

Research



Cite this article: Baciadonna L, Solvi C, del Vecchio F, Pilenga C, Baracchi D, Bandoli F, Isaja V, Gamba M, Favaro L. 2022 Vocal accommodation in penguins (*Spheniscus demersus*) as a result of social environment. *Proc. R. Soc. B* **289**: 20220626. <https://doi.org/10.1098/rspb.2022.0626>

Received: 1 April 2022
Accepted: 24 June 2022

Subject Category:
Behaviour

Subject Areas:
behaviour, cognition

Keywords:
African penguins, Bird communication,
Vocal learning, Social accommodation

Authors for correspondence:
Luigi Baciadonna
e-mail: luigi.baciadonna@unito.it
Livio Favaro
e-mail: livio.favaro@unito.it

†These authors contributed equally.

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6070394>.

Vocal accommodation in penguins (*Spheniscus demersus*) as a result of social environment

Luigi Baciadonna^{1,†}, Cwyn Solvi^{2,†}, Flavia del Vecchio¹, Cristina Pilenga³, David Baracchi⁴, Francesca Bandoli⁵, Valentina Isaja⁶, Marco Gamba¹ and Livio Favaro¹

¹Department of Life Sciences and Systems Biology, University of Turin, Turin, Italy

²Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland

³Zoomarine Italia, Torvaianica-Pomezia, Rome, Italy

⁴Department of Biology, University of Florence, Firenze, Italy

⁵Giardino Zoologico di Pistoia, Pistoia, Italy

⁶Fondazione Zoom, Cumiana, Turin, Italy

id LB, 0000-0003-0011-801X; CS, 0000-0003-2517-6179; CP, 0000-0003-4883-092X; DB, 0000-0003-1308-0612; FB, 0000-0002-2082-6577; MG, 0000-0001-9545-2242; LF, 0000-0002-8698-472X

The ability to vary the characteristics of one's voice is a critical feature of human communication. Understanding whether and how animals change their calls will provide insights into the evolution of language. We asked to what extent the vocalizations of penguins, a phylogenetically distant species from those capable of explicit vocal learning, are flexible and responsive to their social environment. Using a principal components (PCs) analysis, we reduced 14 vocal parameters of penguin's contact calls to four PCs, each comprising highly correlated parameters and which can be categorized as fundamental frequency, formant frequency, frequency modulation, and amplitude modulation rate and duration. We compared how these differed between individuals with varying degrees of social interactions: same-colony versus different-colony, same colony over 3 years and partners versus non-partners. Our analyses indicate that the more penguins experience each other's calls, the more similar their calls become over time, that vocal convergence requires a long time and relative stability in colony membership, and that partners' unique social bond may affect vocal convergence differently than non-partners. Our results suggest that this implicit form of vocal plasticity is perhaps more widespread across the animal kingdom than previously thought and may be a fundamental capacity of vertebrate vocalization.

1. Introduction

A fundamental prerequisite for the development of speech is the ability to modify one's vocalizations. Humans do this relatively spontaneously from infancy through to adulthood when learning new sounds, words and languages. To help reconstruct the evolution of language and the mechanisms underlying all types of vocal learning, it is essential to understand whether and to what extent the vocalizations of phylogenetically distant species are amenable [1,2]. Here, following the broad definition used by Janik & Slater [3], we consider vocal learning to be any vocal signals that are modified in form as a result of experience with any external acoustic stimuli.

Songbirds (Passeriformes) are by far the most studied animals when it comes to vocal learning [1]. Many of these birds require exposure to another bird (or model) to learn their normal songs [1], can acquire new vocalizations via listening to conspecifics [4,5], and/or can even learn to mimic non-species-related sounds [5]. The vast work with songbirds regarding these types of explicit vocal learning has revealed many of the behavioural, neural and genetic processes involved in vocal learning. By contrast, outside of songbirds (and hummingbirds and parrots

[1]), the vocalizations of most animals including our closest relatives (non-human primates), are largely innate [6]. Evidence suggests these animals lack the neural projections to control the structure of their calls [7]. Although many vocal parameters seem to be fixed by both neural circuitry limitations and the set physical structure of an animal's vocal organ, some vocal aspects can still be modified. For example, the duration of a vocal call and the pauses between calls rely on the very flexible changes that can occur in the respiratory system, and therefore are susceptible to modification by the environment [8,9].

