	2.72	1.35	2.12	2.96	3.38	1.37
	n	5	2	7	3	8	2	6	5	6	7	6	4

TABLE 5

CHARACTERISTICS OF SINGLE NOTED CALLS

		Squeak	Whine		Sky call		Sky moo	
		Laysan	Lays.	Blkft.	Lays.	Blkft.	Lays.	Blkft.
Duration (sec)	$\overline{X}$	0.05	1.33	1.77	1.03	0.84	0.98	0.79
	SD	0.003	0.48	0.65	0.11	0.09	0.11	0.13
	n	10	19	8	18	7	17	9
Number of harmonics	$\overline{X}$	3.49	4.04	3.52	25+	25+	25+	25+
	SD	0.69	1.06	1.12				
	n	9	22	11	20	7	17	9
Frequency (kHz)								
Basic	$\overline{X}$	2.95	3.48	3.15	1.13	0.65	0.78	0.55
	SD	0.57	0.26	0.45	0.38	0.06	0.27	0.06
	n	9	22	11	20	7	17	9
Fundamental	$\overline{X}$	2.95	3.48	3.15	0.08	0.11	0.09	0.09
	SD	0.57	0.26	0.45	0.12	0.68	0.16	0.28
	n	9	22	11	20	7	16	9
High	$\overline{X}$	27.81	15.95	14.39	5.78	6.03	4.27	4.67
	SD	5.17	2.24	2.74	1.55	1.86	1.18	1.47
	n	8	21	11	20	7	16	9
Modulation	$\overline{X}$	0.16	0.60	0.17	[1]	[1]	[1]	[1]
	SD	0.22	0.26	0.17				
	n	9	22	10				

[1] Unable to determine.

101 harmonic, 28 noiselike "ehs"; agonistic behavior, 29 harmonic, 44 noiselike "ehs").

Two pairs of Laysans in nest exchange serve as further examples of the relationship between context and call. Female 11-1 repeatedly tried to take over incubation by shoving her mate off the nest. As she shoved, she gave a three-noted call (Fig. 2A). She gave the first note as she contacted the male's side. Her second note closely resembled her typical "eh" and was given as she shoved. The long third note was a moan given as she strained against the male's weight. One of the few variations of the female's "eh" was after she assumed incubation and arched her neck, moving the bill to within 2 inches of the egg. The notes that accompanied this behavior had prolonged portions of low frequency (Fig. 1E). Male 11-1 gave notes with very clear harmonic bands separated by 1 kHz intervals when only the female was present, but changed to noisier notes and squeaks when other birds passed (Fig. 2B).

The second pair's vocalizations corresponded to changes found in the first pair. Most of the "ehs" between mates were harmonic while the male responded to passing birds with noiselike "ehs" and squeaks. The last part of the female's "eh" was prolonged and low in frequency as she bent over the egg.

The only significant intersexual difference found in the "eh" call was a shorter duration of notes in the female Black-foot (0.128 ± 0.003 sec, n = 7) than in the male (0.150 ± 0.002 sec, n = 8) ($P < 0.05$, Student's *t*-test).

Spectrograms of harmonic "ehs" are often helpful in distinguishing individual albatrosses. The most useful features are patterns of frequency modulation, internote interval length, and the presence of transients. As examples of individual distinctiveness in the Laysan, male 13-4 (Fig. 2C) has a sinusoidal frequency modulation, fairly short notes, and a basic frequency of 830 Hz while male 14-2 (Fig. 2D) also has a sinusoidal pattern of modulation, but of lower amplitude than 13-4, moderately long notes, and a basic frequency of 1 kHz. Other spectrograms are presented in Figs. 2E and 2F for additional comparison.

