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Geographical variation in Cape fur seals' in-air vocalizations across Southern Africa (Namibia and South Africa)

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Abstract

The use of acoustic signals to communicate is widespread among marine mammals and vocalizations are involved in all their social interactions. Due to many factors, acoustic features of a species' vocalizations may differ among populations. The present study investigated both micro- and macro-geographical variation in the vocalizations of Cape fur seal females, males, and pups. Acoustic measurements were performed on calls recorded at four South African and two Namibian sites (maximum range ∼ 1,000 km). Comparisons among close sites in South Africa revealed no micro-geographical variation (maximum range ∼130 km) in females' and pups' vocalizations. Barks of subadult males had different features among sites, which may be explained mostly by the context of call production. At the macro-geographical scale (South Africa vs. Namibia), all call types varied significantly among sites. Several extrinsic and intrinsic factors were suggested to drive such differences. For females' and pups' calls, differences might be explained by environmental factors, whereas for males' barks, behavioral differences are the most likely explanation for acoustic differences (breeding vs. resting sites). Such investigations help understand how

acoustic communication in marine mammals is shaped by ecological drivers.

1 | INTRODUCTION

Marine mammal species use acoustic signals to communicate. Vocalizations are involved in the establishment and maintenance of all types of social interactions, including mate-attraction, territorial defense, parental care, and group coordination (Dudzinski et al., 2009). To ensure efficiency in an acoustic communication system, the usage of the different types of calls, as well as their acoustic features, must exhibit a certain degree of homogeneity and consistency within the vocal repertoire of a species, allowing durable transmission of information among individuals and over time or generations (Bradbury & Vehrencamp, 2011). However, subtle variations in call usage and/or in the intrinsic acoustic characteristics of vocalizations can occur in a species' vocal repertoire. When differences are found between populations (as opposed to interindividual variation for example), they are referred to as geographical variations. Geographical variation can be understood at different scales: micro-geographical variation (also called "dialects") concern neighboring populations that have the ability to interbreed or interact with one another, whereas macro-geographical variation refers to differences between populations separated by large distances, preventing them from mixing (Mundinger, 1982).

Geographical variation in acoustic signals has been described in various marine mammal species, including in mysticetes (e.g., Ford & Fisher, 1983; Stafford et al., 2001; Winn et al., 1981), odontocetes (e.g., Luís et al., 2021; Rendell & Whitehead, 2003; Van Cise et al., 2018), and pinnipeds. A large proportion of these studies focus on underwater and airborne vocalizations of phocids (e.g., Cleator et al., 1989; Collins & Terhune, 2007; Le Boeuf & Peterson, 1969; Nikolich et al., 2016; Terhune et al., 2008; Thomas et al., 1988; Van Opzeeland et al., 2009; Van Parijs et al., 2000) but there are also a few studies on otariids' airborne calls (Ahonen et al., 2014, 2018; Attard et al., 2010; Martin et al., 2021; Trimble & Charrier, 2011), leaving a general lack of information in this area. Several drivers are suggested to cause geographical variation in acoustic signals of marine mammals: geographical isolation and/or genetic drift between isolated populations (Cleator et al., 1989; Mundinger, 1982; Stafford et al., 2001; Thomas et al., 1988), adaptation to environmental effects—known as the "acoustic adaptation hypothesis" (Morton, 1975), such as habitat propagation properties and/or background noise (Martin et al., 2021; Trimble & Charrier, 2011) or cultural transmission of learned signals (Luís et al., 2021; Rendell & Whitehead, 2003). The study of geographical variation in vocalizations is a major factor in understanding how acoustic signals (call usage as well as their acoustic features) are shaped by social, behavioral, or environmental factors and to enhance our knowledge of the evolution of communication systems in animal species.

In this study, we focused on geographical variation in the airborne vocalizations of the Cape fur seal (*Arctocephalus pusillus pusillus*), an emblematic marine mammal of Africa, as the only pinniped species to breed on this continent. Like other otariid species, Cape fur seals are colonial breeders. Each year from late October to January, pupping and mating take place in colonies along the southwest and south coasts of Southern Africa (from Baia dos Tigres in southern Angola to Algoa Bay in South Africa). Such wide repartition results in a significant fragmentation of the species with about 40 breeding colonies located on both the mainland and islands. Colonies inhabit very different terrain, from sites characterized by bare rock, boulders, or ledges to open sandy beaches. About 60% of the pup production occurs in Namibia and 40% in South Africa (Hofmeyr, 2017). Cape fur seals are highly vocal and rely on acoustic communication for the vast majority of their social interactions on land, which are primarily related to

reproduction. Females and pups produce attraction calls to communicate with each other (Martin et al., 2021). Barks are short calls always emitted in sequence and produced by males for territorial defense, as well as during agonistic interactions (Martin et al., 2021). Females also produce barks during agonistic interactions with conspecifics (Martin et al., 2021). The importance of vocal signals in establishing relationships among individuals (inter- and intrasexual interactions, territoriality, maternal care), the separation of individuals into colonies along the range of distribution, and the dispersal/movement of individuals between breeding colonies are reasons to investigate geographical variation in the vocalizations of Cape fur seals.

A recent study revealed micro-geographical variations in seven types of Cape fur seal calls between two colonies of central Namibia separated by approximately 150 km: Pelican Point and Cape Cross (Martin et al., 2021). Calls from Cape Cross were higher pitched compared to calls recorded at Pelican Point. Differences in body size—due to possible variation in population density, food availability, and/or genetics—as well as environmental factors (such as the background noise produced by waves) were suggested to contribute to this variation (Martin et al., 2021). The present study aimed to investigate the extent of geographical variation in airborne vocalizations produced by Cape fur seals at a broader scale. We first looked at the micro-geographical variation among neighboring colonies or haul-out sites in the Western Cape, South Africa (approximately 1,300 km to the south of the Namibian study sites). Secondly, macro-geographical variation was examined by incorporating published data from Namibia (vocalizations recorded at Pelican Point and Cape Cross; Martin et al., 2021) to that of South Africa. This allowed us to compare distant and likely noninterconnected seals colonies, at a broader scale.

