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RESEARCH ARTICLE

Neighbors matter: Vocal variation in Gentoo Penguins depends on the species composition of their colony

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ABSTRACT

When suitable nesting habitat is rare, birds may have to share it with heterospecific individuals with similar nesting requirements. The resulting species mosaic may in turn affect how breeding birds communicate vocally with each other. For instance, they may modify their vocalizations if the ambient noise produced by heterospecifics interferes with their own vocalizations. The colonies of Gentoo Penguins (*Pygoscelis papua ellsworthi*) are interesting to examine whether such a vocal variation occurs in colonial seabirds, as these birds frequently breed in the same colony as Adélie (*P. adeliae*) or Chinstrap (*P. antarcticus*) penguins. We investigated whether the presence of congeneric penguins breeding in the same colony as Gentoo Penguins affected the acoustic characteristics of their most common vocalization, the ecstatic display call. Based on vocalizations recorded in 23 breeding colonies along the Antarctic Peninsula during 3 field seasons, we found that the frequency of ecstatic display calls of Gentoo Penguins was consistently lower (average exhale phrase ~460 Hz lower, average inhale phrase ~370 Hz lower) as well as decreased in energy distribution when they bred in mixed colonies with Adélie Penguins than when they bred only in proximity to conspecifics. In contrast, the frequency of both inhale and exhale phrases was unaffected by the presence of Chinstrap Penguins, potentially due to the already greater frequency difference between these 2 species. The apparent vocal plasticity, in mixed colonies with Adélie Penguins, likely allows Gentoo Penguins to adjust the quality of their vocalizations depending on the acoustic space available in their colonies, and hence possibly enhance signal transmission between conspecifics. However, whether this acoustic adjustment is sufficient to increase the detectability of vocalizations and localization of individuals has yet to be determined.

Keywords: Antarctic Peninsula, ecstatic display call, Gentoo Penguins, mixed colonies, *Pygoscelis papua ellsworthi*, vocal variation

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LAY SUMMARY
- We examined whether Gentoo Penguin calls differ between breeding colonies that included multiple species of penguins and those where only Gentoo Penguins bred.
- We compared call parameters including frequency, structure, and duration between individual Gentoo Penguins breeding in colonies with and without the presence of Adélie or Chinstrap penguins along the Antarctic Peninsula during three austral summers.
- We found that the calls of Gentoo Penguins showed a lower frequency and narrower energy distribution when they bred in proximity to Adélie Penguins but did not change when they bred in proximity to Chinstrap Penguins with higher main frequency vocalizations..
- This suggests that penguins can adjust the quality of their vocalizations according to the social (and presumably acoustic) environment of their colonies.

Los vecinos importan: La variación vocal en *Pygoscelis papua ellsworthi* depende de la composición de especies de su colonia

RESUMEN
Cuando el hábitat de anidación adecuado es raro, las aves pueden tener que compartirlo con individuos heteroespecíficos con requisitos de anidación similares. El mosaico de especies resultante puede, a su vez, afectar la forma en que las aves reproductoras se comunican vocalmente entre sí. Por ejemplo, pueden modificar sus vocalizaciones si el ruido ambiental

producido por los individuos heteroespecíficos interfiere con sus propias vocalizaciones. Las colonias de *Pygoscelis papua ellsworthi* son interesantes para examinar si tal variación vocal ocurre en las aves marinas coloniales, ya que estas aves frecuentemente se reproducen en la misma colonia que *P. adeliae* o *P. antarcticus*. Investigamos si la presencia de pingüinos congéneres que se reproducen en la misma colonia que *P. p. ellsworthi* afecta las características acústicas de su vocalización más común, la llamada de despliegue extático. Con base en las vocalizaciones registradas en 23 colonias de reproducción a lo largo de la Península Antártica durante tres temporadas de campo, encontramos que la frecuencia de las llamadas de despliegue extático de *P. p. ellsworthi* fue consistentemente más baja (frase de exhalación promedio ~ 460 Hz más baja, frase de inhalación promedio ~370 Hz más baja) y disminuyó en la distribución de energía cuando se reproduce en colonias mixtas con *P. adeliae* que cuando se reproduce solo en la proximidad de sus congéneres. En contraste, la frecuencia de las frases de inhalación y exhalación no se vio afectada por la presencia de *P. antarcticus*, posiblemente debido a la diferencia de frecuencia ya mayor entre estas dos especies. La plasticidad vocal aparente, en colonias mixtas con *P. adeliae*, probablemente le permite a *P. p. ellsworthi* ajustar la calidad de sus vocalizaciones según el espacio acústico disponible en sus colonias y, por lo tanto, posiblemente mejorar la transmisión de señales entre congéneres. Sin embargo, aún no se ha determinado si este ajuste acústico es suficiente para aumentar la detectabilidad de las vocalizaciones y la localización de los individuos.

Palabras clave: colonias mixtas, llamada de despliegue extático, Península Antártica, *Pygoscelis papua ellsworthi*, variación vocal

INTRODUCTION

Birds may nest in association with other bird species that simultaneously share similar nesting requirements because of heterospecific attraction or the paucity of available breeding sites (Mönkkönen and Forsman 2002, Morinay et al. 2020). The costs and benefits of such breeding associations between birds appear to be context dependent (Brussee et al. 2016, Swift et al. 2018, 2020) but for such associations to persist, the related benefits (e.g., better access to resources, predator detection, nest defense, information transfer) have to overcome the related costs (resource competition, disease transmission, nest parasitism; Farine et al. 2014).

These preponderant advantages likely underlie the existence of large bird colonies (i.e., aggregates of breeding birds nesting at a given site at a higher probability than predicted by a free distribution) that can be not only monospecific but also heterospecific (Evans et al. 2015). Specifically in seabirds, coloniality has been shown to be the most favored breeding structure, with 98% of seabird species being colonial species (Evans et al. 2015).