TABLE 6
REPRESENTATIVE SEQUENCES OF LAYSAN ADVERTISEMENT VOCALIZATIONS INCORPORATED INTO THE DANCE

Pair 1		Pair 2		Pairs 3 & 4 (one silent)	
Bird 1	Bird 2	Bird 1	Bird 2	Pair 3	Pair 4
"Eh" call		"Eh" call		"Eh" call	"Eh" call
Whinny	Whinny	Whinny	Whinny	Inhalation	Whinny
Inhalation	Whinny	"Eh" call	Inhalation	Whinny	Whinny
Whinny	Inhalation	Whinny	Ahh	Inhalation	Inhalation
	Whinny	Whinny	"Eh" call	Ahh	"Eh" call
		Inhalation	Whinny	Whinny	Whinny
		Ahh	Inhalation		
		Whinny			

Black-foot male 16-2 (Fig. 3A) is characterized by a moderate degree of modulation, a noisy note (second note) among harmonic notes, and diffuse frequency bands in the note following the noisy note. Male 18-4 (Fig. 3B) has a distinct couplet arrangement of intervals and a relatively high degree of frequency modulation. Other individual patterns are shown in Figs. 3C to 3F.

Squeak.—The squeak is a short, high-pitched note associated with the "eh" call during agonistic and nest approach behaviors of the Laysan (Table 5, Fig. 1F). The high frequencies attained in this note are remarkable; four of the nine birds giving the call have notes exceeding 20 kHz and the highest frequency is 32 kHz. Squeaks occur singly either separated from or within "ehs" (e.g. first squeak, Fig. 1F).

Whinny.—The whinny has a sinusoidal frequency modulation with a few, clear frequency bands. Greenewalt (1968) published a spectrograph of this call and remarked on its high frequency. The call may be composed of either one long note, several short notes, or both. To a human, the call sounds like the whinny of a young colt (H. Fisher 1971). During this study the call was only heard in epigamic displays such as enticement and dance.

Although the Laysan's whinny is unlike either "eh" note (Table 3, Fig. 4C), the Black-foot's is quite similar to its harmonic "eh" and to the Laysan's whinny. Interspecific differences include a lower fundamental frequency ($P < 0.001$, Student's t-test), and shorter durations of notes ($P < 0.05$, Welch's approximate t) and syllables ($P < 0.05$, Student's t-test) in the Black-foot. Black-foots may also whinny less often than Laysans (H. Fisher 1972, pers.obs.).

Within the Laysan, the durations of syllables exceed those of notes that exceed

TABLE 7
REPRESENTATIVE SEQUENCES OF BLACK-FOOT ADVERTISEMENT VOCALIZATIONS INCORPORATED INTO THE DANCE

A		B	
Male	Female	Male	Female
"Eh" call		Whinny	
Whine		Inhalation	
Inhalation		"Eh" call	
"Eh" call		Whinny	
Inhalation		Inhalation	
Whinny		"Eh" call	
Inhalation	Head-up clacker	Inhalation	Scapular action
Whine		Whine	
Inhalation	Head-up clacker	Inhalation	

TABLE 8
SUMMARY OF ALBATROSS SOUNDS

Sound	Occurrence		Context	Interspecific differences
	Laysan	Black-foot		
Bill snaps	X	X	Most	Not significant
Bill clapping	X	X	Most	Not significant
Bow clacker	X	X	Dance	All temporal
Head-up clacker	X	X	Dance	Snaps, duration
Head flick	X		Dance	
Rapping	X	X	Dance	Not analyzed
Harmonic "eh"	X	X	Courtship	Frequency, notes, duration
Noiselike "eh"	X	X	Agonistic	Duration
Sky call	X	X	Dance	Frequency
Sky moo	X	X	Conflict	Frequency
Squeak	X		Agonistic	
Whine	X	X	Dance, agonistic	Not significant
Whinny	X	X	Courtship	Duration, basic frequency
Yammer	X	X	Agonistic	Not tested
Inhalations	X	X	Physical exertion	Not tested
Moans	X	X	Physical exertion	Not tested

those of intervals. Combined durations of notes and intervals (0.115 ± 0.002 sec) are not significantly different from those of syllables (0.109 ± 0.002 sec). Black-foot whinnies with distinct notes were too few to analyze.

My data confirm H. Fisher's (1971) suggestion that female Laysans whinny less frequently than males. Of 35 individuals giving the whinny, 29 were males. In general, whinnies could not be used to discriminate individuals because of extensive intraindividual variation and interindividual similarities in single-noted whinnies.

Whines.—Whines are long, unmodulated, single-noted calls that onomatopoeically sound like drawn out "e's". They have clear frequency bands.

