

A COMPARISON OF THE VOCAL REPERTOIRES OF CAPTIVE *SPHENISCUS* PENGUINS

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SUMMARY

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This study characterized the vocal repertoires of captive African *Spheniscus demersus*, Humboldt *S. humboldti*, and Magellanic *S. magellanicus* Penguins. The contexts of the calls observed in captivity were consistent with the functions reported in the wild. However, the number and types of calls appeared to be influenced by the stability and density of the captive populations. Significant individual and species level variation occurred in temporal and frequency parameters of the Haw and Bray calls. No significant variation was apparent at the population level; however, these were artificial zoo populations and wild populations should be examined. The implications of the results as related to ecological factors are also considered.

INTRODUCTION

In penguins vocalizations are believed to be of primary importance in communication (Pettingill 1960, Stonehouse 1960, Boersma 1974, Spurr 1975, Scheich 1980a,b, Jouventin 1982). A detailed study of the Mutual Display call of the Emperor Penguin *Aptenodytes forsteri* revealed significant individual variation (Robisson *et al.* 1993). Such individuality of the calls is proposed as being particularly important for southern species which live in large dense colonies and in areas lacking landmarks. The barren habitat increases the need for vocal recognition of mates, chicks, and neighbours to locate nesting sites. To date vocal studies have primarily concentrated on these sub-Antarctic and Antarctic species (Stonehouse 1960, Penny 1964, Jouventin 1982, Robisson *et al.* 1993).

The genus *Spheniscus*, which includes African or Jackass *S. demersus*, Galapagos *S. mendiculus*, Humboldt *S. humboldti*, and Magellanic *S. magellanicus* Penguins, represents the most northerly distributed penguins. Members of this genus are island and coastal inhabitants, nesting mainly in burrows and crevices in areas possessing a variety of landmarks. Colony size is highly variable, ranging from 10–225 000 breeding pairs (Araya 1983, Boersma *et al.* 1990). It could be reasoned that the more northerly distributed penguins which generally live in less dense colonies and inhabit areas possessing numerous landmarks should be less reliant on vocalizations. However, *Spheniscus* penguins are primarily active on land at night. This nocturnal activity may limit the use of vision and increase the use of vocal communication. Consequently, they would be expected to show some variation in the structure of their calls.

Although some behaviours have been studied in all *Spheniscus* penguins, only basic information exists concerning vocalizations (Boersma 1974, 1976, Eggleton & Siegfried 1979, Scolaro 1987). Boersma (1974) identified six different calls in the Galapagos Penguin: Yell, Throb, Haw, Bray, Courtship

Bray and Peep. Yelling is a high intensity threat which corresponds to the Aggressive Bray or Bark in the African Penguin (Boersma 1974, Eggleton & Siegfried 1979). Throbs are very soft calls given when a mate returns to the nest and may serve to reinforce pair bonding (Boersma 1974). The Haw call is usually given by lone birds and used to locate other birds mainly while foraging at sea (Boersma 1974). It has also been described as the Contact call for African, Humboldt, and Magellanic Penguins (Jouventin 1982). The Bray occurs during the breeding period and is given only by the male in Galapagos Penguins to advertise availability and to establish a territory (Boersma 1974). The Bray corresponds to the Ecstatic Display of African and Magellanic Penguins which is given by both sexes (Eggleton & Siegfried 1979, Jouventin 1982). Finally, the Peep is only given by chicks and believed to be individually identifiable so parents feed the correct chicks (Jouventin 1982).

In this study we analyse the acoustic structure of the calls in three *Spheniscus* species (African, Humboldt, Magellanic) to determine if individuals, sexes, populations, or species consistently differ in their calling patterns. We also compare the context of the calls between the wild and captive situations.

