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Vocalizations in *Aptenodytes* Penguins: Application of the Two-voice Theory

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Aptenodytes penguins are colonial seabirds that have no nest but incubate a single egg on their feet. There are two species in the genus: the Emperor Penguin (*A. forsteri*) breeds during the harsh antarctic winter on the sea ice, and the King Penguin (*A. patagonicus*) breeds in subantarctic regions on beaches. Both sexes in each species produce a mutual display call that facilitates the search for a partner at the pairing period. When these penguins return from the sea to resume responsibility for the egg or chick, they use

the same call to achieve mutual recognition of the incubating partner and its mate (Stonehouse 1960, Prévost 1961, Jouventin 1982). King Penguins head towards the restricted area of the colony where their partners are incubating and call to be recognized. However, partner reunion would appear to be particularly difficult for the Emperor Penguin because these birds exhibit a wandering incubation that enables them to regulate the microclimate of the colony by gathering in dense huddles, thus withstanding the

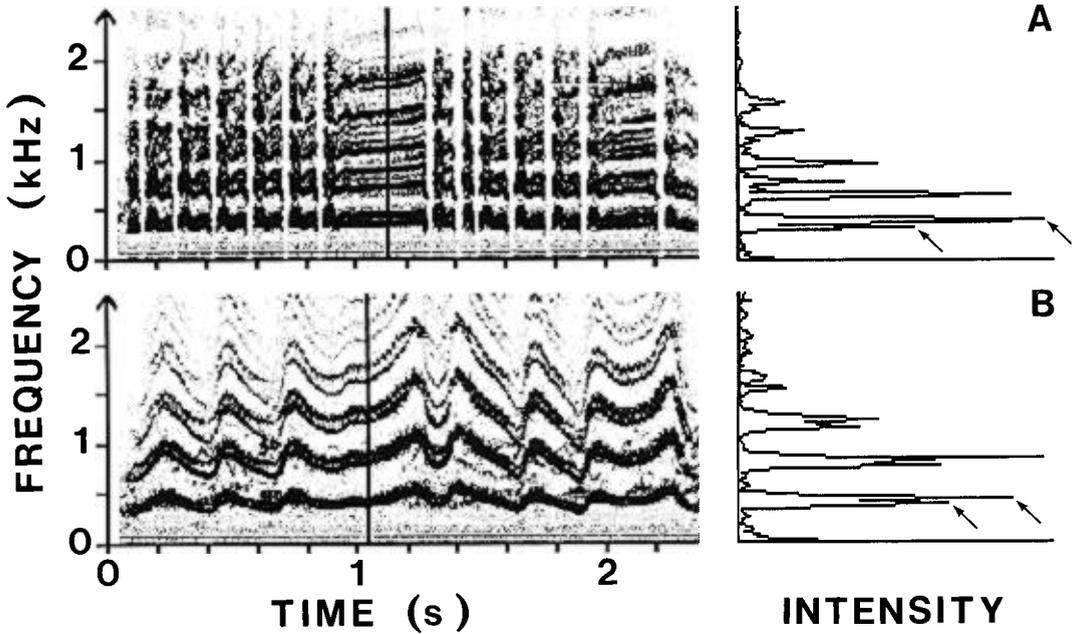


Fig. 1. Sonograms (at a sampling rate of 6,512 Hz and a FFT of 256 points; frequency bandwidth 25.4 Hz) of the individual-specific calls in: (A) a male Emperor Penguin; and (B) a male King Penguin. On spectral slices performed at vertical line of sonograms in long syllable of first series of syllables, arrows indicate the two voices.

extreme weather conditions (Prévost 1961). The birds also can move freely to more favorable places when necessary. This mobility demands that each time a bird returns from foraging, it may have to search among thousands of other birds, and the reunion is achieved only by vocalizations. Thus, in both species, but especially in the Emperor Penguin, the lack of a nest would be predicted to make the reunion of mates difficult. The *Aptenodytes* mutual display call is specific to individuals (Jouventin 1982), and a bird must deal with the complexity of this specificity in order to distinguish its partner from conspecifics. Acoustic communication would be expected to exhibit marked adaptations to such extreme circumstances.

The mutual-display call is composed of syllables separated by amplitude declines. These declines coincide with falls in frequency for King Penguins, and are further pronounced to the extent that they appear as silences for Emperor Penguins (Fig. 1; Jouventin 1982, Brémond et al. 1990). Syllables are grouped in repetitive series and a series is defined as a group of syllables terminated by a long syllable. A call is composed of one to four series. Syllables of the Emperor Penguin call have two frequency bands with their respective harmonics (Brémond et al. 1990). The interaction of these frequencies generates a beat, which Brémond et al. (1990) suggested conveyed information of individual identity. Other studies (Robisson et al. 1989, Robisson 1990) have demonstrated the

importance of the syllable structure for individual recognition in the genus *Aptenodytes*. Finally, bird species are well known to be able accurately to resolve minor differences in frequency (Dooling 1980, Kuhn et al. 1980, Stebbins 1983, Hulse et al. 1984), which has been suggested as a means to categorize notes (Weary 1990) and to discriminate among individuals (Brooks and Falls 1975, Falls 1982, Nelson 1989, Weisman et al. 1990). This led me to study frequency attributes of the mutual-display call of *Aptenodytes* penguins.