2 | METHODS

2.1 | Study sites and animals

Cape fur seal vocalizations were recorded at four study sites located in South Africa, in the Western Cape Province: Lambert's Bay, Duiker Island, Seal Island, and Cape Town harbor (Figure 1), from April to early May 2021, when pups were 5–6 months old. Acoustic recordings performed at Pelican Point and Cape Cross (Namibia) during the 2019–2020 breeding season (between November and February) were included to allow for comparisons at a macro-geographical scale. These data were previously used in the description of the species' vocal repertoire and the assessment of micro-geographical variation in Namibia (Martin et al., 2021). All calls of females and males were included in the present study, while only 2–4-month-old pups' calls were included (calls from pups under the age of 2 months were not selected) to limit the difference in pups' age between study sites.

2.2 | Recording procedure

At all sites vocalizations were recorded at a 44.1 kHz sampling rate, using a Sennheiser ME67 directional shotgun microphone (frequency range: 40–20,000 Hz ± 2.5 dB). The microphone was connected to either a Nagra LB or Roland R26 digital audio recorder. At Duiker Island and Seal Island, recording sessions were performed from a boat. The microphone was mounted at the tip of a 3-m vertical pole to reduce the background noise of the swell and waves hitting the rocks and the boat. Distance from focal animals ranged from 5 to 10 m at Duiker Island and from 10 to 20 m at Seal Island. For the other study sites, recordings were land-based and the distance between the microphone and focal animals ranged from 0.5 to 6 m. To limit the risk of resampling the same individuals, recordings were performed at different locations within study sites, and over several recording sessions and/or days. In addition, at Pelican Point (Namibia) some individuals (males and pups) were individually marked (oil-based paint or hair-dye marks applied for other scientific purposes), which ensured that the same individual was not recorded twice.
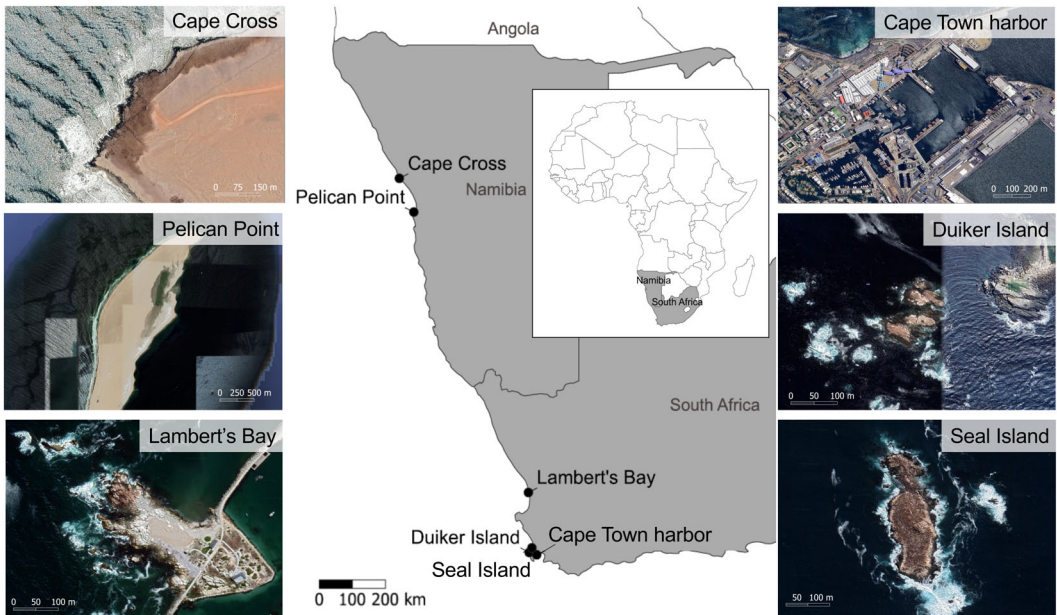
FIGURE 1   Location and satellite view (©2022, Google) of the six study sites in Namibia and South Africa.

To investigate geographical variation in the vocal repertoire of the Cape fur seal, we focused our analysis on three call types: pup-attraction calls, female-attraction calls, and barks. Pup- and female-attraction calls are produced by females and pups, respectively, to communicate with each other at both short- and long-distances (Martin et al. 2021). We recorded barks produced by females during agonistic interactions and barks produced by subadult males when interacting with other individuals. While recording a calling individual with the shotgun microphone, the experimenter described the identity (for marked individuals), as well as the age and/or sex of the target individual (for both marked and unmarked individuals) using a second microphone (lapel microphone) plugged into a separate channel of the recorder.

2.3 | Acoustic measurements

From the stereo recordings, the first channel containing the recorded vocalizations was extracted and resampled at 22.05 kHz as the highest frequencies of Cape fur seal vocalizations do not exceed 10 kHz (Martin et al. 2021). Acoustic analyses were performed using Avisoft SAS Lab Pro (R. Specht, v. 5.2.14, Avisoft Bioacoustics, Berlin, Germany) and spectrograms were calculated with a 1,024-point fast Fourier transform (FFT), 75% overlap and a Hamming window (frequency resolution = 21.5 Hz). Only good-quality calls with low background noise and no overlap with other vocalizations were selected. We included between 1 and 10 pup- or female-attraction calls per individual in the analysis. As barks are vocalizations produced in sequences composed of many repetitions, measurements were performed on five bark units randomly chosen from each bark sequence, and several sequences were analyzed (maximum of 10 sequences per recorded individual). For each vocalization (pup-attraction call, female-attraction call, or bark unit), we measured a set of six acoustic features: total duration of the call (*Dur*, ms), fundamental frequency (*f0*, Hz; measured with the harmonic cursor function), the frequency values of the first, second, and third energy peak (*Fmax1*, *Fmax2*, *Fmax3*, Hz), and the frequency bandwidth within which the energy falls within 12 dB of the first peak (*Bdw12*; Hz). For barks, we measured a seventh variable, corresponding to the

interbark duration, i.e., duration of the silence between the end of the measured bark and the beginning of the next one (*Interbark duration*, ms). Spectral features such as the quartiles of energy spectrum were not included in this study as some sites are highly exposed to abiotic noise, in particular Seal Island and Duiker Island, which are subject to swell and waves hitting the rocks. Such ambient noise may influence the spectral measurements taken from the simultaneous call, and thus bias the comparisons between sites.