METHODS

Observations were made on captive birds during breeding periods, mainly prior to and just after egg-laying, because most of the calling occurred at those times. The microphone was placed inside the exhibit within 1–5 m of the birds, but observations were made from outside the exhibit to minimise disturbance. Individuals were identified by flipper band colour. General behaviour was observed throughout the day from 08h00–17h00. Periodic observations made from 17h00–23h00 indicated little nocturnal activity which was supported by the comments of night keepers. Calls were defined in accordance with Boersma (1974) and measured using

behavioural sampling and continuous recording methods (Martin & Bateson 1986). Vocalizations were recorded throughout the period on a cassette recorder (Aiwa HSJ 500) using a cardioid Nakamichi (CM 100) microphone. The Galapagos Penguin was not included in the study because no captive populations were available. Table 1 indicates the number of penguins studied at each zoo, their housing condition, and periods observed. Note that throughout this study the term population refers to artificial groups of penguins housed at the different zoos.

The calls were analysed using a Kay 7800 Digital Sona-Graph (150-Hz band width) and digitised using a Sigma Scan Program (1988). For the single syllable Haw call the minimum, main, and maximum frequency and the duration of the call were measured. For the multi-syllable Bray call the number of syllables per call, total duration of the call, sum of inter-syllable intervals, duration of the longest syllable, and minimum, main, and maximum frequency of the longest syllable were measured. In both calls, the main frequency was represented by the darkest band in the sonogram of the call. The minimum and maximum frequencies were the lowest and highest bands respectively regardless of darkness. Recording birds from a very close fixed position in captivity reduced the amount variation in vocal parameters. These temporal and frequency variables were selected to assess the acoustical structure of the Haw and Bray calls because they could be consistently measured.

Sufficient data were collected for statistical analysis of variation in the Haw and Bray calls among individuals, sexes, zoo populations, and species for several of the *Spheniscus* penguins (Table 1). The data set was drawn only from calls where the caller had been identified. It was also limited to individuals for whom we had a total of two or more recordings for a given call. Variables were tested for normality and log or square root transformed as necessary. Since all analyses were unbalanced mixed models, SAS Type I error sum of squares was used (Milliken & Johnson 1984). For each call and for as many species as possible, a nested ANOVA (SAS procedure GLM, SAS Institute Inc. 1988) was used to determine the significance of individual and population level variation in each measured variable. Nested ANOVAs were used to examine population differences even though they were artificial zoo populations for the following reasons:

1) Since most of the zoo populations were formed by acquiring

a group of penguins from a single breeding ground in the wild, these do mimic natural populations.

2) Since very little is known about the development of penguin vocalizations (innate vs. learned components), the nested analysis provides for the potential of learning calls within populations. For variables that showed a significant difference at the individual level the percentage of total variance explained by differences among individuals within populations was calculated (SAS procedure VARCOMP). A sufficient number of vocalizations by both sexes was recorded only for the Haw call in the Humboldt Penguin. Therefore, in this case only, a nested ANOVA was used to determine the effect of sex on each measured variable and the amount of variation among individuals within sex.

For each type of call, the data sets from the three *Spheniscus* species were pooled and an ANOVA of individuals nested within populations within species, and populations nested within species was used to determine the effect of species on each measured variable. For variables which had significant variation among species, Gabriel's test was run to determine which pairs of species' means differed significantly. The percentages of total variance explained by differences among individuals within populations and among populations within species were calculated.

RESULTS

Overall, captive *Spheniscus* penguins have a complement of calls that is similar in basic structure and function. The context of the calls in captivity appeared to concur with their function described in the wild (Boersma 1974, Eggleton & Siegfried 1979, Jouventin 1982). However, some individual and species differences are apparent in frequency and temporal components of the Haw and Bray calls.

Call context: descriptive analyses

The Yell was a warning call directed at an individual that had approached too closely to another adult or pair of adults (Fig. 4b). In all three species if the vocal warning went unheeded the calling bird would peck at or chase the other bird away. In the Humboldt Penguin the Yell was heard fairly frequently (3–4 calls/hour) at the Brookfield Zoo (150 hours' observations) and the St. Louis Zoo (65 hours), but was never heard at the

TABLE 1

Zoos where vocalizations of *Spheniscus* penguins were recorded with the number of individuals maintained and recorded, exhibit type, and period observed noted. 'indoor + outdoor' indicates that the birds were brought inside during cold weather