Seabirds, including penguins, exchange information with conspecifics mostly through vocalizations with specific acoustic characteristics. Within breeding grounds, these vocalizations are essential for partner recognition and bonding, feeding, and parent–chick recognition (Boucaud et al. 2016, Tyson et al. 2017). However, the active space of vocalizations (i.e., the area around the signal source over which the signal remains detectable and recognizable) may extend beyond the nest, which may help conspecifics nesting in the surroundings to synchronize their phenology and ultimately optimize their breeding performance. Such a situation can be observed in seabird colonies where nests are close to each other (Waas et al. 2005). In such dense colonies, acoustic space is limited and has to be shared between individuals occupying the same

active space if the characteristics of their vocalizations overlap. Within breeding grounds shared by multiple species, competition for acoustic space may occur between birds of different species. To reduce such vocal competition, coexisting species may show distinct vocalizations, reduce distances between conspecifics (through the creation of meeting points) and a "courtesy rule" (i.e., abstention from calling when another individual is calling) may apply (Aubin and Jouventin 2002). If acoustic overlap persists, one of the species competing within the acoustic space may have to modify the quality of its vocalizations to optimize vocal transmission between conspecifics (acoustic avoidance hypothesis; Brumm and Slabbekoorn 2005). Just as birds may increase the frequency of their vocalizations in the presence of anthropogenic noise (Katti and Warren 2004, Patricelli and Blickley 2006, Nemeth et al. 2013), birds may also have to alter the characteristics of their vocalizations when exposed to heterospecific vocalizations. Thus, within breeding grounds, the available acoustic environment may be partitioned between bird species.

Suitable rocky habitats for breeding are relatively rare and fragmented along the Antarctic coastline, and as such, many Antarctic seabirds breed in close proximity and sometimes in multispecies colonies, as observed for *Pygoscelis* spp. penguins—Gentoo (*P. papua*), Adélie (*P. adeliae*) and Chinstrap (*P. antarctica*) penguins, though all 3 species are rarely found breeding in the same area. This association is made possible because of the use of different ecological feeding niches by each species, with Gentoo Penguins feeding mostly inshore on fish whereas Adélie and Chinstrap penguins forage more extensively on krill in more oceanic areas (Trivelpiece et al. 1987). Moreover, Gentoo Penguins show a higher foraging plasticity than Adélie and Chinstrap penguins (Miller et al. 2009, Casanovas et al. 2015) as well as a greater plasticity in breeding phenology (Lynch et al. 2012a), which may

make them more resilient to environmental variation. This higher plasticity may explain why Gentoo Penguins represent the most abundant penguin species along the western Antarctic peninsula (Herman et al. 2020).

Similar to many seabirds, penguins use vocalizations mainly for the recognition and localization of their partner and offspring within colonies, and to maintain social relationships and group cohesion (Jouventin 1982, Favaro et al. 2014). They may show some vocal plasticity, as demonstrated in King Penguins (*Aptenodytes patagonicus*) that increase their number of calls and syllables per call to be better audible to their partner in response to noisy windy conditions (Lengagne et al. 1999). In *Pygoscelis* penguins, the ecstatic display call is the most frequent call used during the breeding period. It is hypothesized that it serves both to attract and identify partners and as an advertisement display of nest occupancy (Jouventin 1982, Favaro et al. 2014).

To our knowledge, how sympatric *Pygoscelis* penguins share their acoustic space in mixed colonies has not been examined so far. Despite very different display vocalizations between species and even though *Pygoscelis* penguins use frequency bands for individual recognition (Aubin and Jouventin 2002), vocalizations overlap considerably in frequency among Gentoo, Adélie, and Chinstrap penguins (mean main frequency: ~1,285, 1,430, 2,000 Hz, respectively; maximum frequency: ~ 6,535, 4,325, 4,000 Hz, respectively; Jouventin and Dobson 2017). Because of this acoustic overlap, one or more of these species might be limited in the use of the available acoustic space when breeding in contact with other species and have to alter the characteristics of its vocalizations to occupy a new vocal niche. It was recently found that colonies of Gentoo Penguins breeding along the Antarctic Peninsula differed in the frequency of their ecstatic display calls, with much variations coming from differences among colonies and individuals within colonies (Lynch and Lynch 2017). Because no clear correlation was found between the characteristics of these vocalizations and the geographical distribution of colonies, the reasons for this vocal variation between colonies remained unclear (Lynch and Lynch 2017). As these differences may lie in the acoustic properties of each colony (Nottebohm 1975) as well as in the interrelationship of phylogenetic affinities, ecological requirements, and acoustic similarities (Littlejohn 1977, Duellman and Pyles 1983), we hypothesize here that the presence of other sympatrically breeding *Pygoscelis* penguins may contribute to vocal differences between colonies of Gentoo Penguins. Such vocal adjustments may be highly adaptive, as Gentoo Penguins occupying mixed colonies are constantly exposed to the ambient noise caused by heterospecific vocalizations. Specifically, we expect Gentoo Penguins, on which we focused in our study, to be limited to using the frequency bands that are mostly inhabited by other species. Because the main frequency of Gentoo Penguins' vocalizations is closer to that of Adélie Penguins' vocalizations than to that of Chinstrap Penguins' vocalizations (Jouventin 1982, Jouventin and Dobson 2017), we predict that this frequency shift should be more dramatic when Gentoo Penguins breed in proximity to Adélie Penguins.

METHODS

Acoustic Recordings

Passive audio recordings were conducted during three austral summers (2014/2015, 2018/2019, 2019/2020) in a total of 23 Gentoo Penguin colonies (*P. papua ellsworthi*; Pertierra et al. 2020, Tyler et al. 2020) along the Western Antarctic Peninsula and the South Shetland Islands. The colonies were classified as exclusive species colonies with only Gentoo Penguins (G), or multispecies colonies of Gentoo and Adélie penguins (GA) or Gentoo and Chinstrap penguins (GC, Figure 1). Recordings were conducted at the end of the incubation stage and at the beginning of the chick-rearing period. The spatial distribution of the multispecies colonies that we sampled in our study reflects the natural distribution of the different penguin species along the Antarctic Peninsula (Black 2016).