Rice and Kenyon (1962) and Meseth (1975) delineated three types of whines. Although whines occur in three contexts (dancing, fighting, and escape), my data reveal only one, possibly two whines (Table 5). The victory scream (Figs. 4D, 4E) and head-shake-and whine (Meseth 1968) are actually the same sound while the distress scream (Fig. 4F) differs slightly by being softer and shorter in duration.

The Whines of the two species show no significant differences. Black-foot males may whine more often than Laysan males (Tables 6 and 7), but this has not been firmly established. Males of both species appear to whine more often than females in the dance and only males give the victory scream in agonistic displays.

Sky call and sky moo.—These calls are long, single notes with a compact, unmodulated frequency. The sky call occurs in the dance while the sky moo is given in conflicts and in thwarting situations such as after a male tries unsuccessfully to entice a female or immediately after a bird lands.

Within either species sky calls have lower basic and high frequencies ($P < 0.05$, DMRT) and longer durations ($P < 0.05$) than sky moos (Table 5). The Black-foot and Laysan (Fig. 4A) sky calls differ in all of the measured characteristics except high frequency ($P < 0.05$, DMRT). The "moos" of the two species differ in basic frequency, spacing of frequency intervals, and durations ($P < 0.05$). In overall characteristics, the calls of the two species sound and are structurally similar.

Grunts, moans, and inhalations.—This group of vocalizations is characterized by: (1) low frequency ranges with fundamentals lower than 85 Hz, (2) very condensed harmonic structures, and (3) occurrence with physical exertion. Grunts are shorter than moans, and inhalations appear to be made during inspiration of air. All of these calls are easily drowned out by background noise and their analysis is incomplete in some cases.

Grunts accompany bill snaps before and after bill-under-wing clapping. Laysan grunts (wide mark, Fig. 1A) have a basic frequency of 1.43 ± 0.14 kHz and a high frequency of 7.14 ± 0.39 kHz (n = 12) while the respective frequencies in the Black-foot are 1.02 ± 0.16 and 5.26 ± 0.51 (n = 6). Grunts preceding the clapping last 0.01 ± 0.003 sec in the Laysan (Black-foot, 0.06 ± 0.01 sec) while those following the clapping are 0.20 ± 0.01 sec (Black-foot, 0.19 ± 0.02 sec). Grunts may also occur during fighting and defecation, but these could not be analyzed.

The yammer (Richdale 1950), best described as "guarar," a growling sound, is the most interesting moan. It is found only in agonistic behavior and lasts from 0.06 sec to 0.41 sec in the Laysan (n = 4) and 0.57 ± 0.13 sec in the Black-foot (n = 10). Basic and high frequencies are around 2 and 8 kHz respectively for both species. Other moans occur in nest exchange and egg-laying.

Inhalation sounds have not (so far as I can tell) been previously described for any species of bird. Both albatrosses have very loud inhalations during the dance and enticement. One form of inhalation or "ahh" (Fig. 4B) has distinct harmonics and usually precedes whines or whinnies. The Laysan call has the following characteristics (Black-foot in parentheses when different): (1) 7.85 ± 1.65 frequency bands; (2) basic frequency, 2.38 ± 0.14 kHz (1.47 ± 0.18 kHz); (3) fundamental frequency, 0.09 ± 0.02 kHz (0.31 ± 0.52 kHz); (4) high frequency, 7.45 ± 0.85 kHz (4.64 ± 0.38 kHz); (5) duration, 1.36 ± 0.27 sec (0.25 ± 0.04 sec); n = 10 (17). The Black-foot has a second type of inhalation between harmonic "ehs" (Figs. 3B, 3C, 3D) that lasts approximately 0.25 sec.

Organization of vocalizations.—During the dance and enticement both species organize their "ehs", whines, and whinnies into a form of song (Thorpe 1961). The Laysan's song is loosely structured and varies considerably between and within individuals (Table 6). Black-foot songs are more stereotyped; five of the six songs recorded have the pattern shown in Table 7A while the sixth one, shown in Table 7B, varies in the number of whines and whinnies and in female contribution.

Table 8 summarizes the sounds of the two species.

DISCUSSION

Functional analysis.—Lanyon (1969) described the difficulty in correctly determining the function of a call without the use of playback experiments. Field studies may reveal contexts in which calls occur and thereby clarify the call's function. The following discussion is based upon observations during a limited portion of the breeding season and may pertain only to mature birds.