Zoo/Species	Number of individuals			Exhibit type	Period observed
	Maintained	Recorded			
		Bray	Haw		
Milwaukee County					Feb 1986–May 1987
Humboldt Penguin	11	5	4	outdoor	Feb–Mar 1988
Brookfield, Chicago: Humboldt Penguin	9	6	2	indoor	Nov 1987–Apr 1988
St. Louis: Humboldt Penguin	12	9	3	indoor + outdoor	Oct 1988
Henry Villas, Madison: African Penguin	7	5	3	indoor + outdoor	Jan–Apr 1988
Racine: African Penguin	8	3	3	indoor + outdoor	Feb–Mar 1990
Cincinnati: Magellanic Penguin	8	2	0	outdoor	Apr 1988

Milwaukee County Zoo (190 hours). At the Brookfield Zoo it was usually directed at the two youngest penguins (one with immature plumage and the other with his first adult plumage), but was also occasionally directed at a newly introduced adult male. At the St. Louis Zoo about half of the colony was newly introduced birds. Although all populations had approximately the same number of birds, Brookfield's enclosure and St. Louis's outdoor enclosure were about one-half the size of Milwaukee's exhibit. The greater density of penguins at the Brookfield and St. Louis Zoos apparently resulted in more con-

tact between birds, more territorial behaviour, and more Yells.

Density was observed to affect other aggressive behaviours in the Milwaukee County Zoo's population. Aggression within the Milwaukee population increased as indicated by pecking (20 pecks/18 hours' observations) when the birds were temporarily moved to a holding enclosure one-third the size of their normal exhibit. In fact, a distinct 'pecking' order became apparent from contests over the preferred standing areas in the holding enclosure. Virtually no pecking (32 pecks/190 hours'

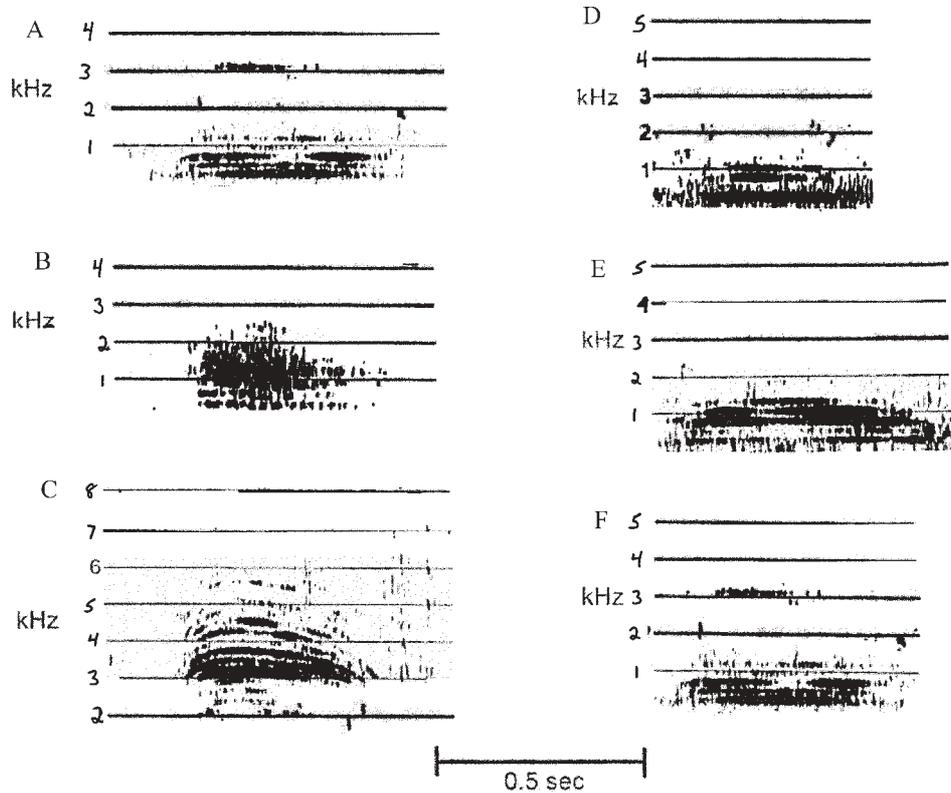


Fig. 1. Representative sonograms of the Haw call of *Spheniscus* penguins. (a) Humboldt Penguin, (b) African Penguin, and (c) Magellanic Penguin, (d-f) three different Humboldt Penguins.