There is a growing body of literature suggesting that some animals, from which there is no evidence of explicit vocal learning, e.g. producing a new song or call through modelling or mimicking, can still modify their calls in response to the environment. This phenomenon has been referred to as 'vocal accommodation' and can occur in response to noisy/changing surroundings (environmental accommodation; [10]), e.g. increasing the loudness of a call with increased background noise [11], or in response to the structure of their social environment (social accommodation; [10]), e.g. convergence of calls in response to closer and more frequent social interactions [10]. However, outside of animals that are capable of explicit vocal learning (e.g. songbirds, hummingbirds, parrots [1], bats [12], cetaceans [13] and elephants [14]), the only animals that have shown evidence of vocal accommodation are primates [10,15]. For example, the acoustic structure of male baboons' calls was found to be more similar between males that spent more time together even when genetic relatedness was taken into account [16]. These results and similar findings [10,17] suggest that even when a primate is not capable of explicit vocal learning, their vocalizations can be modified in response to social interactions. In particular, the more pairs of individuals experience each other's calls, the more their calls change to sound similar. Whether this type of social accommodation occurs outside of primates is unknown.

Here, we examined whether the calls of African penguins (figure 1a; *Spheniscus demersus*) are amenable to their social environment. These penguins are an ideal species to investigate social accommodation for two major reasons. They are phylogenetically distant from any species known to be explicit vocal learners, having separated from the nearest of those, i.e. parrots, more than 60 Ma [18]. Determining whether and how social accommodation occurs in this species will shed light on the distant origins of vocal flexibility, a pre-requisite of vocal learning [1].

African penguins also form large colonies where they frequently hear the calls of their colony mates and form different types of social bonds with other penguins within their community, providing an ideal scenario to test whether social accommodation takes place in these animals. We hypothesized that penguins which have spent more time closer together, and therefore experienced a greater number of each other's vocalizations, should have more similar calls. Here, we tested this hypothesis by measuring and comparing several acoustic parameters within the contact calls, distinctive short calls expressing isolation from groups or their colony mates, [19,20] of African penguins with different social histories.

2. Methods

(a) Penguins

The vocal comparison across years, between partners and non-partners, and the behavioural experiment were performed with

African penguins housed at the Zoomarine Roma marine park (Torvaianica, Italy). The vocal comparison across colonies was performed with penguins in the Zoomarine Roma marine park (Torvaianica, Italy), the Zoom Torino (Cumiana, Italy) and the Zoological Garden of Pistoia (Pistoia, Italy).

The Zoomarine Roma colony was established in 2014 with penguins from the Burger Zoo (Netherlands) and the Bioparc Les Sables D'Olonne (France) (electronic supplementary material, table S1). The Zoom Torino colony was established in 2009 with penguins from the South Lake Park Wild Animal Park (Dalton in Furness, UK) and subsequently adding penguins from the Wilhelma Zoo (Stuttgart, Germany), the Bird Park Avifauna (Alphen an den Rijn, Netherlands) and the Artis Royal Zoo (Amsterdam, Netherlands). The Zoological Garden Pistoia colony was established in 2011 with penguins from the Warszawskie Zoo (Poland) and later added penguins from the Nausicaä Centre (France).

(b) Behavioural data collection

The behavioural data were collected from the colony hosted at Zoomarine Roma. An instantaneous sampling was made every 10 min for the entire group and any penguins that were within one body width of each other were recorded as associating (proximity). In between the samplings, we carried out group observations of affiliative and aggressive behaviours. We recorded three affiliative behaviours [21]—allopreening, extreme/intermediate bow and vibratory head shaking. Five aggressive behaviours were recorded—point, displacement, fight, sideway stare and gape (electronic supplementary material, table S2). Depending on the daily husbandry regimes and weather conditions, 1–3 h of data were recorded between 7.00 and 13.00 each day (a total of 30 h of observations) from October 2020 to November 2020. The entire colony was always visible from where the experimenter conducted the observations.

(c) Acoustic data collection

Vocalizations were collected from all three colonies using the focal animal sampling method [22]. The acoustic data from the Zoomarine Roma colony was collected between February and May 2017 (7.00–13.00; 60 days; 300 h total) and between February and October 2020 (7.00–13.00; 44 days; 220 h total). The acoustic data from Zoom Torino were collected between October 2014 and April 2015 (9.00–16.00; 50 days; 100 h total). The acoustic data from the Zoological Garden of Pistoia colony were collected between October 2016 and June 2017 (8.00–18.00; 68 days; 230 h total). All recordings were collected at 3–10 m from the vocalizing individuals with a RODE NTG-2 shotgun microphone (flat frequency response 20 Hz to 20 kHz, max SPL 131 dB) connected to a TASCAM DR-680 (2017 Zoomarine Roma), a ZOOM H5 (2020 Zoomarine Roma and Zoom Torino) or a ZOOM H4n (Zoological Garden Pistoia) handy recorder (48 kHz sampling rate). Audio files were saved in WAV format (16-bit amplitude resolution) and stored on a secure digital memory card.

(d) Behavioural analysis

The strength of dyadic proximity, and affiliative and aggressive relationships between penguins housed at Zoomarine Roma were measured using a modified version of the dyadic composite sociality index (DSI; [23,24]). The DSI index, which ranges from 0 to ∞ , was calculated for each pair of penguins and for each behaviour considered using the following formula: $DSI = (X_{ij} / X_{\text{mean}\lambda})$; where X_{ij} represents the behavioural occurrences for a certain dyad i and j , and $X_{\text{mean}\lambda}$ represents the mean occurrences for the same behaviour across all dyads.

