

LONG CALL DISPLAYS OF SYMPATRIC SOUTH POLAR AND BROWN SKUAS

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ABSTRACT.—Several aspects of the skua long call display were examined to determine their species specificity. Acoustical parameters were examined for 70 long calls of 24 South Polar Skuas (*Catharacta maccormicki*) and 61 long calls of 17 Brown Skuas (*C. lonnbergi*) at Palmer Station, Antarctica. I found no significant species differences in call composition (notes/call), call duration, or note duration. Despite large range overlaps, the species differed significantly in four parameters. On average, South Polar Skua notes had a faster repetition rate, lower pitch, lower average frequency, and more harmonics than those of Brown Skuas. Differences among individuals were apparent for all acoustic parameters, but again were most marked for note repetition rate, pitch, average frequency, and number of harmonics.

Film analysis of 109 long calls made by over 30 South Polar Skuas and of 44 calls made by 12 Brown Skuas revealed that South Polar Skuas tended to lean farther back at some point in the long call display. About 25% of the birds, however, gave displays that some previous researchers considered atypical for these species, and more than 36% of the birds showed intra-individual variation in display postures.

Variation limits the value of these visual and acoustic aspects of the long call display for individual and species recognition of skuas at Palmer. The value of these parameters for answering evolutionary and taxonomic questions about skuas, however, has yet to be assessed.

Skuas (Stercorariidae) have been the subject of taxonomic controversy at both the generic and specific levels for well over a century (Pietz 1984). I follow Brooke (1978) in separating skuas (*Catharacta*) from jaegers (*Stercorarius*) on the basis of derived juvenal plumage characteristics. Within the genus *Catharacta*, the taxonomic picture is more complicated; morphological features do not provide clear bases for making some taxonomic decisions. Currently, at least five groups are recognized as either species or sub-species. These include the Great Skua (*C. skua*) of the North Atlantic, the Chilean and Falkland skuas (*chilensis* and *antarctica*, respectively) of southern South America, the Brown Skua (*lonnbergi*) of the sub-Antarctic, and the South Polar Skua (*maccormicki*) of the Antarctic.

Based on morphological characteristics, some authorities lump the Falkland, Brown, and Great skuas and assign full species status to both the Chilean and South Polar skuas. Hybridization has been documented, however, between Chilean and Falkland skuas (Devillers 1978), and between Brown and South Polar skuas (Watson et al. 1971, Parmelee et al. 1977) in their respective zones of sympatry. Pending resolution of their taxonomy, I will refer to them all as separate species.

Overlaps in size and plumage characteristics among geographically distant populations of

these groups have long been recognized (Hamilton 1934, Murphy 1936). As a result, there is interest in using other traits for species identification, and for evaluating evolutionary and taxonomic relationships in this genus. Some biologists (e.g., Watson 1975, Devillers 1978, Jouventin and Guillotin 1979) have suggested that acoustic and visual aspects of the skua's "long call" display (Moynihan 1955) may help to distinguish species.

The long call display, as described by numerous authors (e.g., Stonehouse 1956, Perdeck 1960, Moynihan 1962, Burton 1968, Spellerberg 1971, Devillers 1978), is by far the most visible and audible display of those in the skua's behavioral repertoire. It is also one of the most common, employed for territorial advertisement as well as for greeting mates. Moynihan (1955) considered this display to be homologous with the long call and "oblique" postures of gulls. Visual components typically associated with the skua's long call include "wing raising" (Perdeck 1960) and the "bent neck" (Moynihan 1962), as well as the oblique. The display resulting from the integration of these components is sometimes referred to as the "long call complex," and several variations have been noted in the sequencing of components (Perdeck 1960, Spellerberg 1971).

With respect to its multiple functions, the skua's long call is analogous to that of many

larids (Moynihan 1962), such as the Laughing Gull (*Larus atricilla*) described by Beer (1975). Beer (1972) noted that the long call of the Laughing Gull is species-specific in gross acoustic characteristics, yet includes elements of variation both among and within individuals. Some intra-individual variation is attributed to contextual differences related to multiple functions (Beer 1970, 1975). Despite this variation, Beer (1970) believed he could identify individuals by the sound of their long calls. Playback experiments (Beer 1970, 1973) demonstrated that the gulls themselves could use this call for individual recognition.

In the family Stercorariidae, Andersson (1971, 1973) and Cramp and Simmons (1983) provided information on the long calls of jaegers and Great Skuas of the North Atlantic. Comparative studies of the long calls of other skua species have not been made. Nevertheless, biologists occasionally refer to inter-taxon differences in skua calls. Devillers (1978) stated that the call of the Chilean Skua was higher pitched and more nasal than that of the Falkland Skua. Jouventin and Guillotin (1979) believed the Antarctic or South Polar Skua had a lower-pitched call ("cri plus grave") than the sub-Antarctic or Brown Skua. Watson (1975) mentioned the possibility of a pitch difference between Brown and South Polar skuas, but felt that comparative work was needed.

Differences in long call display postures also have been reported among skua groups. Devillers (1978) suggested that in this respect the Falkland, Chilean, Brown, and Great skuas were very similar, but that differences in details could be seen between this group and the South Polar Skua. His diagrammatic drawings of Falkland and South Polar skuas indicated that the two groups differed most and overlapped least in the angles of the neck relative to the body. In South Polar Skuas, the head generally appeared to be pulled backward, whereas in birds of the other groups, it was thrust forward relative to a normal standing posture. Burton (1968) filmed long call displays of Brown Skuas on Signy Island (60°43'S, 45°38'W) and noted several postural variants, including one that Devillers (1978) considered more typical of the South Polar Skua. Having noted these conflicting assessments of the Brown Skua display, Devillers expressed the need for a clarification.