During the breeding season of 2014/2015, passive soundscape recorders (Song Meter SM2+, 24,000 Hz sampling rate, stereo recordings) were placed 3–5 m from one or more small subgroups of nesting penguins (for more details see Lynch and Lynch 2017 from which part of the data was used). In the breeding seasons of 2018/2019 and 2019/2020, recordings were carried out by a person positioned at the edge of a subgroup (i.e., the individuals whose vocalizations we could record above the noise during a recording session, ~10 nests; Mustafa et al. 2017) of nesting Gentoo Penguins and using a unidirectional microphone (Sennheiser ME66 and ME67, Wedemark, Germany, a frequency response rate of 40–20,000 Hz, the sensitivity of 50 mV/Pa ± 2.5 dB at 1kHz) connected to a recorder (Olympus LS 100, Tokyo, Japan; internal amplification level 2–5 (5 = +4.4 dB), 48–96 kHz sampling rate of 16–24-bit resolution, respectively) and directed towards a given penguin showing ecstatic displays in the absence of its mate. Each location was only recorded at one resolution rate in the same year. To additionally make sure that bit resolution did not have an effect on the recordings or measurements, we ran a playback experiment, recording exactly the same call, one time with 16-bit resolution, the other time with 24-bit resolution. We could not find any difference. The microphone was mounted on a boom pole to better approach and target specific penguins at 3–5 m distance and was protected with a windjammer. The sensitivity of the microphones was confirmed before fieldwork by the manufacturer and by using a Brüel & Kjaer
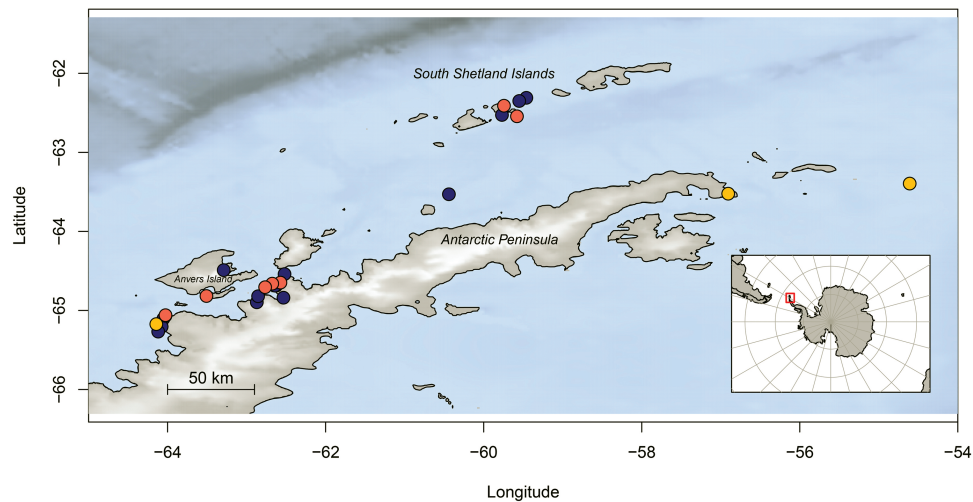
FIGURE 1. Map showing the sampling locations along the Antarctic peninsula and the South Shetland Islands. Navy colored dots indicate exclusive Gentoo colonies (G), red dots indicate Gentoo colonies mixed with Chinstrap Penguins (GC) and yellow dots indicate Gentoo colonies mixed with Adélie Penguins (GA) (map created in R with marmap and getNOAA.bathy; Pante and Simon-Bouhet 2013).

4230 sound calibrator (SPL = 94 dB–1kHz) both before and after fieldwork. In addition to the recording of Gentoo Penguins, we also recorded some ecstatic display calls of Adélie (*n* = 20) and Chinstrap (*n* = 37) penguins, to estimate how the calls emitted by Gentoo Penguins acoustically compared with those of other species.

Analysis of Acoustic Sequences
Recordings were screened using Adobe Audition* 3.0 (Adobe Systems Inc., San Jose, CA, USA) and ecstatic display calls were manually selected from the recordings. An ecstatic display call was defined as any display call performed by a single individual with a repeated series of long, low-frequency exhale phrases and short, higher-frequency inhale phrases (Jouventin 1982, Lynch and Lynch 2017; Figure 2). Signal to noise ratio (SNR) was obtained in Raven sound analysis software (Raven Pro 1.5, Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY) by taking the difference between the measured energy of the selected area with the signal and the selected area without any signal at the same recording period. For further analysis, we only selected high-quality calls (SNR > 11 dB, without any background interference, e.g., of strong wind noise, calling chicks, and other individuals calling at the same time) resulting in a total of 706 individual ecstatic display calls. Among these calls, 419 came from 13 exclusive Gentoo Penguin colonies, 104 came from three colonies mixed with Adélie Penguins, and 183 from 7 colonies mixed with Chinstrap Penguins (Table 1).

To exclude low-frequency background wind noise, each selected call was filtered, with Raven sound analysis software (at 100 or 150 Hz) for the 2014/2015 recordings and for better control of filter settings with a custom-written script (MATLAB R2019a, 7th order Butterworth high pass filter at 100 Hz) for the 2018/2019 and 2019/2020 recordings. All adjusted ecstatic display calls were analyzed with Raven sound analysis software (window size = 625 samples, overlap = 65%, discrete Fourier transform (DFT) size = 2,048 samples). We measured energy [dB re 20 µPa], 90% duration [s], center frequency [Hz], 5% frequency [Hz], 95% frequency [Hz], peak frequency contour (PFC), PFC slope and peak frequency inflection points (for definitions, see Table 2; Charif et al. 2010). After filtering, 95% frequency of background noise was consistently below the 5% frequency of any ecstatic call measured, minimizing the possibility that background noise or variation in filtering interfered with our analysis. Due to the highly repetitive and variable number of phrases, we included in the analysis only measurements for the whole call and the first exhale and first inhale phrase. The first phrases are the clearest and are sufficient for individual identification (Jouventin and Aubin 2002). Received levels were only determined to rule out major transmission loss from off-axis or far distant calls but were not further analyzed because they could not be standardized between recordings due to variable distance between penguins and microphone, and variable orientation of the penguin relative to the microphone. Energy distribution within the ecstatic display calls was measured as aggregate entropy from the spectrogram (Raven Pro 1.5, Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca, NY) of Gentoo Penguins in exclusive colonies (*n* = 364), Gentoo Penguins in mixed colonies (*n* = 275), as well as Adélie Penguins (*n* = 22) and Chinstrap Penguins (*n* = 33) from opportunistically taken mixed colonies, as well as Chinstrap Penguins (*n* = 9) in an exclusive colony. Aggregate entropy measures disorder in a sound by analyzing the energy distribution within a selection. Higher
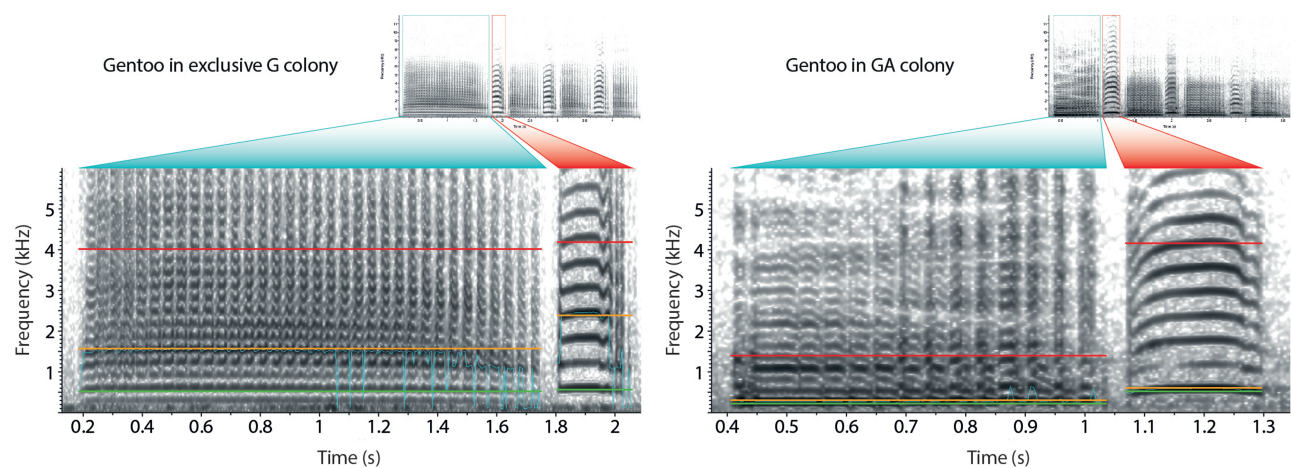
FIGURE 2. Shown are spectrograms of a selected typical complete ecstatic display call by a Gentoo Penguin with the repeating series of the starting longer exhale (broadband pulses) and shorter following inhale phrases (harmonic stacks) and a zoomed in display of only the first exhale and inhale phrases in an exclusive Gentoo colony (G) and in a mixed Gentoo and Adélie penguin colony (GA). Darker hues indicate more power at that frequency. Also visible in the zoomed in spectrograms are the 5% frequency (bottom green line), center frequency (middle yellow line), 95% frequency (top red line), and the PFC (light blue squiggly line). Blue and red boxes show the selection windows. Spectrogram details: Window type: Hann, window size = 625 samples, overlap = 65%, DFT size = 8,192 and 4,096 samples with a 96 and 48 kHz sampling rate, respectively.