I recorded Emperor Penguins on the Pointe Géologie Archipelago, Antarctica (66°40'S, 140°01'E) in the austral winter of 1987, and King Penguins on the Crozet Islands, Indian Ocean (46°50'S, 37°45'E) in the austral summer of 1989. I used an omnidirectional Beyer Dynamic M69 microphone connected to a Nagra III or Uher 4000C tape-recorder (19.05 cm/s). Calls were displayed and analyzed on an Amiga microcomputer associated with an analytic package that calculated a Fast Fourier Transform (FFT) with 256 consecutive points and performed a spectrographic representation (Richard 1991). Figure 1 represented spectrograms with a frequency precision of ± 12.7 Hz (sampling frequency of 6,512 Hz), whereas I measured frequencies with a precision of ± 6.4 Hz (sampling frequency of 3,256 Hz). Frequency maxima and minima of each syllable of the first series were measured. I calculated the average values for the lower

TABLE 1. Means (\pm SD) of frequency features of mutual-display call in King and Emperor penguins. The following numbers of calls, each produced by a different bird, were analyzed: King Penguin, males 28, females 30; Emperor Penguin, males 23, females 24. All units in Hertz. Levels of significance two-tailed *t*-test. ***, $P < 0.001$; ns, $P > 0.05$.

Sex	Variable	Penguin		Species differences
		King	Emperor	
Male	Lower voice	456.4 \pm 29.9	370.7 \pm 24.2	10.92***
	Upper voice	480.1 \pm 24.5	431.5 \pm 25.0	6.88***
	Beat	23.6 \pm 17.1	60.4 \pm 13.7	8.45***
Female	Lower voice	501.6 \pm 50.0	432.5 \pm 43.2	5.36***
	Upper voice	528.0 \pm 46.4	528.3 \pm 53.7	0.02 ns
	Beat	27.1 \pm 22.0	95.9 \pm 25.3	10.51***
Sex differences (<i>t</i> -values)	Lower voice	6.30***	8.54***	
	Upper voice	8.18***	10.04***	
	Beat	0.68 ns	0.99 ns	

and upper frequency bands, and the interval frequency between the two bands. Frequency features were compared between species and between sexes (*t*-test), and between individuals (single-factor analysis of variance; *F*-test).

Both *Aptenodytes* species produced a signal consisting of a continuous pattern of two simultaneous series of harmonically related bands of slightly differing frequencies (Figs. 1A and B; see arrows). Such a signal corresponds closely with what other workers have termed a "two-voice" signal, which many birds are stated to produce through the elaboration of syrinx anatomy. Located at the junction of the two primary bronchi, each half of this two-part organ has an independent set of muscles and membranes thought to be involved in phonation and controlled separately by the tracheosyringealis branches of the right and left hypoglossus nerves. This double system enables birds to produce two voices simultaneously, as evidenced by results of many studies on avian anatomy (Stein 1968, Gaunt et al. 1982, Gaunt 1983) and physiology (Nottebohm 1971, 1972, Nottebohm and Nottebohm 1976, Nowicki and Capranica 1986, Suthers 1990), as well as by the spectrographic analyses of songs (Greenewalt 1968, Stein 1968, Latimer 1977, King and West 1983, Adret-Hausberger and Jenkins 1988) and calls (Stoddard and Beecher 1983, Beecher et al. 1985, Aubin 1986, Weisman et al. 1990). Therefore, the application of the two-voice theory (Greenewalt 1968) to the double-frequency structure of *Aptenodytes* calls is entirely reasonable.

Between-species comparison showed that the pitch of the call was greater in King than in Emperor Penguins except for the upper voice for females, and beat frequency was significantly greater for Emperor than for King penguins (Table 1). This indicated that frequency characteristics were species-specific. Lower and upper frequencies were significantly higher for females than for males in Emperor and King penguins, while no significant difference was found for the beat

frequency. The sex differences in frequency features are clear in Table 1, though it is not these features that render the calls of the two sexes so distinct to the human ear. Rather, it is the differences in the temporal patterning of syllables (Jouventin 1982).

I recorded seven male Emperor Penguins and seven male King Penguins from 5 to 10 times each. This gave a total of 47 Emperor Penguin calls and 53 King Penguin calls. An *F*-test showed significantly greater inter- than intraindividual variations for absolute frequencies and beat frequency in Emperor Penguins (lower voice, $F = 80.1$, $df = 6$ and 40 , $P < 0.001$; upper voice, $F = 99.5$, $df = 6$ and 40 , $P < 0.001$; beat, $F = 98.6$, $df = 6$ and 40 , $P < 0.001$) and King Penguins (lower voice, $F = 293.7$, $df = 6$ and 46 , $P < 0.001$; upper voice, $F = 264.8$, $df = 6$ and 46 , $P < 0.001$; beat, $F = 120.2$, $df = 6$ and 46 , $P < 0.001$). I suggest this represents a significant variability of frequency features, demonstrating their potential role as individual markers.