Using sound and film recordings of South Polar and Brown skuas at Palmer Station, Antarctica, I have attempted to (1) clarify the observational discrepancies cited by Devillers (1978), (2) provide pitch comparisons called for by Watson (1975), and (3) quantify several additional long call parameters. These data

serve to determine the value of the measured parameters as tools for field identification of skuas, and provide useful information for studies of skua systematics.

Reliable field characteristics are important at Palmer, where long-term, comparative studies of Brown and South Polar skua ecology (Neilson 1983, Pietz 1984) depend on a researcher's ability to identify individuals by species. If measurements of a long call parameter fall into discrete groups, that characteristic is potentially useful in field identification.

Use of these data in studies of skua systematics must await the availability of comparable data from other skua populations. In conjunction with information from allopatric populations of Brown and South Polar skuas, these data can be used to evaluate the specific status of the two skua groups. In conjunction with data from populations of other species or subspecies, these data may help to assess evolutionary relationships within the genus.

STUDY AREA

Palmer Station (64°46'S, 64°03'W) is situated on the southwest coast of Anvers Island, off the west side of the Antarctic Peninsula. I conducted my study on several small islands and peninsulas within a 5-km radius of the station. In the austral summer, these areas are largely exposed rock, which in many places support a rich growth of lichens and mosses. They provide nesting areas for nearly a dozen species of birds (Parmelee et al. 1977), including over 200 pairs of South Polar Skuas and up to 12 pairs of Brown Skuas.

The sympatric nesting of Brown and South Polar skuas makes the Palmer area particularly suited to comparative studies of their ecology and behavior. Nesting conditions among allopatric populations can vary dramatically (e.g., in dense vegetation [Young 1978] or on barren rock [Eklund 1961]), but at Palmer, these species nest in the same conditions (Pietz 1984). In fact, nest sites occupied by Brown Skuas in some years have been used by South Polar Skuas in other years.

That these two skua groups are closely related is evidenced by hybridization; at least one mixed-species pair occurs each year. Viability of hybrid offspring has been well established (Parmelee et al. 1977, Neilson 1983, Pietz 1984), and their fertility has been documented as well (Parmelee and Rimmer, pers. comm.).

Given the success of these mixed-species matings, it is not surprising that I found no difference in the behavioral repertoires of Brown and South Polar skuas at Palmer. Calls and displays were used interspecifically.

The primary differences between the two skuas at Palmer relate to their feeding ecology. Brown Skuas generally feed on penguin eggs and chicks, and defend a nesting/feeding territory that encompasses groups of breeding penguins. South Polar Skuas feed primarily on fish at sea and defend only a nesting territory. Correlates of these two feeding ecologies are seen in nesting chronology, breeding success, time budgets, and daily activity patterns (Pietz 1984).

METHODS

During the 1979–1980 and 1980–1981 austral summers, I filmed long call displays of South Polar and Brown skuas using a super-8 movie camera. Film was analyzed for postural differences with the aid of a Timelapse Data Analyzer Projector 3420.

Displays were grouped into five types, defined as follows: (1) the entire head is in front of the chest and the upper mandible is typically level with or below the horizontal; (2) only the front edge of the head is in front of the chest and the bisector of the open bill is generally on the horizontal or slightly below it; (3) the head is directly above the chest, often with neck stretched upward and bill bisector on the horizontal; (4) the front edge of the head is slightly behind the front edge of the chest and the bill bisector is on the horizontal or above it; and (5) the head is far behind the front edge of the chest and the lower mandible is typically above the horizontal. Birds often assumed several of these postures during a single call (see Perdeck [1960] for description). To standardize the procedure for assigning a display to one type, I judged the display when the bird's head and body were tilted farthest backward.

Sound recordings of long calls were made on the territories of breeding skuas during four austral summers. I used recordings made by D. R. Neilson in 1976–1977 and 1977–1978, and by me in 1979–1980 and 1980–1981. All recordings were made with a Uher 4200 tape recorder and a uni-direction microphone.

Sonagrams of calls or parts of calls were made using a Kay 7030A sound spectrograph set at the 80–8,000 Hz frequency range. Both wide-band (300 Hz) and narrow-band (30 Hz) displays were made for each call or call segment. Wide- and narrow-band displays were used to measure time and frequency parameters, respectively.

For individual notes in these displays, I calculated fundamental frequency (Hz), note duration (s), number of harmonics, relative energy content of each harmonic (weighted from 0 to 3), and average frequency (Hz). Average frequency was calculated using the formula,

$$\frac{\sum_{i=1}^n (\text{fund. freq.}) \times (\text{no. of } i^{\text{th}} \text{ harmonic}) \times (\text{wt. of } i^{\text{th}} \text{ harmonic})}{\sum_{i=1}^n (\text{wt. of } i^{\text{th}} \text{ harmonic})}$$

For use in this formula, harmonics were numbered as integer multiples of the fundamental frequency (f.f. = harmonic #1), with weights assigned as zero for missing bands. On the other hand, when counting the number of harmonics in a note (a separate test parameter), I included only those harmonics with sound energy weighted as one or greater.

The average frequency formula used in this study was devised in an attempt to measure timbre, a qualitative element of sound that traditionally has eluded quantification. Timbre depends on the number of harmonics present and their relative amplitude (Marler 1969). This formula provides a means of comparing and statistically analyzing these aspects of timbre, by reducing to a single number the complex pattern of energy distributed over several harmonic levels.