TABLE 1. Summary of the recording sessions of 3 field seasons along the Western Antarctic Peninsula and at the South Shetland Islands. Location, number of Gentoo Penguin ecstatic display calls recorded, and the species breeding are noted for each colony; G = Gentoo Penguins, A = Adélie Penguins, C = Chinstrap Penguins.

Colony composition	Colony location	Number of calls per field season			Total
		2014/15	2018/19	2019/20	
G		207	98	114	419
	Brown Station	12	6	12	30
	Gabriel Gonzalez Videla			10	10
	Cuverville Island	22		14	36
	East Corner Cuverville Island			18	18
	Mikkelsen Harbour-Borget Point		14		14
	Moot Point	20			20
	Neko Harbour	40		19	59
	North-East coast Rongé Island			34	34
	Pleneau Island	21			21
	Port Lockroy-Damoy Point		31		31
	Port Lockroy-Jougla Point		12	7	19
	Cape Tuxen	60			60
	Yankee Harbour	32	35		67
GA		73		31	104
	Brown Bluff	31		17	48
	Heroina Island	12			12
	Petermann Island	30		14	44
GC		94	10	79	183
	Barrientos Island			28	28
	Booth Island	28		13	41
	Fort Point	11			11
	Georges Point	42	10		52
	Ketley Point			20	20
	Orne Island			18	18
	Selvick Cove	13			13
Total		374	108	224	706

TABLE 2. Descriptions of spectrogram measurements used in our analysis.

Measurement	Description
90% duration (s)	The difference in time between two points that contain 5% and 95% of the time (the middle 90% of the time).
Center frequency (Hz)	The frequency that divides the selection into two frequency intervals of equal energy (is the smallest discrete frequency where the summed energy exceeds 50% of the energy).
95% frequency (Hz)	The frequency that divides the selection into two frequency intervals containing between 95% and 5% of the energy in the selection (the summed energy has to exceed 95% of the total energy).
5% frequency (Hz)	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection (the summed energy has to exceed 5% of the total energy).
Energy (dB re 20 μPa)	The total energy within the selection bounds.
Peak frequency contour (PFC)	A trace of the peak frequency across the duration of the selection.
PFC number of inflection points	The number of inflection points in the trace of peak frequency across the entire selection.
PFC slope	A trace of measurements of slopes between consecutive peak frequency measurements in the PFC.

entropy values correspond to greater disorder in the sound whereas a pure tone with energy in only one frequency bin would have zero entropy. The size of a frequency bin is determined by the spectrogram parameters (Charif et al. 2010). As the DFT size was kept the same throughout the measurements independent of sampling rate, we compared 6 randomly selected calls of 48 kHz and 96 kHz analyzed with a DFT size of 2,048 samples to the adjusted DFT sizes of 4,096 samples or 8,192 samples, respectively and statistically tested for differences. We could not find any significant differences for our here analyzed parameters (paired t-test, df = 11, $P > 0.05$), except for peak frequency inflection points but this was also accounted for in the statistical models. The additional aggregate entropy measurements data were adjusted for differences in sampling rate by a statistically tested consistent factor (determined by the mean difference between randomly chosen original sampled calls and the down sampled version, respectively, 48 kHz + 0.9 and 96 kHz + 1.8; paired t-test, $t = 0.41$, df = 9, $p = 0.7$).

Statistical Analysis
In 2018–2019 and 2019–2020, we could assign a given individual to a given call, as we actively selected given individuals during recording sessions. In contrast, it was not possible to assign a given individual to a given call for vocalizations recorded in 2014–2015, as individuals were passively recorded (Lynch and Lynch 2017). However, in this previous study, a significant variation within colonies in a manner typical of inter-individual variation was found. Combined with a known low rate of recorded repeated calls of identified individuals within one colony, we therefore considered each of the calls analyzed from 2014/2015 in our study was also produced by a given individual.