The sound structures of the functionally identical call in 10 other penguin species were analyzed (three *Pygoscelis* species, three *Eudyptes* species, two *Spheniscus* species, *Megadyptes antipodes*, and *Eudyptula minor*), but only the *Aptenodytes* species employ two frequency bands. It is presumably more than coincidence that these 10 species, and not *Aptenodytes* species, breed on a fixed nest site that appears ideally suited as a rendezvous point. Therefore, I suggest that the exploitation of two acoustic sources represents a means whereby *Aptenodytes* penguins can increase the information content of the call regarding individual identity, which can facilitate the recognition process. This is in accordance with the model proposed by Schleidt (1976) where the number of features is a component of individual distinctiveness. A further possibility is that complexity of the call increased by two voices has evolved in parallel with loss of territoriality. The next step is to test experimentally whether birds actually use two acoustic

sources to generate features relevant to the recognition processes.

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Seasonal Variation in Gene Frequencies in the House Sparrow (*Passer domesticus*)

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Differential survivorship within a population is usually considered to be a result of natural selection. It is, however, difficult to identify specific causes of selection and the levels at which they operate (Endler 1986, Grant 1986). Several avian studies have examined genetic changes in allozymic frequencies in populations across seasons, one period when selection could operate (Fleischer 1983a, b, Burns and Zink 1990, Retzlaff 1989). For allozymes, the question of whether gene frequencies vary seasonally is relevant because of the controversy over whether or not allozymic variation is primarily neutral (Fuerst et al. 1977, Baker and Fox 1978, Barrowclough et al. 1985, Nei 1987, Zink and Watt 1987).

The House Sparrow (*Passer domesticus*) has been analyzed for geographic variation in both allozymes and morphology (reviewed by Parkin 1987). Seasonal variation in morphology attributed to natural selection has been reported by Fleischer and Johnston (1982) for House Sparrows in Manhattan, Kansas. However, there was no seasonal variation in allozymes in the House Sparrow populations from Kansas (Fleischer 1983a, b), and none was found in a similar study on House Sparrows collected in North Dakota (Retzlaff 1989). During 1987-1988, we studied a population of House Sparrows in Baton Rouge, Louisiana, a site with considerably milder winters than Kansas or North Dakota. Baton Rouge winters consist of short cold periods usually lasting for only a few days, and freezing temperatures are recorded only a few times each winter. Temperatures for the 1987-1988 winter followed this pattern, although the mean daily minimum temperature for January 1988 was 2.5°C, which is 2° colder than the long-term monthly mean (N.O.A.A. 1987, 1988). We tested the null hypothesis that recruitment and over-winter survival in this House Sparrow population was independent of an individual's genotype at 29 allozyme loci.

We used mist nets and traps to collect 186 House Sparrows from several sites around the campus of Louisiana State University (LSU), Baton Rouge. All

individuals were collected between September 1987 and June 1988 and prepared as skeletons, which are housed at the Museum of Natural Science, LSU. From each individual, samples of liver, heart and breast muscle were collected and stored at -76°C. Protein electrophoresis followed standard techniques (Selander et al. 1971, Harris and Hopkinson 1976, Zink 1986). During electrophoretic analyses, no attempt was made to sort individuals by date of collection, sex, or age classes, to prevent biased interpretation of the data. In an initial screening, 28 individuals were surveyed for 30 loci, and the following loci (acronyms follow Gerwin and Zink 1989) had little or no variability (frequency of the common allele > 95%): ACON1, ACON2, ADH, ALD, EAP, ESTD, FUMH, GOT1, GOT2, αGPD, GPT, GR, Hb, HK, LDH1, LDH2, ME, MDH1, MDH2, MPI, SDH, SOD1, SOD2. All 186 individuals were surveyed for the six loci most variable: sLDH, mLDH, PGM, 6PGD, and peptidases LA1 and LGG. An additional locus, purine nucleoside phosphorylase (NP), appeared to show substantial variation; however, after a large series of reruns on all individuals, scoring was too inconsistent and the locus was excluded from the analysis.

For analysis, specimens were combined from the several collecting sites (located up to 8 km apart) because no significant differences in heterozygosity or gene frequencies could be detected among sites for any locus. Specimens, divided by sex and age, were divided into three temporal categories: fall (September to 14 December 1987, $n = 64$); winter (24 January to 13 February 1988, $n = 43$); and summer (May and June 1988, $n = 79$). All birds in which the skull was less than 90% ossified were considered immatures. By the end of December, hatching-year (HY) birds probably have completely ossified skulls (Pyle et al. 1987). All birds in the winter sample had ossified skulls, so these groups likely include some HY birds.

Heterozygosities (H) were calculated by direct count for each locus and summed over all loci for each sample category. G -tests were performed on genotype