Pitch of notes was determined independently using auditory matching tests. A single note was played repeatedly on the sonograph tape loop while its pitch was matched to that of sound waves produced by a Wavetek Voltage Controlled Generator, Model III. The duration of the generated wave was matched to that of the skua note using a manually controlled momentary contact switch.

For whole calls, I examined call duration (s), call composition (no. of notes/call), and note repetition rate (no. of notes/s). Call duration was measured by timing tape recordings of full calls played at normal speed.

Statistical examination of call and note parameters included one-way analyses of variance and covariance (SPSS package) and nested two-way analysis of variance, using maximum likelihood estimations (BMDP package). I calculated the degree of variation between and within species, and among and within individuals of each species.

In preliminary analyses, I noted that fully developed calls often exhibited a build-up, then a diminution in pitch, average frequency, and intensity of notes as the call progressed. This crescendo-decrescendo pattern was sometimes apparent in note duration and repetition rate as well. Beginning and/or ending notes often corresponded to a bent neck component in the display (e.g., Fig. 1*d*, first frame, and Fig. 2*b*, fourth frame). Notes with highest values tended to correspond to the peak of the visual display, when wings were fully raised and the bird's

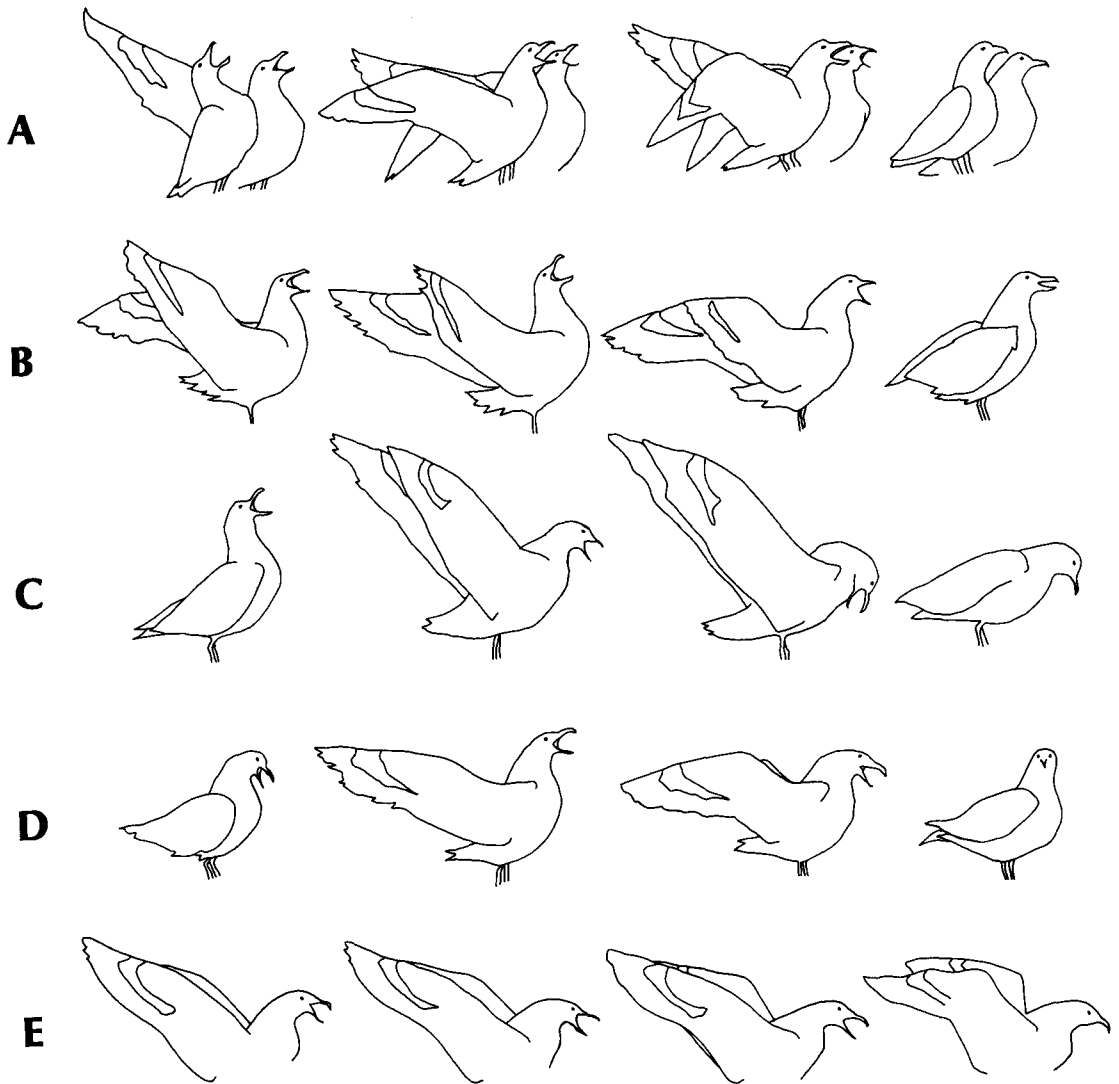


FIGURE 1. Examples of long call displays of South Polar Skuas. Each row contains tracings from four frames of movie film, representing four different positions assumed during one long call display. The displays of six different birds are shown; row *a* represents a breeding pair calling together.

body and head were tilted farthest back (e.g., Figs. 1*b* and 2*a*, second frame). To control for this source of variation, I used only fully developed calls (i.e., those with wing raising), and notes from the central part of fully developed calls in statistical calculations. For examination of pitch, average frequency, and note duration, I selected the highest pitched central note from each full call. Null hypotheses of no difference between species or between individuals were rejected at $P < 0.05$.