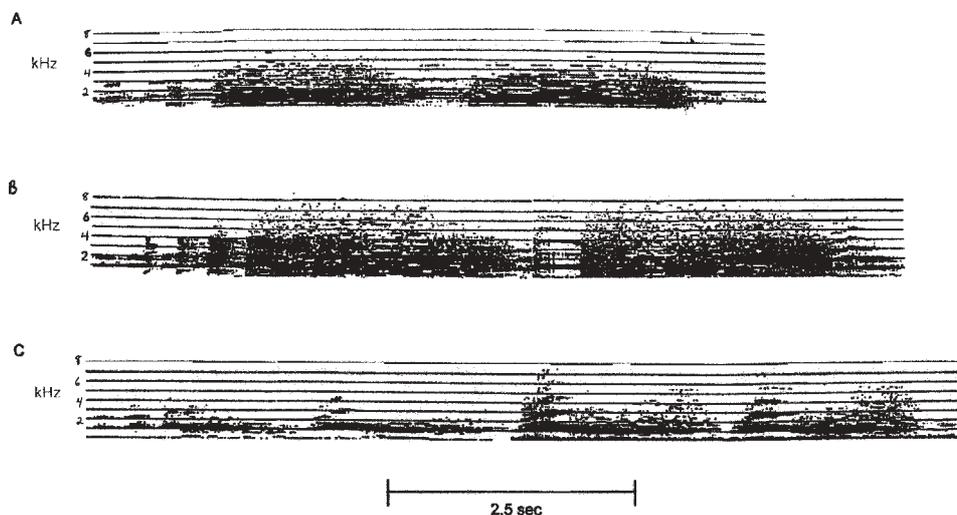


Fig. 2. Representative sonograms of the Bray call of *Spheniscus* penguins. (a) African Penguin, (b) Magellanic Penguin, and (c) Humboldt Penguin.

observations) was observed in the normal exhibit prior to or after the move.

In Humboldt Penguins the increase in aggressive behaviour (pecking) in the denser populations resulted from the preferred standing locations being closer together and along commonly travelled routes. The Yell was heard frequently (9 calls/hour) in the Magellanic Penguin population (50 hours' observations), but was most common (13–14 calls/hour) in the African Penguin populations (75 hours). Keepers commented and we observed that African Penguins fought more with each other and were more aggressive toward keepers than were Magellanic Penguins, and Magellanic Penguins were more ag-

gressive towards each other and to keepers than were Humboldt Penguins. These observations were made on populations with approximately the same densities.

The Throb calls were very soft calls given by pairs at the nest. Although these calls were difficult to detect, we heard them in Humboldt Penguins at the Brookfield and Milwaukee County Zoos and in African Penguins at the Madison Zoo (Fig. 4c). In all cases incubating birds called when their mates returned to the nest. Throbs have not been reported in Magellanic Penguins, but this is most likely due to the low volume of the call and the limited vocal studies on Magellanic Penguins.

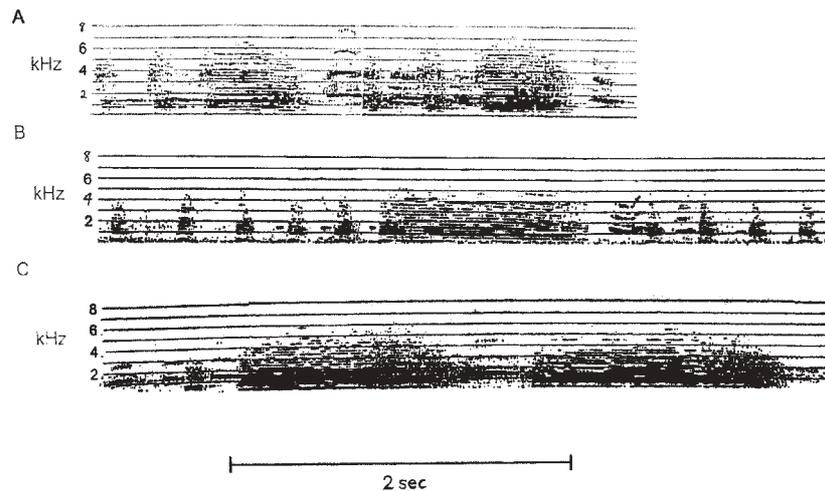


Fig. 3. Sonograms of the Bray call showing individual variation among three different Humboldt Penguins.