Due to the highly correlated number of inhale and exhale phrases per call ($r_s = 0.84$, $P < 0.001$), both variables were combined into one (total number of phrases per call) for further analyses. To reduce the number of vocal parameters to analyze, we then conducted principal component analyses (PCA). PCA loadings were limited to components with an eigenvalue ≥ 1 and varimax rotated

for easier visual differentiation. The PCA model that was used for further analysis contained components explaining the highest variance (83%, Table 3) and variables showing no cross-loadings on different axes. We then used PC1 to PC5 scores in generalized linear mixed-effect models (GLMMs; Gaussian distribution) with colony composition as an explanatory variable (fixed factor) and, year and location nested within the year as random variables (to also account for differences in recording methods between years). We also repeated these analyses within each year to examine the repeatability of our results despite the use of different approaches in the field. The normality of residuals was checked through the visual inspection of QQ-plots and by conducting Shapiro–Wilk tests. Data were log-transformed (and mirrored in case of left skewed data) when their distribution was not normal. When this transformation was not sufficient for residuals to be normally distributed, a Gamma error distribution (log link function) was used in the GLMM (*lme4* package; Bates et al. 2015). Using an analysis of variance (ANOVA), we tested the significance of a "full model" comprising both the fixed and random factors against a "null model" comprising the random factor only. We additionally re-conducted statistical tests for relevant acoustic parameters (95% frequency and aggregate entropy; see Results) independently to examine more precisely how colony composition affected individual acoustic parameters (when those reflected PC scores or parameters that were affected by colony composition). A nonparametric comparison (Kruskal–Wallis test) was used to test for significant differences between means and a Wilcoxon test for variation across years. To ensure that geographic distance alone did not explain the acoustic variation described here, we performed a Spearman's rank correlation test to assess whether a correlation existed between divergence in Gentoo acoustic features (using the difference in mean PC1 scores) and latitude or longitude across all colonies.

All statistical tests were conducted in R for Windows (The R Foundation 2022) with R Studio* 1.1.456. Data are provided in the result section as median ± SD.

TABLE 3. Listed are loadings of variables of the best-fitting principal component analysis (PCA) where the first 5 components (PC1–PC5) explain 83% of variance.

Measurement	PC1 (36%)	PC2 (16%)	PC3 (14%)	PC4 (9%)	PC5 (8%)
90% duration exhale phrase [s]		0.112			**0.843**
Center frequency exhale phrase [Hz]	0.205	**0.325**	−0.104	0.115	0.118
95% frequency exhale phrase [Hz]	**0.483**				0.138
PFC number of inflection points exhale phrase	−0.129	**0.560**			0.139
90% duration inhale phrase [s]	0.107	−0.223		**−0.788**	
Center frequency inhale phrase [Hz]	0.260	0.188			**−0.311**
95% frequency inhale phrase [Hz]	**0.521**				
PFC number of inflection points inhale phrase		0.298		**−0.588**	
90% duration complete call [s]			**0.664**		0.227
Center frequency complete call [Hz]	0.217	**0.337**			−0.147
95% frequency complete call [Hz]	**0.535**				
PFC number of inflection points complete call	−0.117	**0.523**	0.198	−0.101	−0.132
Total phrase amount of call			**0.696**		−0.172

Bold values show the highest loading of the variables in the principal component.

RESULTS

Colony composition significantly affected PC1 scores (ANOVA$_{PC1}$, $\chi^2 = 11.034$, $P = 0.004$; Figure 3), and these results were consistent across years when calls were recorded in the 3 colony compositions, even though the scores were overall lower in 2014/2015 than in 2019/2020 (2014/2015: $\log_e(W_{Wilcoxon}) = 9.26$, $P = <0.001$, $\hat{r} = 0.30$, 95% CI: 0.20–0.40, $n_{obs} = 280$, 2019/2020: $\log_e(W_{Wilcoxon}) = 7.94$, $P = <0.001$, $\hat{r} = 0.42$, 95% CI: 0.27–0.58, $n_{obs} = 145$; Figure 4). Specifically, lower PC1 scores were found when Gentoo Penguins bred in mixed colonies with Adélie Penguins (GLMM, estimate = −0.106, $P < 0.001$; Figure 3). Such a pattern was not found when Gentoo penguins bred in mixed colonies with Chinstrap Penguins (GLMM, estimate = 0.009, $p = 0.75$; Figure 3). Colony composition did not affect any other components of the ecstatic display calls of Gentoo Penguins (ANOVA$_{PC2}$, $\chi^2 = 0.52$, $P = 0.77$, ANOVA$_{PC3}$, $\chi^2 = 0.55$, $P = 0.76$, ANOVA$_{PC4}$, $\chi^2 = 1.50$, $P = 0.47$, ANOVA$_{PC5}$, $\chi^2 = 3.23$, $P = 0.20$).

As PC1 scores mostly reflected the 95% frequency of ecstatic display calls, we re-conducted our analyses for this given parameter. The 95% frequency of the exhale and the inhale phrases was on average 458 Hz and 367 Hz lower, respectively, when Gentoo Penguins bred in mixed colonies with Adélie Penguins than when they bred by themselves or in mixed colonies with Chinstrap Penguins (exhale: $\chi^2 = 29.32$, $P = <0.001$, $\varepsilon^2 = 0.04$, 95% CI: 0.02–0.09, $n_{obs} = 706$; inhale: $\chi^2 = 11.83$, $P = 0.003$, $\varepsilon^2 = 0.02$, 95% CI: 0.003–0.06, $n_{obs} = 706$; Figure 5). Specifically, the complete ecstatic display calls of Gentoo Penguins showed a median 95% frequency of 2,730 ± 691 Hz in the exclusive Gentoo Penguin colonies ($n = 419$) and of 2625 ± 584 Hz in the colonies with Chinstrap Penguins ($n = 183$), whereas it showed a median 95% frequency of 2,344 ± 697 Hz in the colonies shared with Adélie Penguins ($n = 104$).
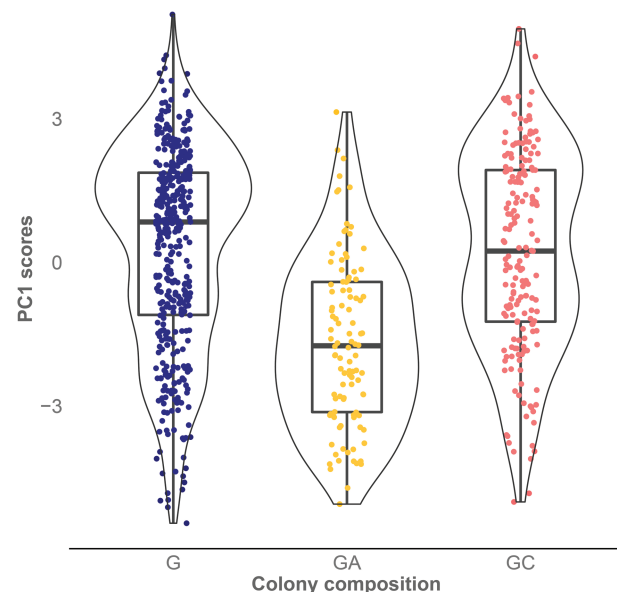
FIGURE 3. PC1 scores of Gentoo calls compared by breeding colony composition (G = exclusive Gentoo Penguins breeding colony, GA = Gentoo and Adélie penguins breeding colony, GC = Gentoo and Chinstrap penguins breeding colony).