RESULTS AND DISCUSSION

Visual components of the long call display were examined for 109 calls made by over 30 South Polar Skuas and for 44 calls made by 12 Brown Skuas. This sample revealed considerable

overlap between species (Figs. 1, 2, and 3), despite their average differences. Nearly one-fourth of the calls and one-fourth of the individuals analyzed showed interspecific overlap in display postures (i.e., South Polar Skua displays of types 2 and 3, Brown Skua displays of types 3 and 4). Thus, postural aspects of the long call display have limited value for species recognition.

Only the most extreme postures, i.e., types 1 and 5, appeared to be species-specific (Fig. 3) and, even here, there was potential overlap. Brown Skuas were never observed in type 5 postures, but South Polar Skuas were seen in type 1 postures on rare occasions. Although the sample of film examined for this paper contained no clear examples (Fig. 1*e* comes

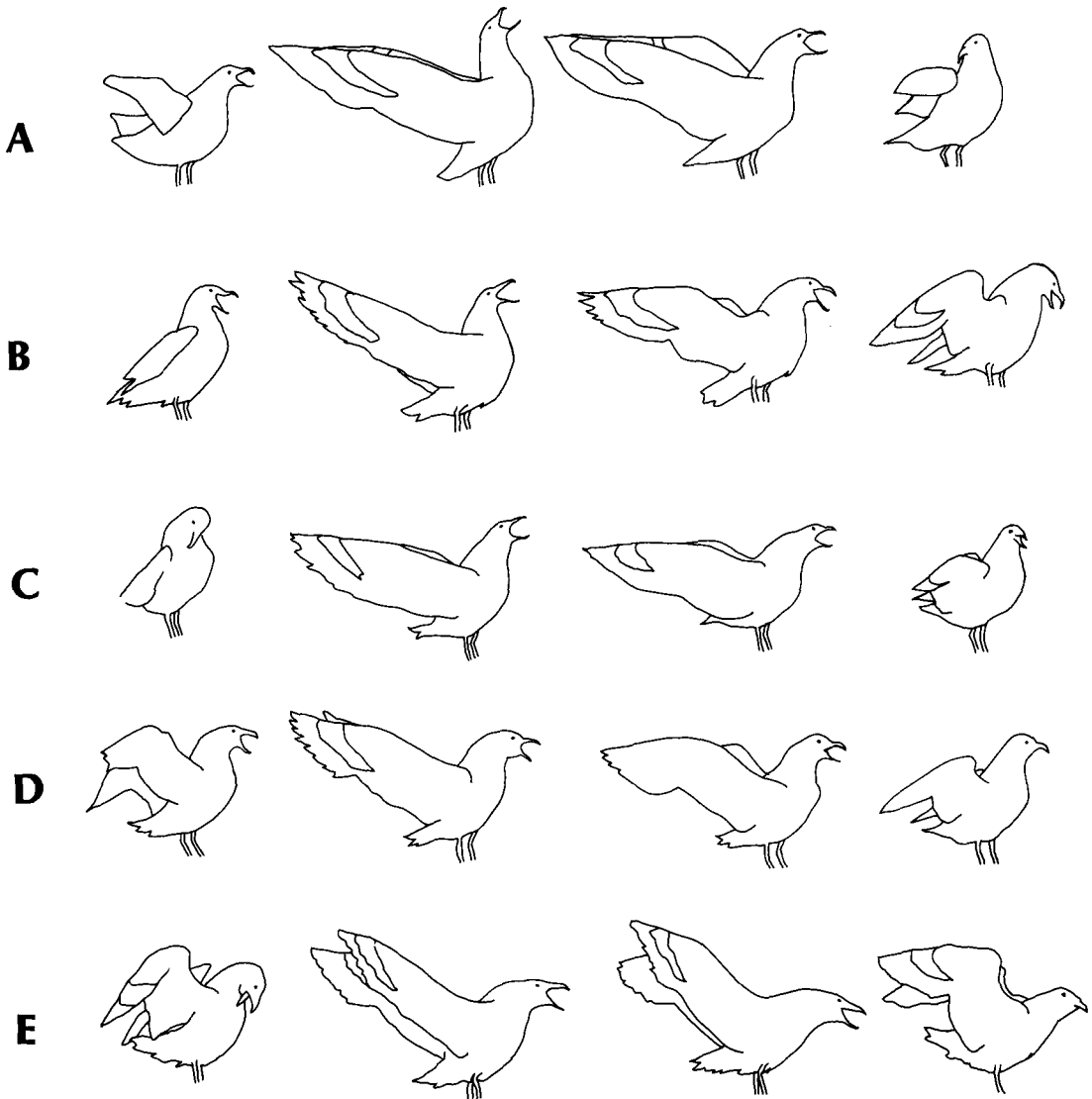


FIGURE 2. Examples of long call displays of Brown Skuas. Each row contains tracings from four frames of movie film, representing four different positions assumed during one long call display. The displays of four different birds are shown; rows *c* and *e* represent the same individual.

close), I observed South Polar Skuas giving type 1 displays when the calling bird was close to and facing an intruder or competitor on the ground. In such instances, the caller leaned toward the other bird and sometimes even walked forward while calling. Such a display might be interpreted as a combination of long call and aggressive approach.