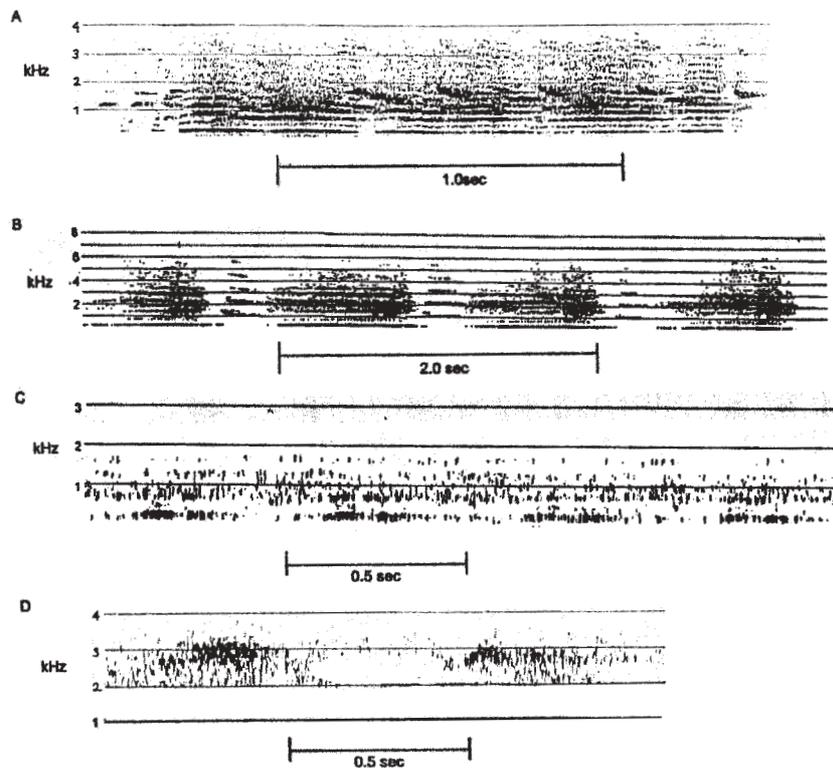


Fig. 4. Representative sonograms of (a) the Courtship Bray call, (b) the Yell call, (c) the Throb call, and (d) the Peep call of the Humboldt Penguin.

The Haw was a short call (c. 0.5 s) heard in all zoo populations. Juveniles often gave this call when alone in the water. In paired birds, the call was often given by either member of a pair when one member was in the water and one was on land.

The Bray was a long call (2–3 s) also heard in all zoo populations and appeared to be used to attract a mate and advertise a territory. The bird stands with its head pointing up and calls while slowly flapping its flippers. In Humboldt Penguins at the Milwaukee County Zoo the Bray was only given by males and occurred most frequently during the pre-laying and pre-

hatching periods. At the Brookfield and St. Louis Zoos the call was given more frequently, by both sexes, and occurred throughout the breeding period.

The Courtship Bray was very similar to the Bray except that it was associated with a different posture and given synchronously by pairs. During a typical Courtship Bray, the birds stand together with their necks and heads pointed up, and their flippers slightly out to the side. This call was observed only in the Humboldt Penguins at the Brookfield Zoo during the pre-laying period (Fig. 4a).

The Peep was given only by chicks when begging for food. All of the chicks that hatched at the zoos during the study period gave this call. These include calls by Humboldt Penguins at the Milwaukee and Brookfield Zoos, African Penguins at the Racine Zoo, and Magellanic Penguins at the John Ball Zoo (Fig. 4d). We were unable to obtain a sufficient number of sonograms to determine statistically whether they were individually distinct. However, siblings were fairly easily distinguished from one another by the human ear.