Most bill sounds appear to convey only generalized information that may accentuate other displays or indicate their intensity. Bill clapping sequences are highly variable and show no consistent correspondence between context and structure (timing, number of strikes). Other bill sounds are more stereotyped and may have more specific functions.

The motor pattern involved in the bow clacker (bowing the head and a forward bending of the body) resembles the movements of nest building. Small bill movements made during nest construction pick up nest material. The similarities suggest that bow clacker may be ritualized nest building. The movements of the head-up clacker (bill pointed at partner, rapid bill movements, and an erect posture) are similar to threat displays and the display may be a form of ritualized agonistic behavior.

Scapular action and bill-under-wing are probably forms of ritualized preening as the motor patterns in the displays and actual preening are virtually identical. The head flick also appears to be ritualized clicking, but its function and origin are unclear.

The "eh" call appears to have two primary functions, depending upon the "eh" involved. Harmonic "ehs" occur primarily in epigamic displays and may function in forming and maintaining the pair bond. They are also used with some modifications when females bend over the egg and vocalize. H. Fisher (1972) suggested that species and parental recognition may have their beginnings in this call. Noiselike "ehs" may serve to disperse birds and prevent territorial transgression for they are found in agonistic behavior. The squeak is found in some of the same contexts and may serve a similar function.

The presence of both harmonic and noiselike "ehs" in the same contexts and even the same sequences may indicate a mixture of two or more behavioral states. In post dance, for example, the male may utter an harmonic "eh" because a receptive female is present, but a noiselike one in response to a conspecific (the female) on its territory.

Whinnies may also serve a dual function. They occur in the male's song and, like songs of other birds (Smith 1963), may serve to announce the presence of a territorial, unmated male in reproductive condition. This information may attract females and discourage conspecific males, thus aiding pair formation and male dispersal.

Whines, particularily the victory and distress screams, are clearly associated with agonistic encounters. Dance whines may establish male dominance.

The sky call occurs only in the dance and probably functions as an epigamic display. Its close resemblance to the sky moo indicates that it may be a ritualized form of "moo". The sky moo, although given in displacement activities, may also attract females. Fisher (1971) noted that females may turn and reapproach after leaving an enticing male if he "moos", which my observations confirm. This attracting quality may have developed after ritualization of the sky call or may have facilitated the ritualization.

The function of most of the moans, grunts, and inhalations is less certain. The yammer appears to function as a threat display. The other sounds of this group appear to be analogous to human "ughs" and "oofs", that is, as a result of physical exertion, and contain little or no information.

Isolating mechanisms.—Marler (1957) stated that optimal efficiency in preventing breeding between two sympatric, physiologically interfertile species would be through similarities in agonistic displays and differences in epigamic displays. Similarities would lead to dispersal while differences would inhibit interspecific courting. Albatross vocalizations seem to have these two characteristics.

The most obvious example of a potential isolating mechanism is the "eh" call. The agonistic noiselike "ehs" of the two species are similar in all respects except the number of notes in a sequence. They may be distinguished by the human ear, and observations indicate that albatrosses interpret the "ehs" of the other species correctly; territorial encroachers moved away after a territory holder gave a noiselike "eh."

Harmonic "ehs", on the other hand, are interspecifically dissimilar. Laysan harmonic "ehs" are more similar to the Black-foot more noiselike than harmonic "ehs". Observations indicate that Laysans may be more likely to approach enticing or dancing Black-foots than Black-foots are to approach Laysans. This suggests that Black-foot harmonic "ehs" may have superior interspecific attraction.

Bill clackers may also support Marler's theory. Head-up clackers are interspecifically similar and may be derived from agonistic behaviors while bow clackers are derived from nonaggressive behaviors and are different between the species. Similarly,the songs of the two species are very different.

Whines and yammers are agonistic displays and are structurally and acoustically similar between species. Both species give the calls during interspecific battles and may use them in interspecific communication. The dual function of the whinny may have resulted in a compromise between a breakdown in interspecific communication between males and females and the retention of some male dispersal characteristics, hence the degree of interspecific difference is intermediate between that of harmonic "ehs" and whines.