Calling postures appeared to vary depending on the location of the bird's mate as well. One Brown Skua leaned back when its mate was flying directly above it (Fig. 2*a*) and leaned forward when its mate moved away in front of it. Some South Polar Skuas leaned slightly forward when facing their mates, and leaned farther back when calling beside and parallel

to their mates. Such contextual differences may be responsible for the extensive intra-individual variation I saw. Over 36% of the birds gave long call displays of more than one of the five defined categories.

Additional sources of individual variation were noted in other aspects of the visual display. Birds sometimes assumed a bent neck posture both before and after raising the wings, sometimes only before (Figs. 1*d*, 2*c* and *e*), and, at other times, only afterward (Figs. 1*c*, 2*b*). Birds showed extreme bent neck postures on some occasions (Fig. 2*c* and *e*) and showed little or no bend in the neck on other occasions (Figs. 1*a* and *b*, 2*a*). Some South Polar Skuas tilted their head and body farthest back at the

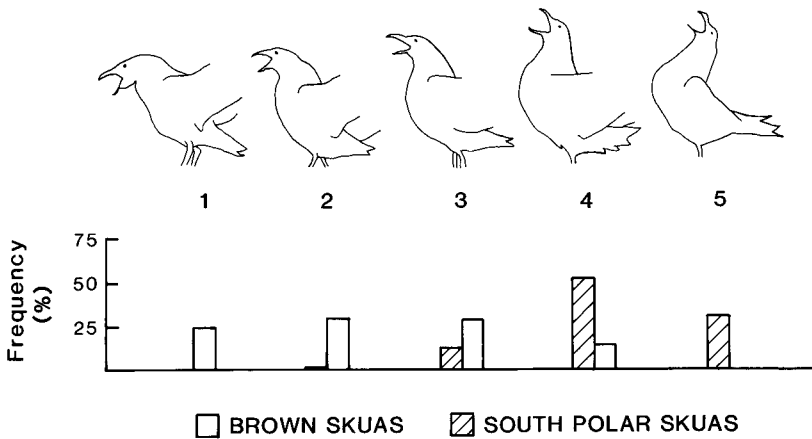


FIGURE 3. Frequency of five types of long call displays from films of 30 South Polar Skuas and 12 Brown Skuas. Percentages represent the number of individuals giving displays of that type divided by the sum of those numbers across types (sums were 45 for South Polar Skuas, 20 for Brown Skuas). The line drawings represent the most extreme backward position of head and body exhibited during displays of each type.

beginning of the call, before wing raising (Fig. 1*a* and *c*); others reached this extreme only during wing raising (Fig. 1*b*, 2*a*). Some of these display components may be useful for individual recognition, but their value is limited by overlap among individuals and variation within individuals.

Acoustical analyses were based on sonagrams of 79 long calls made by 24 South Polar Skuas and 61 calls made by 17 Brown Skuas. Examples of wide-band sonagrams of full calls (Figs. 4 and 5) show typical features as well as the extent of variation within species and individuals.

Summary statistics (Table 1) indicate that the species overlapped widely in all acoustic parameters that I measured. This overlap is exemplified in Figure 6, which displays the median pitch of each bird by species. Despite such overlaps, maximum likelihood tests showed significant differences between species in pitch, average frequency, number of harmonics, and note repetition rate.

Nearly all parameters differed among individuals as well. Maximum likelihood tests indicated weak individual differences only in note duration. Even for this parameter, one-way ANOVA tests within species revealed significant differences among Brown Skuas ($P < 0.05$). Lack of homogeneity of variances among South Polar Skuas made the result of their ANOVA test on note duration ($P > 0.20$) unreliable.

The large variances in note duration of some South Polar Skuas were due to the frequent occurrence of temporally split notes (e.g., Fig. 4*b*, note 5; 4*e*, note 7) or notes with introductory components (e.g., Fig. 4*c* and *f*). Because individuals that produced such notes also pro-

duced temporally "solid" notes (often within the same call), measurements of note duration varied more for these birds than for birds that produced only solid notes. Acoustically, these introductory components were heard as changes in pitch within a note; sometimes the note seemed to slide from a higher to lower pitch, and sometimes the note broke abruptly as it changed from one pitch to another.

Brown Skua calls also contained notes with sliding changes or sharp breaks in pitch (e.g., Fig. 5*d* and *e*, latter notes; 5*c*, central notes). Nevertheless, these notes did not exhibit the temporal gaps and complexities of the South Polar Skuas' split notes and introductory phrases. Brown Skua notes were invariably "solid" and, thus, tended to vary less in duration.

Some of the temporal gaps in South Polar Skua calls lasted more than 0.10 s and, thus, should be discernible to the avian ear (Dooling [1982] estimated gap detection thresholds for birds to be 2–3 ms). Many birds were inconsistent in the production and form of these more complex notes, both within and between calls, however; it therefore seems unlikely that these temporal features are important for individual recognition.

The use of acoustic characteristics for individual recognition appears to be widespread in birds (see reviews by Beer 1970 and 1972, Falls 1982). In skuas at Palmer, strong individual differences in pitch, average frequency, note repetition rate, and number of harmonics (Table 1) suggest that these parameters provide potential sources of information for individual recognition. Skuas may rarely need this information on the breeding grounds at Palmer, given the almost continual access to visual cues