TABLE 2

Mean and standard deviation of the variables in the Haw call for the three species of *Spheniscus* penguins

Variable	Species		
	Humboldt	African	Magellanic
Sample size	32	12	2
Duration of call (s)	0.62±0.11	0.57±0.24	0.58±0.16
Minimum frequency (kHz)	0.26±0.16	0.11±0.09	0.16±0.12
Maximum frequency (kHz)	2.92±1.21	1.10±0.20	3.36±0.10
Main frequency (kHz)	0.89±0.87	0.70±0.18	0.41±0.04

TABLE 3

ANOVAs based on 32 observations of the haw call of Humboldt Penguins for six individuals nested within three captive populations and six individuals nested within two sexes

	Degrees of freedom	Sum of squares	% of total variance	F ^a
Duration of call				
Pop	2	0.088		1.77
Indiv within Pop	3	0.074	32	3.27*
Sex	1	0.045		1.56
Indiv within Sex	4	0.117	44	3.85*
Minimum frequency				
Pop	2	3.598		3.56
Indiv within Pop	3	1.516	38	4.07*
Sex	1	0.277		0.23
Indiv within Sex	4	4.837	71	9.74***
Main frequency				
Pop	2	0.455		1.58
Indiv within Pop	3	0.432		0.19
Sex	1	0.104		0.53
Indiv within Sex	4	0.783		0.26
Maximum frequency				
Pop	2	24.184		2.80
Indiv within Pop	3	12.965	72	13.82***
Sex	1	6.099		0.79
Indiv within Sex	4	31.050	87	24.82***

^aSignificance of F: * = $P < 0.05$, *** = $P < 0.0001$.

Frequency and temporal variation: statistical analyses

The Haw call was very common and was similar in basic structure in all the *Spheniscus* species (Fig. 1a–c, Table 2). Individual variation was apparent in the sonograms of Humboldt Penguins (Fig. 1d–f). The parameters of the Haw call in Humboldt Penguins showed significant ($P < 0.04$) individual variation in the duration of the call and minimum and maximum frequencies, but not in the main frequency (Table 3). There was no significant variation among captive populations or sexes for any variable tested when individual variation was taken into account (Table 3). Individual variation could not be determined in the African and Magellanic Penguins because

TABLE 4

ANOVAs based on 57 observations of the Haw call of *Spheniscus* penguins for 10 individuals nested within six captive populations nested within three species

	Degrees of freedom	Sum of squares	% of total variance	F ^a
Duration of call				
Species	3	0.089		0.14
Pop within Species	3	0.626	78	8.41
Indiv within Pop within Species	3	0.074	5	2.78
Minimum frequency				
Species	3	19.404		2.13
Pop within Species	3	9.119	60	6.02
Indiv within Pop within Species	3	1.516	3	1.39
Maximum frequency				
Species	3	63.116		2.59
Pop within Species	3	24.411	48	1.88
Indiv within Pop within Species	3	12.965	34	10.53***
Main frequency				
Species	3	19.006		22.16*
Pop within Species	3	0.858	4	1.98
Indiv within Pop within Species	3	0.432	0	0.34

^aSignificance of F: * = $P < 0.05$, *** = $P < 0.0001$.

a sufficient number of recordings was not obtained. The Haw call showed significant ($P < 0.02$) variation among species (Humboldt, African, Magellanic) only for the main frequency (Table 4). Gabriel's test of the species' means indicated that there were no significant differences in means among the *Spheniscus* penguins.

The Bray had a similar basic structure in all *Spheniscus* species (Fig. 2, Table 5). Within each species, individual penguins showed distinct differences in their sonograms (Fig. 3). In Humboldt Penguins the Bray call showed significant ($P < 0.0001$) variation among individuals in all variables: number of syllables per call, total duration of the call, sum of inter-syllable intervals, duration of the longest syllable, and minimum, main, and maximum frequency of the longest syllable (Table 6). Again no significant variation was found among captive populations. In African Penguins significant ($P < 0.05$) variation was found among individuals for number of syllables, duration of the longest syllable, and main frequency of the longest syllable (Table 6). There was no significant variation among captive populations. In Magellanic Penguins only one population was analysed, so only individual variation within that population was examined. Individuals varied significantly ($P < 0.05$) for duration of the longest syllable, sum of inter-syllable intervals, and maximum frequency of the longest syllable (Table 6). The Bray call showed significant ($P < 0.02$) variation among species (Humboldt, African and Magellanic,) for number of syllables, total duration of the call, and main frequency of the longest syllable (Table 7). Gabriel's test of the species' means indicated that for syllable number there were significant differences of the means between African and Humboldt Penguins.