The sky call and sky moo are more difficult to apply to Marler's theory. Although they are interspecifically similar, the epigamic sky call contains more differences between species than the sky moo. There may have been less pressure on the sky moo to become different in relation to its less significant communicatory function.

The bill-under-wing and scapular action clappings do not appear to conform easily to the general theory, for they are epigamic displays that show few interspecific differences, though bill-under-wing motor patterns differ between species (H. Fisher 1972). If, as Meseth (1968) suggested, the scapular action synchronizes the dance and emphasizes future steps, then the similarities may actually accentuate the differences in the dance of a mixed pair.

Occasionally all of these potential isolating mechanisms and others mentioned by H. Fisher (1972) break down. During this study two hybrids were on the atoll. A hybrid female on Sand Island was incubating an egg when first seen, but was later replaced by a pair of Laysans. A hybrid male was seen in the same part of Eastern Island for several continuous days. Neither of the hybrids were seen to court or defend a territory. The few observations made on these birds indicated that hybrids are ignored or not tolerated by either species.

Many questions about communication, sympatry, and hybridization between these birds still remain unanswered, and their tameness and behavior provide an excellent situation for further study.

ACKNOWLEDGMENTS

I thank H. I. Fisher, T. Anthoney, and W. Klimstra for reviewing the original manuscript that served as my master's thesis. L. Oring reviewed the manuscript prepared for publication. Financial support and equipment were provided by the National Geographic Society and the Department of Zoology, Southern Illinois University, Carbondale. I also thank my wife, Paulette, for her help during the preparation of my thesis.

LITERATURE CITED

BAILEY, A. M. 1952. Laysan and Black-footed Albatrosses. Mus. Pict. No. 6. Denver, Denver Mus. Nat. Hist.

FISHER, H. I. 1971. The Laysan Albatross: its incubating, hatching, and associated behaviors. Living Bird 10: 19–78.

———. 1972. Sympatry of Laysan and Black-footed Albatrosses. Auk 89: 381–402.

FISHER, W. K. 1903. Birds of Laysan and the Leeward Islands, Hawaiian Group. U.S. Comm. Fish and Fish. Bull.

———. 1904a. On the habits of the Laysan Albatross. Auk 21: 8–20.

———. 1904b. The albatross dance at sea. Condor 6: 78.

GREENEWALT, C. N. 1968. Bird song: acoustics and physiology. Washington, D.C., Smithsonian Inst. Press.

HADDEN, C. F. 1941. Midway Islands. Hawaiian Planters Record 45: 179–221.

LANYON, W. E. 1969. Vocal characters and avian systematics. Pp. 291–310 *in* Bird vocalizations (R. A. Hinde, Ed.). Cambridge, Cambridge Univ. Press.

MARLER, P. 1957. Specific distinctiveness in the communication signals of birds. Behaviour 11: 13–39.

MESETH, E. M. 1975. The dance of the Laysan Albatross, *Diomedea immutabilis*. Behaviour 54: 217–257.

RICE, D. W., AND K. W. KENYON. 1962. Breeding cycles and behavior of Laysan and Black-footed Albatrosses. Auk 79: 517–567.

RICHDALE, L. E. 1950. The pre-egg stage in the albatross family. Biol. Monogr. No. 3. Dunedin, New Zealand. Otago Daily Times and Witness Newspapers Co. Ltd.

———. 1952. Post-egg period in albatrosses. Biol. Monogr. No. 4. Dunedin, New Zealand. Otago Daily Times and Witness Newspapers Co. Ltd.

SMITH, J. W. 1963. Vocal communication of information in birds. Amer. Naturalist 98: 117–125.

SPARLING, D. W. 1975. Vocalizations and sounds of the Laysan (*Diomedea immutabilis*) and Black-footed (*D. nigripes*) Albatrosses. Unpublished M.A. thesis, Carbondale, Southern Illinois Univ.

THORPE, W. H. 1961. Bird song: the biology of vocal communication and expression in birds. Cambridge, Cambridge Univ. Press.

YOCUM, C. 1947. Notes of behavior and abundance of the Black-footed Albatross in the Pacific waters off the coastal North American shores. Auk 64: 507–523.