In comparison, random selected ecstatic display calls of Adélie ($n = 22$) and Chinstrap ($n = 33$) penguins showed a median 95% frequency of 2,625 ± 482 and 2,953 ± 666 Hz, respectively (Figures 2 and 7).

Energy distribution in the complete ecstatic display calls of Gentoo Penguins narrowed down to fewer frequencies used when Gentoo Penguins bred in mixed colonies with Adélie Penguins than when they bred by themselves or in mixed colonies with Chinstrap Penguins ($\chi^2 = 52.86$, df = 2, $P < 0.0001$, $\varepsilon^2 = 0.083$, 95% CI: 0.042–0.132, $n_{obs} = 639$; Figures 6A and 7). Energy distribution in the complete ecstatic display calls of Gentoo Penguins in
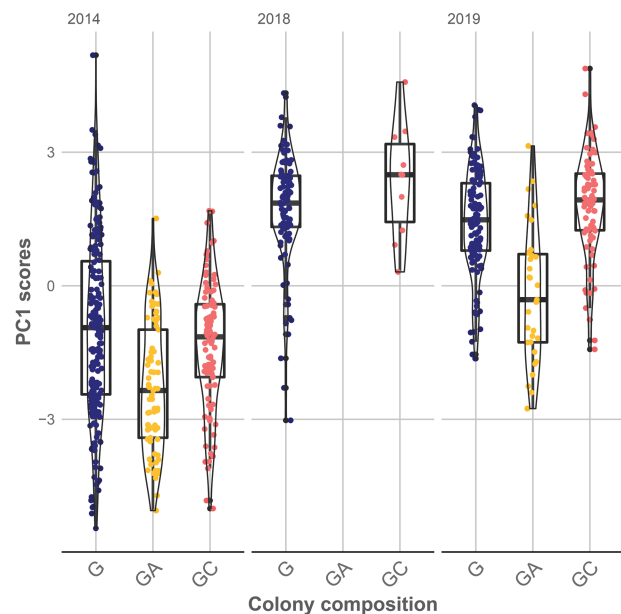
FIGURE 4. PC1 scores plotted as grouped by year and by colony composition (G = exclusive Gentoo Penguins breeding colony [blue dots], GA = Gentoo and Adélie penguins breeding colony [yellow dots], GC = Gentoo and Chinstrap penguins breeding colony [red dots]).

FIGURE 5. Box-violin plots showing the median and quartiles (**A**) 95% frequency of the first exhale and (**B**) first inhale phrase of ecstatic display calls of Gentoo Penguins plotted as grouped by colony composition (G = exclusive Gentoo Penguins breeding colony, GA = Gentoo and Adélie penguins breeding colony, GC = Gentoo and Chinstrap penguins breeding colony).

mixed colonies with either Adélie or Chinstrap Penguins is lower compared to calls of Adélie Penguins (χ^2 = 21.98, $P < 0.0001$, df = 1, n_{obs} = 127) and Chinstrap Penguins (χ^2 = 4.22, $P = 0.04$, df = 1, n_{obs} = 203; Figures 6B–C and 7). Chinstrap Penguin ecstatic display calls in an exclusive Chinstrap penguin colony showed no change in energy distribution compared to when they bred in mixed colonies with Gentoo Penguins (χ^2 = 0.12, $P = 0.72$, df = 1, n_{obs} = 42; Figure 6D).

There was no significant correlation between geographic locations of all colonies by latitude or longitude, and acoustic parameters (mean PC1 scores) of the Gentoo Penguins ecstatic display calls (latitude: $P = 0.67$, r_s [1,836] = 0.09; longitude: $P = 0.54$, r_s [2,294] = −0.13).

DISCUSSION

We found that the presence of other penguin species breeding in colonies of Gentoo Penguins was associated with a qualitative change in their vocalizations (frequency, duration, contour). Interestingly, this difference between colonies, mostly reflecting a change in the frequency and energy distribution of vocalizations, was only observed when Gentoo Penguins bred in proximity to Adélie Penguins but not when they bred in proximity to Chinstrap Penguins, presumably because of a stronger acoustical overlap between the vocalizations of Gentoo and Adélie penguins. The geographic locations of colonies
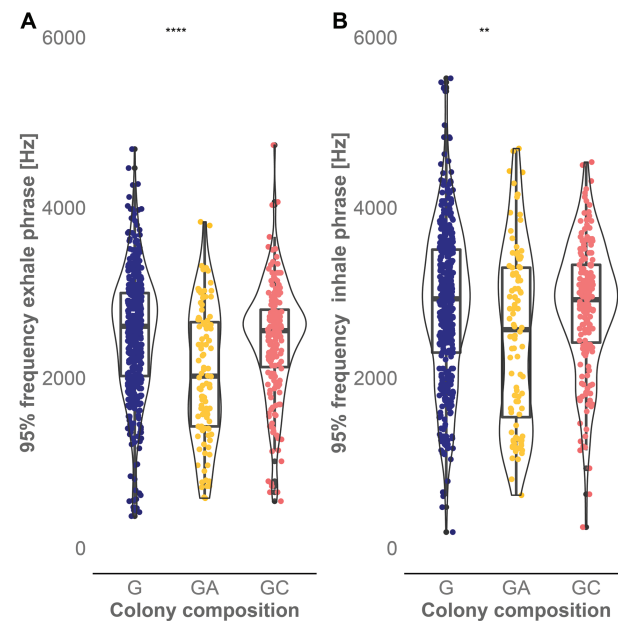
along the Antarctic Peninsula did not explain the vocal variation described here. Based on these results, our original hypothesis stipulating that birds sympatrically breeding with other birds need to adjust the use of their acoustic space by modulating their vocalizations therefore cannot be rejected.