DISCUSSION

Given their common evolutionary origin and the simple acoustical structure of their calls, it is not surprising that the functions of *Spheniscus* penguin calls appears to be consistent among species and between the captive and wild state. However, the stability and density of captive populations seems to influence greatly the amount and types of calls occurring. Since *Spheniscus* penguins are known to vary greatly in colony size and density in the wild (Araya 1983, Boersma *et al.* 1990), it is important to record these parameters in wild populations and collect quantitative vocal data.

Vocal studies on wild populations are necessary to substantiate any of the tendencies suggested by this captive study. For

example, population stability may be correlated with the braying of females. Females brayed at the Brookfield and St. Louis Zoos where pairs were still forming or females were competing for mates. However, only males brayed at the Milwaukee County Zoo which has had a stable adult population for over five years. It would be interesting to look at wild populations to determine if female braying is helpful in assessing or tracking their stability over time.

Even though these penguins inhabit areas containing numerous landmarks for locating nests, mates and chicks, significant individual variation occurred in both the Haw and Bray calls. Of course, this variation can be attributed to other ecological factors. For example, vocal identification and warning calls could be particularly important in *Spheniscus* penguins because they often nest in dark burrows and crevices and some populations are exposed to terrestrial predators.

In addition, variation in both temporal and frequency parameters of the Haw call could provide a mechanism whereby individuals could find one another on land or at sea. Since adult *Spheniscus* penguins (except Galapagos) primarily forage in groups at sea, the Haw call could be important in bringing foraging groups together (Wilson *et al.* 1987). No significant differences were found among captive populations in the parameters we measured. However, the zoo populations are artificial and wild populations should be examined before any conclusion is reached concerning population differences. The Haw call also exhibited little variation at the species level even between sympatric species. This overlap at the species level within *Spheniscus* would be interesting to examine in more detail since there are several potential explanations. For example, there would be little selection pressure for divergence of this locating call if a lone or lost penguin has a better chance of survival if it finds any other penguin regardless of species.

The individual variation found in the temporal and frequency parameters of the Bray call should make it easier for birds to find their colony and for mates to locate each other when returning from the sea at dusk. Species showed a marked difference in the number of syllables per call, total duration of the call, and the main frequency of the longest syllable. There was sufficient species-level variation for a phenetic analysis of taxonomic relationships (Thumser *et al.* 1996). The resulting phylogeny showed a closer relationship between Magellanic and African Penguins than either has to Humboldt Penguins, which corresponds with phylogenies based on allozyme data (Grant *et al.* 1994, Thumser &

TABLE 5

Mean and standard deviation of the variables in the Bray call for the three species of *Spheniscus* penguins

Variable	Species		
	Humboldt	African	Magellanic
Sample size	100	54	8
Syllable number	5.39±1.91	9.82 ±2.83	13.75±2.66
Total duration of call (s)	5.30±1.43	6.00±1.27	6.65±1.78
Total inter-syllable interval (s)	1.00±0.82	1.04±0.66	2.59±0.83
Duration of longest syllable (s)	2.09±0.58	1.46±0.35	1.61±0.30
Minimum frequency of longest syllable (kHz)	0.41±0.30	0.21±0.05	0.24±0.05
Maximum frequency of longest syllable (kHz)	5.57±1.82	7.14±1.16	6.92±1.07
Main frequency of longest syllable (kHz)	1.48±0.64	1.24±0.26	1.97±1.29

Karron 1994, Thumser *et al.* 1996). Since the Bray is associated with attracting mates, it is not surprising that it was found to vary at the individual and species levels.

The three *Spheniscus* penguins studied have clearly retained a similar repertoire of calls. However, individuals and species consistently showed significant differences in several frequency and temporal aspects of the Haw and Bray calls. Similar to other seabirds, penguins have a significant amount of variation in the structure of their calls below the species level (Bretagnolle 1996). This pattern appears to be widespread since it occurs in the strictly Antarctic Emperor Penguin and in the northern *Spheniscus* penguins.