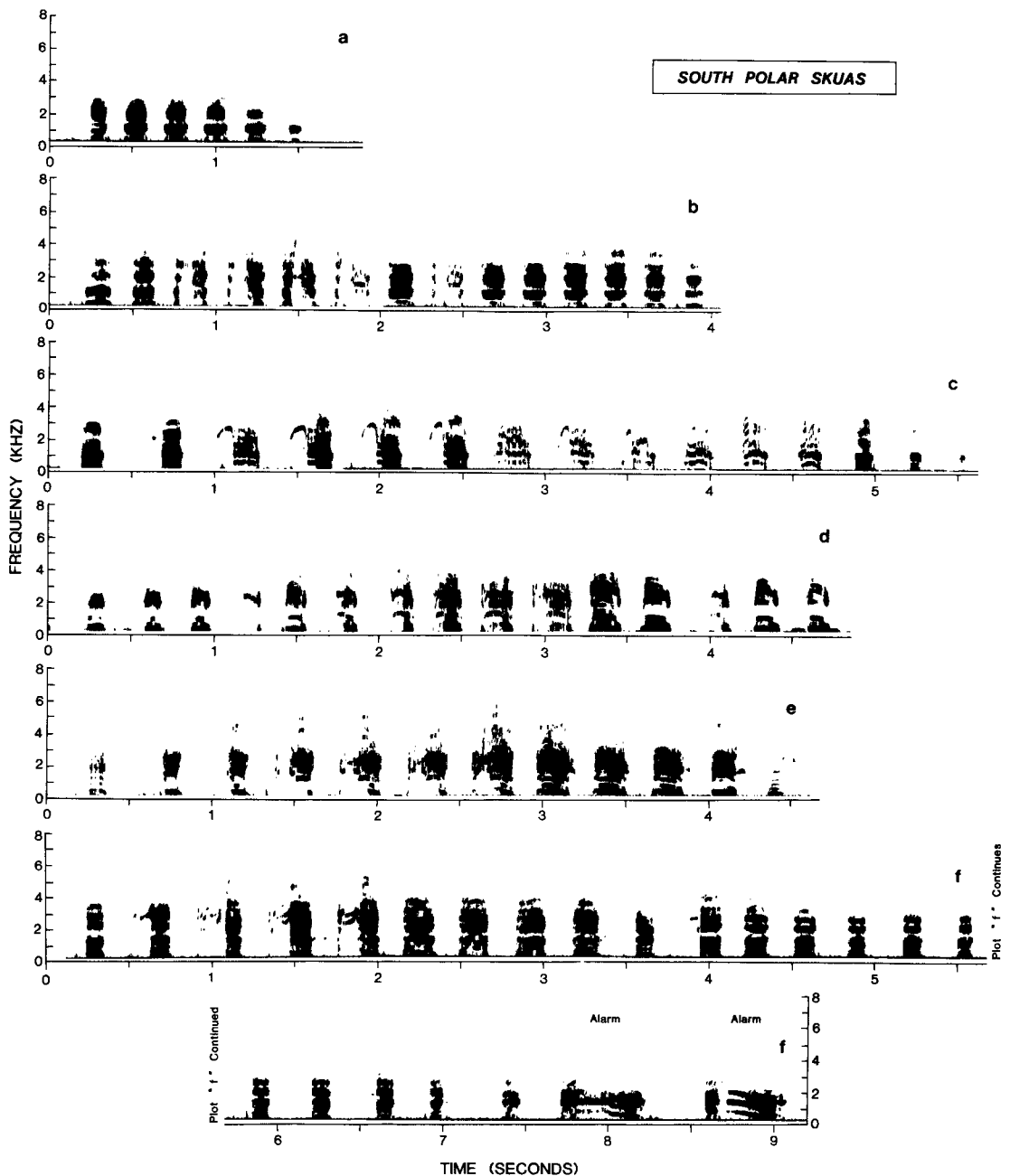


FIGURE 4. Wide-band sonograms of South Polar Skua long calls. Calls *a* and *b* were made by the same individual; *c* through *f* represent four additional individuals.

that their open habitat allows. Some open-habitat larids, however, appear capable of using either vocal or visual cues for recognizing individuals (e.g., Herring Gulls [*Larus argentatus*], Tinbergen 1953; Black-legged Kittiwakes [*Rissa tridactyla*] and some terns, Thorpe 1961). This may be the case with skuas as well.

Several species of gulls perform a long call that is closely related to that of skuas in both form and function. In the Laughing Gull, Beer (1970) reported that the number, duration, shape, and harmonic spectra of "short notes"

and the time intervals between them were individually characteristic. He speculated that pitch or timbre of the call as a whole might be individually characteristic also, but this impression was based more on his experience of identifying individuals by ear than on his examination of sonograms.

My data for skuas suggest that individuals differed in both pitch and timbre. Timbre, as measured by average frequency, was statistically correlated to pitch; however, in ANOVA tests controlling for the covariance of pitch,