In mixed colonies with Adélie and Gentoo penguins, Adélie Penguins occupy similar acoustic space as Gentoo Penguins use in exclusive colonies. In mixed colonies, the average frequency difference of ~300 Hz that we detected between both penguin species might be biologically meaningful, as it corresponds to the critical ratio bandwidth difference for each species to distinguish conspecific vocalizations (Langemann et al. 1995). Average Chinstrap vocalizations already exceed that ~300 Hz frequency difference to Gentoo Penguin ecstatic display calls and would render relative frequency change unnecessary. Frequency values of harmonics and timbre have been shown to be important factors for parent chick recognition in penguins, and the associated critical bandwidth can be as low as 25–50 Hz in the main frequency of Gentoo and Adélie penguins (Jouventin and Aubin 2002). Due to characteristics of cochlear processing, the detection of lower frequencies has a smaller critical bandwidth than higher frequencies, which might explain the lowering in Gentoo Penguin call frequency as well as the narrowing of energy distribution we observed in mixed colonies (instead of
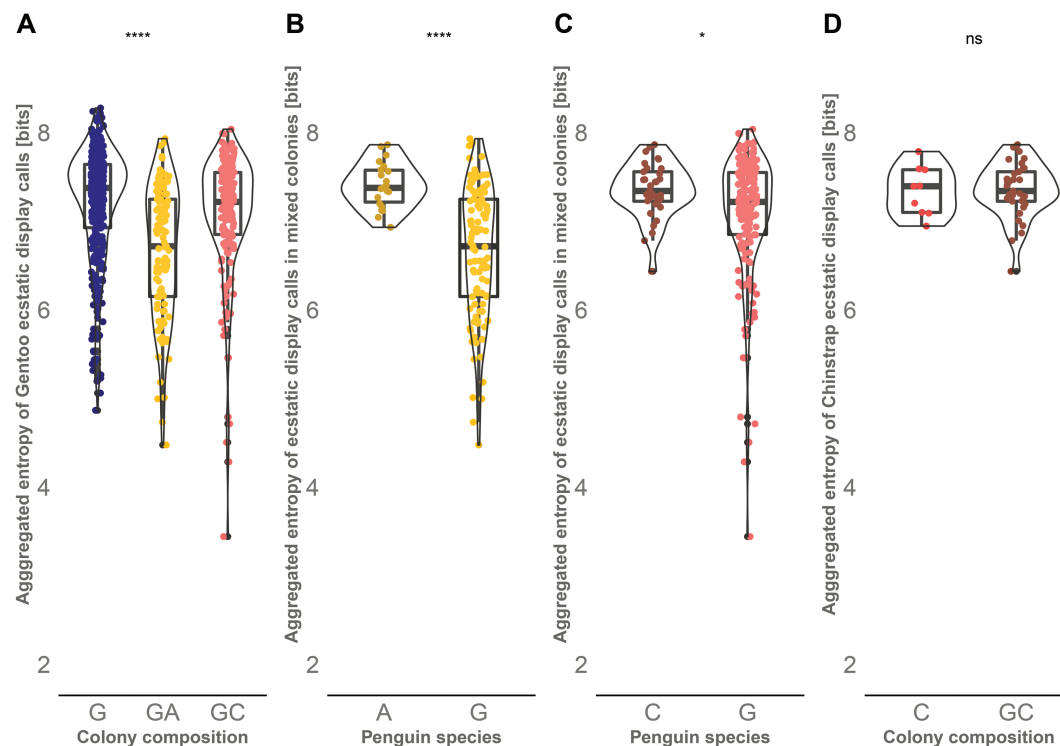
FIGURE 6.   Box-violin plots showing the median and quartiles aggregate entropy (**A**) of ecstatic display calls of Gentoo Penguins grouped by colony composition (G = exclusive Gentoo Penguins breeding colony, GA = Gentoo and Adélie penguins breeding colony, GC = Gentoo and Chinstrap penguins breeding colony); (**B**) of ecstatic display calls grouped by penguin species in mixed GA colonies (A = Adélie Penguins, G = Gentoo Penguins); (**C**) of ecstatic display calls grouped by penguin species in mixed GC colonies (C = Chinstrap Penguins and G = Gentoo Penguins); (**D**) of ecstatic display calls of Chinstrap Penguins plotted as grouped by colony composition (C = exclusive Chinstrap Penguins breeding colony). Statistical categories shown are: ns (not significant) is p > 0.05, *p ≤ 0.05, **p ≤ 0.01, ***P ≤ 0.001, ****P ≤ 0.0001.

increased frequencies; Langemann et al. 1995, Dooling et al. 2000, Shera et al. 2002, Henry and Lucas 2010). Especially at fundamental frequencies of 200–400 Hz, masking is less pronounced in songbirds, which was suggested to reflect general avian anatomical and physiological mechanisms in the early peripheral auditory system (Dooling et al. 2001). Alternatively, it may be hypothesized that Gentoo Penguins avoid using high frequencies when breeding with Adélie Penguins, as such vocalizations may be associated with a higher cost/benefit ratio under such conditions. Indeed, vocalizations with higher frequencies may be more costly to produce (as a result of a stronger contraction of the syringeal muscles; Suthers et al. 1999) whereas their detectability may be limited when overlapping with other vocalizations with similarly high frequencies. The presumed higher cost of vocalizations with higher frequencies may explain why Gentoo Penguins do not raise the frequency of their vocalizations when breeding with Adélie Penguins, but rather use lower and narrower frequency bands. This vocal plasticity would fit quite well with the general behavioral plasticity of Gentoo Penguins (Miller et al. 2009, Lynch et al. 2012a, Casanovas et al. 2015).

Even though penguins are not known to experience vocal production learning (Tyack 2020), our results suggest that penguins might be able to learn vocal production to some limited extent, by adjusting the acoustic properties of their inherited vocal motor patterns based on the social structure and the acoustic environment of the colony where they were raised (Searcy et al. 2021). Discrimination of neighbors, strangers, and mates in Adélie Penguins supports the learning of calls in high nest fidelity birds (Speirs and Davis 1991, Beaulieu et al. 2009). It would therefore be interesting to examine the ontogeny of calls across the development of chicks in the different types of colonies we considered.