2.4 | Statistical analysis

2.4.1 | Micro-geographical variation among South African study sites

For the comparison of Cape fur seals' vocalizations among sites in South Africa, a linear mixed-effects model (LME) was built for each call type and each acoustic feature to assess differences between sites. A variable containing the identity of recorded individuals was set as a "random effect" to account for the fact that the data set can include several calls from the same individual (maximum of 10 calls or 10 bark sequences). Statistical analyses were performed in R (R Core Team, 2020) with the *lme4* R package (Bates et al., 2015) and a pairwise analysis of estimated marginal means was conducted using the *emmeans* package (Lenth, 2021). It included a Šidák correction for multiple comparisons. Secondly, a classification method was used to assess the discrimination of vocalizations among study sites, based on acoustic variables. We performed Random Forest algorithms on each call type with the six (pup- and female-attraction calls) or seven (barks) acoustic features measured. We set the number of trees at 1,000 and the number of variables to be selected at each node at 2, i.e., the square root of the total number of variables (as suggested by the package). The overall classification rate stabilized at its lowest value using these parameters. To maintain equal sample sizes of each class (i.e., each study site) in the classification and to avoid the over-representation of the biggest classes, we used the "Balanced Random Forest" algorithm (Chen et al., 2004). With this procedure, each tree of the Random Forest was built with the same number of calls per study site, i.e., the number of calls in the smallest class. The confusion matrix resulting from each Random Forest was extracted using the *caret* package (Kuhn, 2021) and classification rates (in percent) were calculated. The performance of the classification is evaluated by comparing the accuracy of the model with the no information rate (NIR) obtained with the *confusionMatrix* function of the previous package.

2.4.2 | Macro-geographical variation between Namibian and South African study sites

Comparisons of Cape fur seal vocalizations on a macro-geographical scale, i.e., between sites in Namibia and South Africa, were performed in the same way as in the previous section. A univariate analysis was built for each type of call and each acoustic feature (LME with the individual identity set as "random effect") supplemented by a Random Forest algorithm (with the same specifications) to classify the vocalizations at the different study sites. To provide a visual two-dimensional representation of call distinctiveness among study sites, we built a multi-dimensional scaling (MDS) plot based on the proximity matrix from the Random Forest algorithm for each call type.

3 | RESULTS

3.1 | Micro-geographical variation among South African study sites

Pup-attraction and female-attraction calls were recorded at all South African study sites, except at Cape Town harbor because this hauling-out site is only occupied by juveniles and subadult or adult males. Barks produced by

TABLE 1 Comparison of the acoustic features (indicated as mean ± *SD*) measured on three Cape fur seal call types between different study sites in South Africa (LB: Lambert's Bay, CT: Cape Town harbor, DI: Duiker Island, SI: Seal Island.). Results of the pairwise analysis of estimated marginal means following the linear mixed-effects model are indicated for each acoustic feature and each study site (no significant difference between sites sharing the same letter; NS means that the LME was not significant).

Micro-geographical variations (South Africa)		Duration (ms)		f0 (Hz)		Fmax1 (Hz)		Fmax2 (Hz)		Fmax3 (Hz)		Bdw12 (Hz)		Interbark duration (ms)
Pup-attraction calls	LB (n = 280)	1,040 ± 304	NS	281 ± 46	NS	825 ± 336	NS	1,027 ± 442	NS	1,121 ± 494	NS	14 ± 13	NS	
	DI (n = 86)	938 ± 247		306 ± 38		778 ± 268		1044 ± 486		1,118 ± 539		18 ± 13		
	SI (n = 117)	949 ± 291		300 ± 45		822 ± 297		1,120 ± 517		1,276 ± 516		15 ± 14		
Female-attraction calls	LB (n = 238)	708 ± 201	ab	330 ± 87	NS	1,069 ± 498	NS	1,448 ± 829	NS	1,553 ± 983	NS	23 ± 25	NS	
	DI (n = 43)	609 ± 169	a	360 ± 42		1,140 ± 485		1,050 ± 813		1,486 ± 849		23 ± 21		
	SI (n = 59)	732 ± 242	b	366 ± 63		1,108 ± 642		1,314 ± 847		1,440 ± 884		16 ± 13		
Subadult male barks	LB (n = 420)	91 ± 19	a	148 ± 24	ab	753 ± 344	ab	844 ± 439	NS	942 ± 578	NS	60 ± 32	b	229 ± 38 NS
	DI (n = 120)	98 ± 31	a	169 ± 25	a	725 ± 232	a	828 ± 482		885 ± 589		70 ± 37	a	218 ± 38
	CT (n = 430)	135 ± 32	b	139 ± 34	b	648 ± 202	b	785 ± 368		864 ± 432		48 ± 25	b	235 ± 59

FIGURE 2 Classification rates (in percent) calculated based on confusion matrices resulting from classifications among South African sites by Random Forest algorithm for pup-attraction calls (a), female-attraction calls (b), and subadult male barks (c). Values represent the percentage of calls assigned in each of the prediction class. Below each matrix is the statistical comparison between the accuracy of the Random Forest model (Acc) and the no information rate (NIR) and the associated *p* value in case of significant difference.

females could only be recorded at one site (Lambert's Bay), so no comparisons could be carried out with other South African study sites. Subadult male barks were compared among all study sites, except Seal Island for which we had too few animals (bark from only two males). A summary of the exact sample size for each location is presented in Table 1.