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TABLE 6

Nested ANOVAs of individuals within populations based on 100 observations of 12 individuals in three captive populations of Humboldt Penguins, 33 observations of five individuals in two populations of African Penguins, and eight observations of two individuals in one population of Magellanic Penguins for the Bray call

	Degrees of freedom	Sum of squares	% of total variance	F ^a		Degrees of freedom	Sum of squares	% of total variance	F ^a
Syllable number					Minimum frequency of longest syllable				
Humboldt Penguin					Humboldt Penguin				
Pop	2	38.670		0.94	Pop	2	10.452		1.01
Indiv within Pop	9	184.890	60	13.27***	Indiv within Pop	9	49.794	74	24.00***
African Penguin					African Penguin				
Pop	1	2.814		0.15	Pop	1	0.007		0.25
Indiv within Pop	3	55.879	32	3.40*	Indiv within Pop	3	0.082	28	2.99*
Magellanic Penguin					Magellanic Penguin				
Indiv	1	4.167		0.55	Indiv	1	0.386		6.49*
Total duration of call					Maximum frequency of longest syllable				
Humboldt Penguin					Humboldt Penguin				
Pop	2	3.929		0.23	Pop	2	60.704		1.84
Indiv within Pop	9	77.464	39	6.28***	Indiv within Pop	9	148.687	58	12.42***
African Penguin					African Penguin				
Pop	1	0.00075		0.0003	Pop	1	6.006		3.54
Indiv within Pop	3	6.606	16	1.95	Indiv within Pop	3	5.085	4	1.19
Magellanic Penguin					Magellanic Penguin				
Indiv	1	4.766		1.65	Indiv	1	4.519		7.71*
Total inter-syllable interval					Main frequency of longest syllable				
Humboldt Penguin					Humboldt Penguin				
Pop	2	17.225		3.65	Pop	2	0.100		0.16
Indiv within Pop	9	21.262	43	7.24***	Indiv within Pop	9	2.748	35	5.49***
African Penguin					African Penguin				
Pop	1	0.235		7.68	Pop	1	0.007		0.25
Indiv within Pop	3	0.092	0	0.39	Indiv within Pop	3	0.082	28	2.99*
Magellanic Penguin					Magellanic Penguin				
Indiv	1	0.118		3.91	Indiv	1	0.428		2.64
Duration of longest syllable									
Humboldt Penguin									
Pop	2	0.220		0.13					
Indiv within Pop	9	7.814	75	26.24***					
African Penguin									
Pop	1	0.083		0.50					
Indiv within Pop	3	0.494	40	4.34					
Magellanic Penguin									
Indiv	1	0.166		24.66**					

^aSignificance of F: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.0001$

TABLE 7

ANOVAs based on 206 observations of the Bray call of *Spheniscus* penguins for 27 individuals nested within six captive populations nested within three species

	Degrees of freedom	Sum of squares	% of total variance	F ^a
Syllable number				
Species	3	1196.41		10.53*
Pop within Species	4	151.44	14	2.46
Indiv within Pop				
within Species	18	276.90	21	3.45***
Total duration of call				
Species	3	220.78		27.63**
Pop within Species	4	10.65	0	0.44
Indiv within Pop				
within Species	18	109.89	26	3.63***
Total inter-syllable interval				
Species	3	13.84		0.91
Pop within Species	4	20.22	23	2.98*
Indiv within Pop				
within Species	18	30.52	31	5.93***
Duration of longest syllable				
Species	3	50.62		3.88
Pop within Species	4	17.40	52	7.94**
Indiv within Pop				
within Species	18	9.86	20	6.63***
Minimum frequency of longest syllable				
Species	3	59.38		3.18
Pop within Species	4	24.91	13	1.95
Indiv within Pop				
within Species	18	57.36	38	6.68***
Maximum frequency of longest syllable				
Species	3	47.58		0.74
Pop within Species	4	85.80	16	2.20
Indiv within Pop				
within Species	18	175.69	37	6.79***
Main frequency of longest syllable				
Species	3	2.674		11.47*
Pop within Species	4	0.311	0	0.30
Indiv within Pop				
within Species	18	4.623	43	6.83***

^aSignificance of F: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.0001$.

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