It might also be hypothesized that Gentoo Penguins able to breed in proximity to Adélie Penguins differ in some traits affecting vocalizations from Gentoo Penguins breeding in exclusive colonies. For instance, body size can affect frequency parameters in birds, with larger individuals typically producing lower frequencies (Ratcliffe and Grant 1985, Podos 1997, 2001). It is therefore possible that only larger Gentoo Penguins, using lower frequencies, are able to breed in colonies shared with Adélie Penguins, thereby
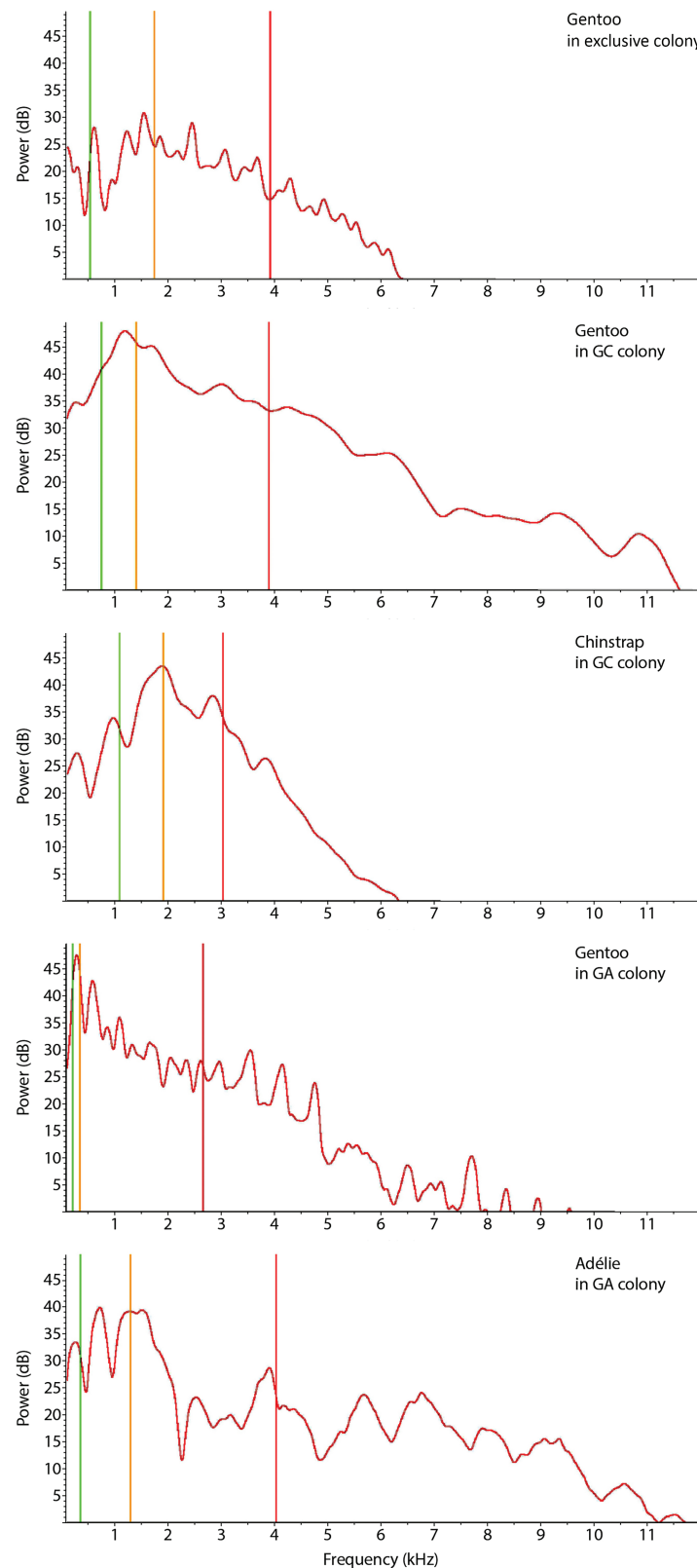
FIGURE 7. Power spectra of examples of typical Gentoo Penguin calls in all different kinds of examined colony types (G exclusive, GA mixed, GC mixed) as well as of Adélie Penguin calls and Chinstrap Penguin calls in the mixed colony type. Green vertical line = 5% frequency measurement, yellow vertical line = center frequency measurement, red vertical line = 95% frequency measurement. Spectrum details: Window type: Hann, window size = 625 samples, overlap = 65%, DFT size = 2,048, 4,096 or 8,192 samples at a 24, 48 or 96 kHz sampling rate, respectively.

explaining the pattern we observed. Thus, the selection for stronger and larger animals nesting in mixed colonies would lead to a lower frequency purely through larger vocal organs and vocal tracts which are better capable to produce and resonate low frequencies, and coupling them to the outside medium (Friis et al. 2021). Such a selection for larger individuals might be possible precisely because the deeper vocalizations of larger individuals provide them with an adaptive advantage by making their vocalizations more distinguishable, thereby facilitating intraspecific communication (Aubin and Jouventin 1998, Jouventin and Aubin 2002). In that case, smaller Gentoo Penguins with higher-frequency vocalizations might be counter-selected from colonies where Adélie Penguins breed because such vocalizations do not allow a proper intraspecific communication under such acoustic conditions. This scenario suggests that Adélie Penguins may limit smaller Gentoo penguins to breed where they could otherwise. Such a potential limitation may explain why colonies of Gentoo Penguins are rarer in association with Adélie Penguins than exclusive Gentoo colonies or colonies of Gentoo Penguins in association with Chinstrap Penguins.

Our correlative results did not enable us to disentangle the possible mechanisms underlying the vocal differences we found between colony compositions (selection for given individuals depending on their size vs. vocal plasticity) and may be affected by some confounding factors (e.g., variable distance to heterospecific nests, colony topography, and structure). Moreover, the number of mixed colonies included in our study was limited (because their number is naturally limited). Finally, because of the few exclusive colonies of Adélie and Chinstrap penguins present along the Antarctic Peninsula, our correlative study focused solely on more frequent colonies of Gentoo Penguins. It is for instance possible that Gentoo Penguins did not modify their vocalizations in the presence of Chinstrap Penguins because Chinstrap Penguins show themselves some vocal plasticity, leading to less acoustic overlap in those mixed colonies. All these limitations call for the use of experimental approaches, such as approaches based on the use of heterospecific playbacks and their effects on the vocalizations of focal individuals. The use of such approaches would allow us to examine whether penguins can directly alter the quality of their vocalizations in response to their exposure to other vocalizations. Moreover, this experimental approach could also be used to examine whether the vocal plasticity of penguins differs between the three *Pygoscelis* species, or even further to assess the applicability of frequency changes as limited vocal learning mechanisms in other colonial bird nesting associations.

The coexistence of the 3 *Pygoscelis* species in colonies along the coast of the Antarctic Peninsula is made possible through the use of different foraging niches (Croxall and Prince 1980, Trivelpiece et al. 1987, Wilson 2010) and breeding phenology niches (Trivelpiece et al. 1987). However, climate change is strongly affecting *Pygoscelis* penguin populations and distributions along the Antarctic Peninsula. As Gentoo Penguins increase in abundance and expand their range southward (Hinke et al. 2007, Lynch et al. 2012b, Herman et al. 2020), interspecies competition for physical space, and subsequently acoustic space may also increase or shift. How climate change and competition for acoustic space interact in bird nesting associations therefore remains an important aspect to explore.

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