For pup-attraction calls, we failed to find significant difference between the three South African locations in any of the six acoustic features considered (Table 1). The Random Forest algorithm, for which the resulting classification rates are presented in Figure 2a, revealed low correct classification rates among the three study sites, with the accuracy of the model being equal to the no-information rate (NIR). Respectively, 28% and 32% of the calls from Duiker Island and Seal Island were assigned to Lambert's Bay site. For female-attraction calls produced by pups, only the total duration of the calls varied significantly between sites, with longer vocalizations at Seal Island (732 ± 242 ms) compared to Duiker Island (609 ± 169 ms) and Lambert's Bay standing between the two (708 ± 201 ms, Table 1). Similar to pup-attraction calls, the classification by the Random Forest revealed an overall accuracy equal to the NIR (Figure 2b). Respectively, 33% and 36% of the calls from Duiker Island and Seal Island were assigned to Lambert's Bay site.

In contrast to pup- and female-attraction calls, significant variation was found for subadult male barks among South African sites. We found significant differences among the three study sites for four out of the seven measured features: *Duration*, *f0*, *Fmax1* and *Bdw12* (Table 1). The bark units were longer in duration at Cape Town harbor (135 ± 32 ms) compared to Duiker Island and Lambert's Bay (respectively, 98 ± 31 ms and 91 ± 19 ms) (Table 1). For the fundamental frequency (*f0*) and the frequency of the first peak of energy (*Fmax1*), values were higher at Duiker Island (average *f0* 169 ± 25 Hz and *Fmax1* 725 ± 232 Hz) compared to Cape Town harbor (average *f0* 139 ± 34 Hz and *Fmax1* 648 ± 202 Hz). Those from barks recorded at Lambert's Bay were intermediate (Table 1). For *Bdw12*, values were also higher at Duiker Island (average *Bdw12* 70 ± 37 Hz) compared to the two other sites (60 ± 32 Hz at Lambert's Bay and 48 ± 25 Hz at Cape Town harbor). The Random Forest algorithm was able to classify subadult male barks between the three study sites (model accuracy significantly higher than NIR; Figure 2c). Correct classification rates were 50% for Duiker Island, 75% for Lambert's Bay and 81% for Cape Town harbor (Figure 2c). The acoustic features that contributed the most to the classification were *Duration* and *f0*.

3.2 | Macro-geographical variation between Namibian and South African study sites

As no significant variation was found in the acoustic features of pup- and female-attraction calls among the South African study sites, these calls were pooled for the macro-geographical scale investigations. This resulted in a

TABLE 2 Comparison of the acoustic features (indicated as mean ± SD) measured on four Cape fur seals calls types between Namibian study sites (CC: Cape Cross, PP: Pelican Point) and South African (SA: grouping of several South-African sites showing no significant difference in the acoustic features of this type of call, LB: Lambert's Bay, CT: Cape Town harbor, DI: Duiker Island, SI: Seal Island). Results of the pairwise analysis of estimated marginal means following the linear mixed-effects model are indicated for each acoustic feature and each study site (no significant difference between sites sharing the same letter; NS means that the LME was not significant).