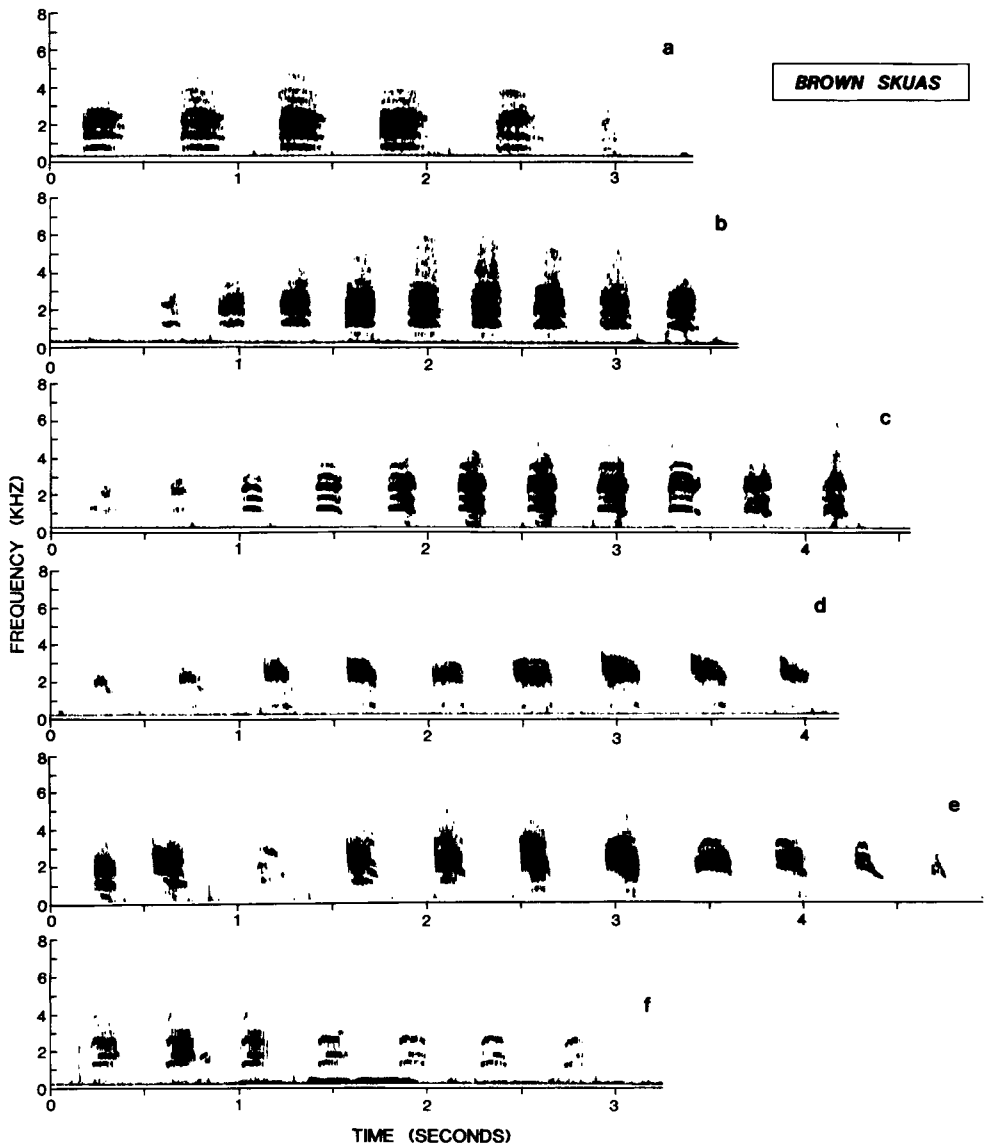


FIGURE 5. Wide-band sonograms of Brown Skua long calls. Calls *d* and *e* were made by the same individual; *a*, *b*, *c*, and *f* represent four additional individuals.

average frequency differences among individuals were still large.

Variation within individuals was large for all parameters examined; no inflexible, stereotypic features were discerned. Emlen (1972) suggested that intra-individual variation in the song of the Indigo Bunting (*Passerina cyanea*) was due primarily to differences in motivational state. Beer (1970) attributed some call variations of individual gulls to differences in context.

Differences in the motivational state of the calling skua appeared to affect all of the note parameters and at least some call parameters that were measured. Figure 4*a* shows a long call typical of a bird not motivated strongly enough to perform the full visual display (i.e., wing raising). Skuas often performed such long

call displays in response to milder territorial threats, e.g., a skua flying past the area. Fewer, shorter, and lower pitched notes characterized such calls.

Occasionally, in much more threatening circumstances, a long call did not end in the typical way, but trailed on, eventually leading into an alarm call (Fig. 4*f*); for example, when an intruder near eggs or chicks failed to retreat after the long call display had been given. Commonly, these obstinate intruders were humans, seals, or penguins.

Sexual dimorphism in acoustic and visual aspects of the long call display could not be rigorously tested because gender had been established (from copulatory position and courtship feeding) for only a small proportion of the Palmer skuas. For a sample of five male and

TABLE 1. Acoustic parameters of long calls given by South Polar and Brown skuas near Palmer Station, Antarctica.

	Call duration (s/call)	Call composition (notes/call)	Note repetition rate (notes/s)	Pitch (Hz)	For central note(s) of each call		Note duration (s)
					Average frequency (Hz)	Number of harmonics	
South Polar Skuas	Weighted \bar{x}	12.0	2.9	462	2,351	11.9	0.1922
	Weighted SE	0.29	0.09	25.5	55.9	0.53	0.0068
	Minimum	1.7	2.5	330	1,421	5	0.135
	Maximum	8.0	4.3	760	3,034	20	0.285
	N (cases) <i>n</i> (individuals)	39 14	39 14	39 14	53 18	68 15	40 18
Brown Skuas	Weighted \bar{x}	4.7	2.4	622	2,705	8.5	0.1826
	Weighted SE	0.32	0.10	27.2	64.1	0.57	0.0075
	Minimum	2.6	1.7	421	2,272	3	0.150
	Maximum	8.0	3.1	1,260	3,130	16	0.248
	N (cases) <i>n</i> (individuals)	27 11	27 11	27 11	44 15	58 11	34 14
Between species	$P = 0.270$	$P = 0.353$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001^*$	$P = 0.486$
Among individuals	$P = 0.008$	$P = 0.044$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001^*$	$P = 0.072$