| Macro-geographical variations		Duration (ms)		f0 (Hz)		Fmax1 (Hz)		Fmax2 (Hz)		Fmax3 (Hz)		Bdw12 (Hz)		Interbark duration (ms)	
Pup-attraction calls	CC (n = 145)	1,130 ± 358	a	275 ± 39	ab	757 ± 278	ab	786 ± 421	a	1,015 ± 479	a	16 ± 14	NS		NS
	PP (n = 620)	1,120 ± 306	a	264 ± 41	a	667 ± 181	a	583 ± 269	b	747 ± 491	b	15 ± 17			
	SA (n = 483)	998 ± 294	b	290 ± 46	b	816 ± 316	b	1,053 ± 470	c	1,158 ± 511	a	15 ± 13			
Female-attraction calls	CC (n = 88)	702 ± 269	NS	381 ± 68	NS	1227 ± 695	a	1,585 ± 1049	a	1,583 ± 1039	a	27 ± 24	NS		NS
	PP (n = 145)	667 ± 233		343 ± 70		826 ± 245	b	683 ± 588	b	1,107 ± 1006	b	29 ± 26			
	SA (n = 340)	699 ± 208		340 ± 80		1085 ± 523	a	1,374 ± 838	a	1,525 ± 949	a	21 ± 23			
Females' barks	CC (n = 135)	118 ± 31	NS	149 ± 32	NS	758 ± 265	NS	786 ± 338	ab	808 ± 443	ab	58 ± 35	NS	226 ± 45	NS
	PP (n = 150)	116 ± 31		164 ± 33		660 ± 206		611 ± 223	a	578 ± 342	a	70 ± 38		254 ± 57	
	LB (n = 185)	98 ± 64		166 ± 44		717 ± 263		858 ± 446	b	933 ± 548	b	66 ± 37		257 ± 57	
Subadult male barks	CC (n = 170)	118 ± 27	abc	130 ± 32	ab	754 ± 176	ab	886 ± 362	ab	1021 ± 509	ab	55 ± 27	ab	209 ± 39	NS
	PP (n = 320)	120 ± 30	bc	128 ± 25	a	642 ± 225	ab	630 ± 270	a	565 ± 308	a	60 ± 41	ab	219 ± 42	
	LB (n = 420)	90 ± 19	a	148 ± 24	ab	771 ± 517	b	846 ± 439	b	940 ± 579	a	60 ± 32	a	229 ± 38	
	CT (n = 430)	135 ± 32	c	139 ± 34	a	648 ± 202	a	785 ± 368	a	864 ± 432	ab	48 ± 25	b	235 ± 59	
	DI (n = 120)	98 ± 31	ab	169 ± 25	b	725 ± 232	b	828 ± 482	ab	885 ± 589	ab	70 ± 37	a	218 ± 38	
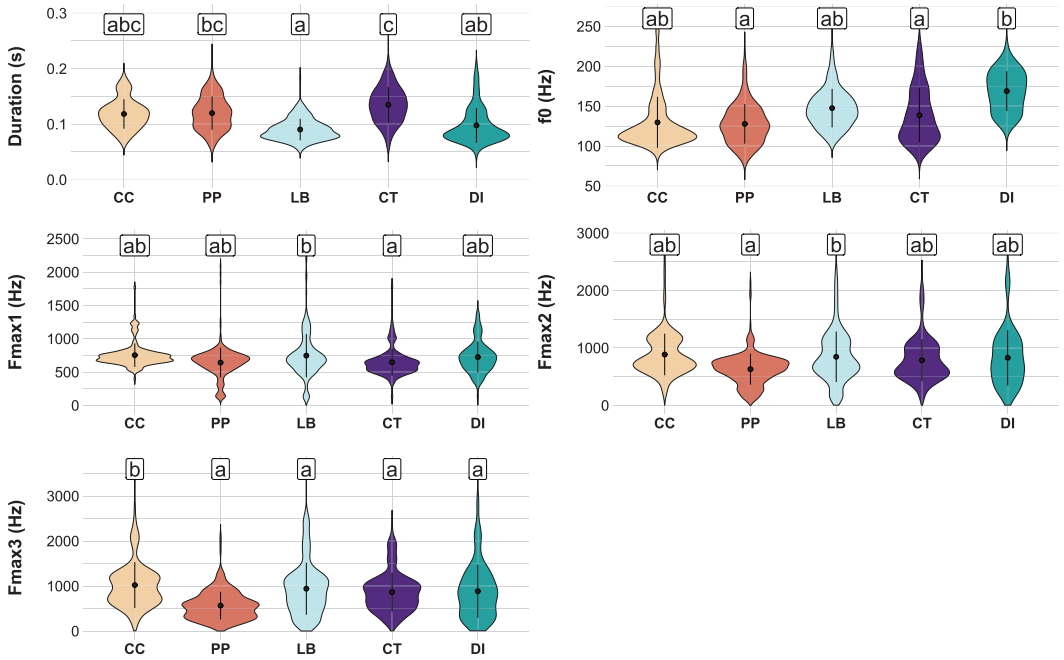
FIGURE 3 Representation of five acoustic features of subadult male barks measured at the five study sites in Namibia (CC: Cape Cross, PP: Pelican Point) and South Africa (LB: Lambert's Bay, CT: Cape Town harbor, DI: Duiker Island). The letters indicate the results of the pairwise analysis of estimated marginal means following the linear mixed-effects model (no significant difference between sites sharing the same letter).
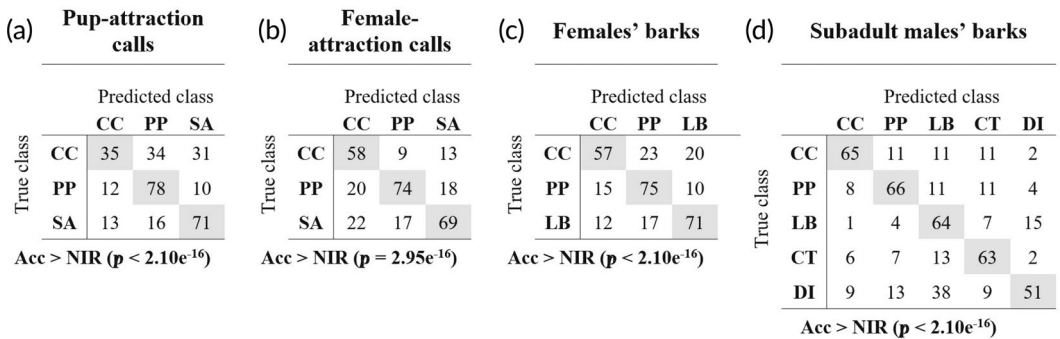

FIGURE 4 Classification rates (in %) calculated based on confusion matrices resulting from classifications between South African and Namibian sites by Random Forest algorithm for pup-attraction calls (a), female-attraction calls (b), female barks (c), and subadult male barks (d). Values represent the percentage of calls assigned in each of the prediction class. Below each matrix is the statistical comparison between the accuracy of the Random Forest model (Acc) and the no information rate (NIR) and the associated p value in case of significant difference.

grouped sample of 483 pup-attraction calls and 340 female-attraction calls, all from South Africa. For subadult male barks, the three South African sites (Duiker Island, Lambert's Bay, and Cape Town harbor) were kept separately as significant differences in their acoustic features occurred among sites.

Calls recorded in Namibia (at Pelican Point and Cape Cross) and previously analyzed for the description of the vocal repertoire of the Cape fur seal (Martin et al., 2021) were included in this analysis to allow comparisons
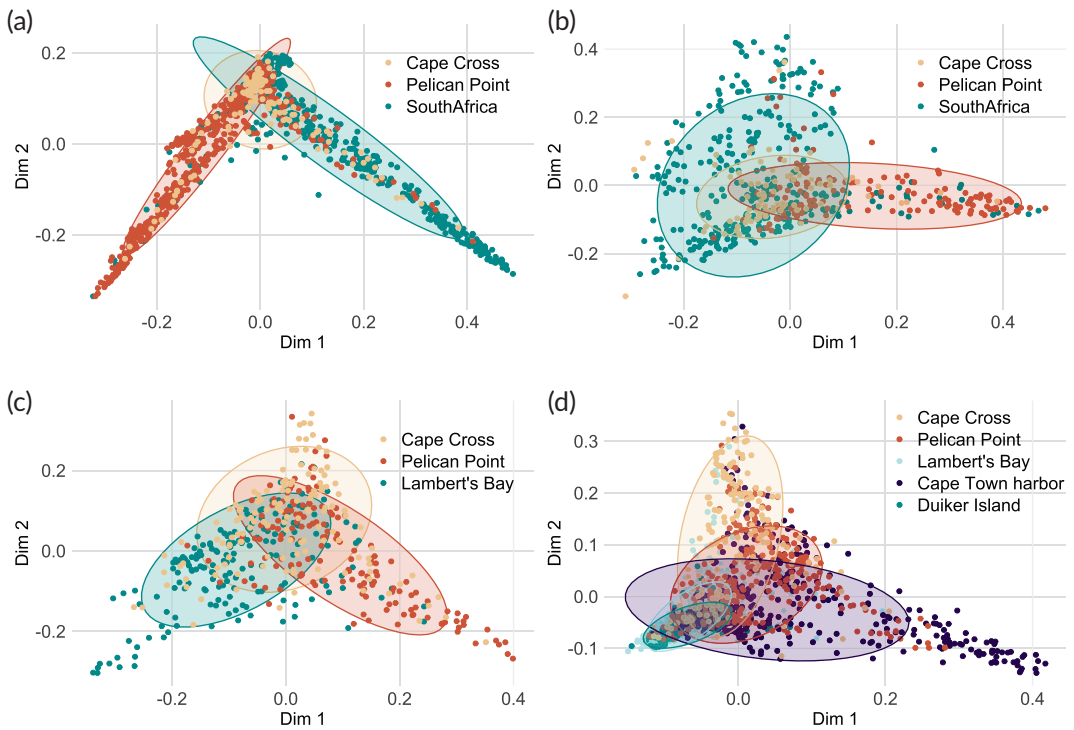
FIGURE 5 Two-dimensional scatter-plot produced by Nonmetric Multidimensional Scaling (MDS) resulting from the classification of calls between South African and Namibian study sites by Random Forest for pup-attraction calls (a), female-attraction calls (b), females' barks (c) and subadult male barks (d). Ellipses contain 80% of the data points.

between South African and Namibian study sites. Data from Pelican Point and Cape Cross were considered separately since micro-geographical variation has been shown between these two sites i.e., significant differences in the acoustic features of pup- and female-attraction calls as well as females' and subadult male barks were found between Pelican Point and Cape Cross (Martin et al. 2021). A total of 765 pup-attraction calls, 233 female-attraction calls, 285 females' barks and 490 subadult male barks from both Namibian colonies were included (Table 2).

Linear mixed-effects models highlighted significant differences among pup-attraction calls for all acoustic features, except $Bdw12$ (Table 2). Females' calls recorded in South Africa had shorter duration than those from Namibia, with an average duration of 998 ± 294 ms against 1,130 ± 358 and 1,120 ± 306 ms at Cape Cross and Pelican Point, respectively (Table 2). For spectral parameters, calls from Pelican Point had lower values of $f0$ and frequency of the first three peaks of energy $Fmax1$, $Fmax2$ and $Fmax3$ compared to females' calls recorded in South Africa (Table 2). Calls from Cape Cross females had intermediate values for these parameters (Table 2). In female-attraction calls produced by pups, a similar trend was found with lower $Fmax1$, $Fmax2$, and $Fmax3$ values at Pelican Point than in South Africa or at Cape Cross. Both call duration and $f0$ did not vary significantly between Namibian and South African colonies (Table 2). Only two acoustic features varied among study sites for females' barks but, similarly to pup- and female-attraction, we reported lower $Fmax2$ and $Fmax3$ values at Pelican Point than South African sites and intermediate values at Cape Cross (Table 2).

For subadult male barks, linear mixed-effects models were all significant, except for the interbark duration (Table 2). However, differences among study sites resulting from the pairwise analysis of estimated marginal means were hard to interpret (Table 2). To better interpret these results, we also plotted our acoustic features values in Figure 3. The shortest bark units were found at Lambert's Bay and Duiker Island (Table 2, Figure 3), and the longest

at Cape Town harbor. Regarding spectral features such as *f0* and energy peaks (*Fmax1-2-3*), we could see a tendency for Pelican Point and Cape Town harbor to show lower values compared to Cape Cross and Lambert's Bay (Table 2, Figure 3).

The Random Forest classifications revealed high correct classification rates for all the four call types investigated, always with a model accuracy significantly above the NIR (Figure 4). For pup-, female-attraction calls and female barks, Cape Cross is the least well predicted location with only 35%, 58%, and 57% of correct classification respectively (Figure 4a–c). Calls from Pelican Point and South Africa were correctly classified at 70% or more for these three call types (Figure 4a–c). For subadult male barks, correct classification rates were lower and ranged from 51% to 66% (Figure 4d). Male barks from Duiker Island and Lambert's Bay were mostly confused with each other while barks from the three other locations (CC, PP, and CT) were confused with all other sites without any specific trend (Figure 4).

MDS plots resulting from Random Forest showed a relatively similar spatial organization of the calls among study sites for pup-attraction calls, female-attraction calls, and female barks: calls from Pelican Point and South Africa are quite distinct, whereas calls from Cape Cross largely overlap with the other two locations (Figure 5a–c), It suggests a sort of "grading," with Cape Cross vocalizations falling between Pelican Point and South African sites (Figure 5a–c). For subadult male barks, calls from Lambert's Bay and Duiker Island totally overlapped and were concentrated in the lower left panel of the MDS plot (Figure 5d), with negative values on both dimensions 1 and 2. Pelican Point's male barks appeared to be interspersed between those of Cape Cross and Cape Town harbor (Figure 5d).