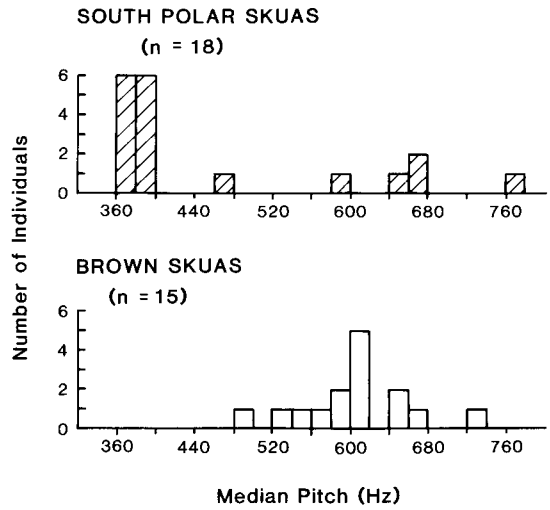
* *P*-values are for test results of ln-transformed data for all parameters except number of harmonics.

FIGURE 6. Median pitch of long calls given by 18 South Polar Skuas and 15 Brown Skuas. Each median was calculated from a sample of calls (mean of three calls/bird, range of 1–14), using the highest pitched note of each call.

four female South Polar Skuas, however, I detected no significant differences in note duration, average frequency, or pitch.

Although the skua long call display may have limited value as a taxonomic field tool, its potential value for evolutionary systematics has yet to be assessed. If birds from allopatric populations overlap in call parameters more than their sympatric counterparts at Palmer, one might suspect that evolutionary divergence was in progress in the zone of overlap. If calls of allopatric populations overlap less than their sympatric counterparts, genetic or cultural convergence would be indicated.

Quantitative data are scarce on long calls of allopatric populations of skuas. Brunton (1982, unpubl. M.Sc. thesis) examined calls of Brown Skuas from the Chatham Islands off New Zealand (44°22'S, 176°11'W). Although our goals and methods of analyses differed in many respects, our data on some parameters warrant comparison.

Brunton reported that long calls of skuas on the Chatham Islands typically consist of 5–9 notes. My examination of sonograms in Brunton's thesis suggested that 5–9 note calls last about 2–4 s. These values fall below the averages I recorded for Brown Skuas at Palmer. This might either represent a real difference between populations, or reflect possible differences in our methods of recording or sampling calls. In my analyses, I tried to include only long calls that had been accompanied by wing-raising displays; this eliminated calls responding to partial or low-level stimulation. Although Brunton presumably did not make this

distinction (which could account for her smaller mean), she did note that call length varies with the motivational state of the bird.

Brunton measured several note parameters, including duration, number of harmonics, and fundamental frequency of a central note. I calculated weighted means for her data on nine birds with five calls each (given in her thesis appendix). Note duration ($\bar{x} = 0.21$ s, range 0.16–0.38 s) and number of harmonics ($\bar{x} = 8.5$, range 5–14) were very similar to those I recorded for Brown Skuas at Palmer. Fundamental frequency, which theoretically is equivalent to pitch, averaged 1,046 Hz in her sample (SE = 25 Hz), with a range of 400–1,300 Hz. This range is nearly identical to that of the Brown Skua sample from Palmer, but the mean is considerably higher. As with call length, this may either indicate a real difference between populations (supporting the possibility of pitch convergence in the zone of sympatry), or reflect methodological differences. Fundamental frequencies calculated from sonagrams may differ from acoustically determined pitches for a number of reasons. Sometimes, for example, the fundamental frequency does not appear on a sonagram (phenomenon of the “missing fundamental”; e.g., see Durlach and Colburn [1978]), and its value must be inferred from interharmonic distances. The accuracy of these measurements, in turn, depends on the quality of the recording and the researcher’s ability to distinguish true harmonics from sounds of other origins.

Acoustical data on long calls of other Stercorariidae are limited primarily to the Great Skua and jaegers of the northern hemisphere (see reviews by Cramp and Simmons [1983]). Andersson (1973) found that the long calls of the Great Skua and Pomarine Jaeger (*Stercorarius pomarinus*) are similar in main features. They consist of notes similar in duration, repeated at 2–4 notes/s, and last about 1–5 s. He contrasted these with the calls of the Parasitic (*S. parasiticus*) and Long-tailed jaegers (*S. longicaudus*), which both produce 2–3 short notes followed by 3–5 long notes. He concluded that the long calls of the Great Skua and Pomarine Jaeger seem to be homologous, whereas those of the other two species may have had a different origin.

The Pomarine Jaeger appears more similar to the Great Skua than to other jaegers in displays as well as calls. Andersson (1973) noted that wing raising and bent neck components commonly occur in the long call displays of Great Skuas and Pomarine Jaegers, but are absent from those of Parasitic and Long-tailed jaegers. He suggested that the Pomarine Jaeger may have diverged from the Great Skua stock

later than the predecessor of the other two jaegers.

The sonagrams I present of South Polar and Brown skua long calls resemble those that Andersson (1973) and Cramp and Simmons (1983) presented for Pomarine Jaegers and Great Skuas. By contrast, the longer notes seen in sonagrams of the other two jaegers (Andersson 1971, 1973; Cramp and Simmons 1983) resemble the alarm notes of Brown and South Polar skuas (Fig. 4f; Burton 1968, Spellerberg 1971). Again, this suggests that Pomarine Jaegers may be more closely related to *Catharacta* species than are other jaegers.

These few inter-taxon comparisons hint at what may be learned when comparable, quantitative data on long calls are collected from all representative populations of Stercorariidae. Data presented here, in conjunction with those from these other populations, may help us assess taxonomic and evolutionary relationships at the subspecific, specific, and generic levels.

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