4 | DISCUSSION

The in-air vocal repertoire of otariids has been widely described in regard to the behavioral context of the production and acoustic features of calls, as well as the different types of information encoded in vocal signals (for review see Charrier, 2021). Fewer studies have focused on the existence and sources of geographical variation in their vocalizations (Ahonen et al., 2014, 2018; Attard et al., 2010; Martin et al., 2021; Trimble & Charrier, 2011). The present study aimed to contribute to filling this gap by investigating geographical variations in the airborne vocalizations of Cape fur seal females, pups, and males, at both micro- and macro-geographical scales, and suggest possible factors shaping acoustic differences.

4.1 | Micro-geographical variation among South African study sites

In a recent study (Martin et al., 2021), we found differences in the spectral features of Cape fur seal vocalizations between two breeding colonies located in central Namibia and separated by about 150 km. Here, similar investigations were performed on four study sites representing both breeding colonies and haul-out sites in South Africa across a similar distance range. Three were located around the city of Cape Town, within a radius of about 30 km (Seal Island, Duiker Island, and Cape Town harbor), while the fourth was about 100 km farther north (Lambert's Bay).

For pup- and female-attraction calls—respectively produced by mothers and pups—no significant difference was found between three sites in South Africa: Lambert's Bay, Duiker Island, and Seal Island. The six measured acoustic features were all similar for females' calls. For pups' calls, call duration was the only parameter that varied significantly among sites, which might not be sufficient to conclude there is geographical variation. Differences in Cape fur seals' vocalizations between Pelican Point and Cape Cross, in Namibia, were suggested to be driven by two factors: differences in individuals' body size (due to genetic variation and/or differences in food availability) and/or differences in their environment (population density of the colony, abiotic noise and/or propagation properties; Martin et al., 2021). Here, we suggest that given their geographical proximity (especially between Seal Island

and Duiker Island), the hypothesis of genetic drift is unlikely within these sites and would thus explain the absence of geographical vocal variation in this area. Indeed, analysis of recoveries of tagged Cape fur seals as well as genetic analyses reported a potential extensive exchange of individuals between sites (juveniles tend to disperse to nonnatal sites during their first years (Oosthuizen, 1991) and a possible lack of female philopatry (Matthee et al., 2006). A second reason for the homogeneity of females' and pups' calls would be that, due to the proximity between sites, seals may have relatively similar food resource levels which would reduce the possibility of significant differences in their body size, and thus variations in the acoustic features of their calls. Although the at-sea movements of females were described for the Seal Island colony (Botha et al., 2020) and not for the other two, several studies have shown that they generally forage at a maximum distance of 150 km from their colony and remain in areas where the maximum depth does not exceed 1,000 m (Botha et al., 2020; Skern-Mauritzen et al., 2009). For these reasons, the foraging area of females from the three study sites likely overlap (at least for Seal Island and Duiker Island) or may show similar resources, providing them with similar quality/quantity of food. Finally, the environment at the three sites is similar (rocky islands or peninsula exposed to wind and waves). This would explain the lack of specific acoustic adaptations linked to their habitat.

In subadult male barks, unlike female and pups calls, several acoustic features differed among the South African study sites. Barks recorded at Cape Town harbor were longer in duration than those from Duiker Island and Lambert's Bay and were lower pitched than Duiker Island with Lambert's Bay values in between. Two main hypotheses could explain these differences: the isolation of sites due to their geographical distance, or the variations in the morphological or physiological characteristics of individuals. Of the three sites, Cape Town harbor and Duiker Island are the closest (about 20 km) so these variations may not be linked to the geographic distance. Similar vocal variations were found at the regional scale in Australian sea lion males' barks (Ahonen et al., 2014; Attard et al., 2010). For this sea lion species, genetic or geographical distances between colonies probably did not explain observed variations and the authors rather suggested the role of environmental or morphological factors.

Because Cape Town harbor is not a breeding colony but a hauling-out site, it is likely that the acoustic differences found in males' barks are due to differences in individuals themselves, including age differences and behavioral states. In Cape fur seals, male barks become lower-pitched with age (Martin et al., 2021) so it is possible that males recorded in Cape Town harbor were older subadults than those from the two breeding colonies Duiker Island and Lambert's Bay, as their calls were found to be lower pitched (Figure 3). A second explanation is that the variation found in male barks among South African sites may be related to differences in behavioral contexts. Indeed, it has been shown that the acoustic features of Cape fur seal male barks vary depending on their arousal state (Martin et al., 2022). Indeed, both the fundamental frequency value and the bark rate increase during high arousal state activities such as territorial confrontations with other males during the breeding season (Martin et al., 2022). On breeding colonies, males socially interact with both males and females, whereas in Cape Town harbor there are only juveniles and subadult males, mostly resting or playing/interacting with conspecifics. Since there is no competition for mating, we suggest that the differences seen at Cape Town harbor are likely explained by a difference in the behavioral context of bark productions.

4.2 | Macro-geographical variation between Namibian and South African study sites

With regards to the macro-geographical scale and comparisons between Namibian and South African sites, consistent results were found for females (pup-attraction calls and barks) and pups calls (female-attraction calls). For all three types of calls, the classification methods and resulting MDS plots showed clear differences between vocalizations recorded in South Africa (all sites) and Pelican Point (Figures 4 and 5). Generally speaking, pup- and female-attraction calls from Pelican Point were lower in frequencies ($Fmax1$–3) compared to those from South African sites. Vocalizations from Cape Cross generally showed intermediate values of spectral features. A similar pattern was found for the female barks, with barks produced at Pelican Point being lower in frequency.

Comparisons between pup calls at Pelican Point and South African sites should be considered with caution as recordings were not made at the same time of year and thus the age of pups differed slightly: 2–4 months old at Pelican Point and 5–6 months old in South Africa. Pup calls are known to become longer in duration with age, and the energy spectrum is also more evenly distributed among harmonics with age (i.e., higher $Fmax1$, $Fmax2$, and $Fmax3$ values) (Martin et al., 2021). Here, we failed to find differences in call duration between pups from Pelican Point and South African sites, suggesting they may be similar, but they tend to have lower $Fmax1$, $Fmax2$, and $Fmax3$ values despite their younger age when recorded. This limits a potential effect of age and strengthens the evidence of geographical vocal variation in pup's calls.

This study reports geographical vocal variation in female and pup calls at the macro-geographical scale, i.e., between populations separated by large distances, preventing them from mixing (Mundinger, 1982). For these call types, the greatest differences were found between two distant locations, separated by more than 1,300 km (Pelican Point and South African sites of the Western Cape Province). Vocalizations from Cape Cross, which is only 150 km further north of Pelican Point—and therefore about 1,450 km distant from Cape Town area had intermediate acoustic features: some were more similar to Pelican Point, whereas others were more similar to South Africa. The lack of relationship between distance and acoustic similarity disproves the effect of geographic isolation on macro-geographical variation for these call types. At a macro-geographical scale, genetic variation (due to geographic isolation) and related morphological differences become more likely than at a regional scale. However, genetic analysis showed that the Cape fur seal population exhibits a higher degree of genetic diversity within colonies rather than among them (Matthee et al., 2006). The population decline caused by uncontrolled harvest prior to the 20th century may have reduced genetic diversity in this species (Matthee et al., 2006). For this reason, it seems unrealistic to assume significant morphological differences related to genetics between colonies. Differences in body size and condition caused by variation in prey availability along the species' range are conceivable, but no data on individual morphology were available to support this hypothesis.

Environmental factors are most likely to explain macro-geographical variation in Cape fur seal females' and pups' calls. Indeed, the gradual variation in acoustic features of females' and pups' calls is consistent with the environmental differences between the study sites. On one hand, Pelican Point and the South African sites are quite different. Pelican Point breeding colony is a flat, open and uniform sandy beach. On its eastern side where the recordings were made, the beach borders a lagoon with shallow water, so seals are not exposed to the swell. In contrast, breeding colonies sampled in South Africa (Lambert's Bay, Seal Island, and Duiker Island) are located on rocky islands consisting of large boulders significantly exposed to the ocean swell. Cape Cross has an intermediate topography as the colony spreads over a sandy beach area in its southern part (high swell exposure compared to the Pelican Point lagoon side) and wide rocky headland exposed to waves in its central and northern part. According to our results, the more the colony is exposed to abiotic noise, such as breaking waves on rocks, the higher the value of the fundamental frequency and/or the frequency value of the first three energy peaks. The same findings were reported in the previous study showing vocal variation between Pelican point and Cape Cross (Martin et al., 2021). As this type of abiotic noise is concentrated on low frequencies (30–500 Hz; Carey & Fitzgerald, 1993), a shift of the calls' energy spectrum towards higher frequencies—avoiding the overlap with noise—was thus suggested (Martin et al. 2021). The present study provides more evidence and reinforces the suggestion of such habitat acoustic adaptation. Our findings are consistent with those found on South American sea lion (*Otaria byronia*) females' and pups' calls: observed macro-geographical variations were suggested to result from environmental differences (obstructed habitat, i.e., rocky area vs. open habitat such as beach) between the two study sites, located 1,200 km apart (Trimble & Charrier, 2011). This is based on the "acoustic adaptation hypothesis," stating that acoustic signals may undergo modifications according to characteristics of the environment, such as the ambient noise level or propagation conditions, to improve their propagation or their discriminability and therefore the transfer of information among individuals (Morton, 1975). Geographical variation resulting from different environment acoustic properties were documented in multiple animal species from several taxa: birds, mammals, and anurans (Ey & Fischer, 2009; Podos & Warren, 2007; Velásquez, 2014).

Finally, macro-geographical variations in the acoustic features of subadult male barks were found between the different study sites in Namibia and South Africa. However, the distinction among locations was not as clear as for females' and pups' calls. Indeed, both uni- and multivariate analyses showed a stronger overlap in their acoustic parameters. Similar findings were reported in barks produced by Australian sea lion (*Neophoca cinerea*) at different breeding sites (Ahonen et al., 2014). The authors explained it by the short duration and narrow frequency bandwidth of the barks, resulting in inevitable overlap among the calls. The classification method we used still successfully differentiated the subadult male barks according to their geographic locations. Barks produced by subadult males at Pelican Point and Cape Town harbor were longer in duration and had lower values for both their fundamental frequency and peak frequencies. In contrast, barks from Lambert's Bay, Duiker Island, and Cape Cross were shorter in duration and of higher frequencies. As explained in the micro-geographical variation section, the nature of the study site (breeding vs. hauling-out site) is likely to explain the differences in the type of males recorded, the context of bark production, and their state of arousal or motivation.

In conclusion, this study was the first to investigate geographical vocal variations at both macro- and micro-geographical scales in several call types from an otariid species' vocal repertoire. It allowed us to suggest the role of extrinsic and intrinsic factors in modulating vocalizations among Cape fur seal populations. Results seem to indicate an effect of environmental characteristics to explain both micro- and macrogeographical vocal variation in this species for females' and pups' calls, and the behavioral context for male barks. Other drivers could play a role in the differentiation of vocalizations but more data on genetics, morphology, or behavior of individuals (breeding site fidelity, dispersal) are still needed. Further investigations would be valuable to understand whether these vocal variations are perceived and recognized by individuals, and whether they are involved in the modulation of social interactions.

AUTHOR CONTRIBUTIONS

Mathilde Martin: Conceptualization; data curation; formal analysis; writing – original draft. **Tess Gridley:** Project administration; writing – review and editing. **Simon Harvey Elwen:** Project administration; writing – review and editing. **Isabelle Charrier:** Data curation; funding acquisition; project administration; supervision; writing – review and editing.

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