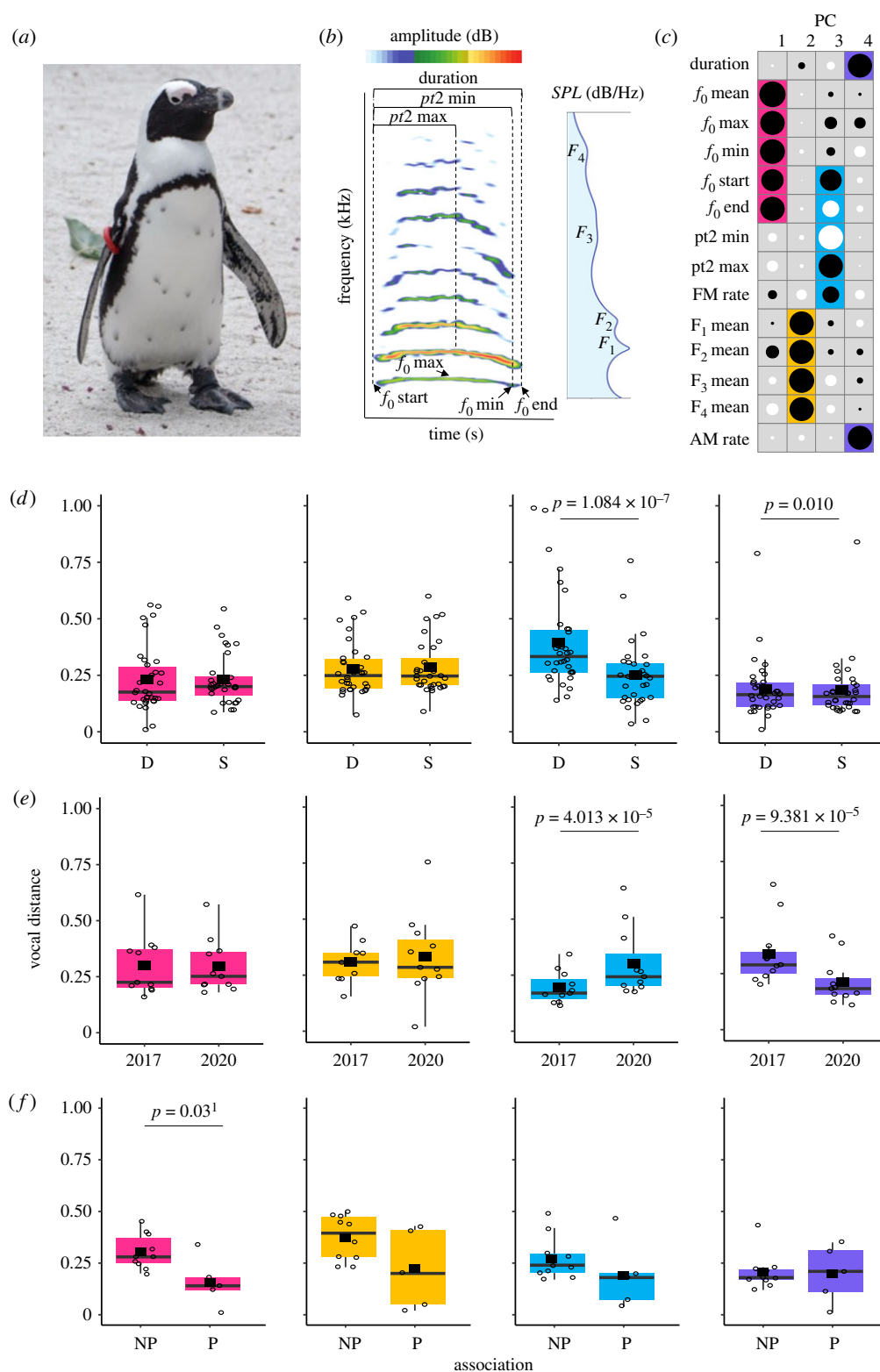


Figure 1. Vocal accommodation in African penguins. (a) Adult African penguin (photo credit: Giulia Olivero). (b) Spectrogram of an example contact call noting the various measured vocal parameters (electronic supplementary material, table S3). For each call, we extracted the fundamental frequency (f_0) contour, which included the frequency value at the start (f_0 start) and end (f_0 end) of a call, and the mean (f_0 mean), minimum (f_0 min) and maximum (f_0 max) frequency values. We also calculated the time between the start of a call to the time of minimum frequency (pt2 min) and maximum frequency (pt2 max), both as percentages of the entire call duration. The number of complete cycles of f_0 modulation per second (FM rate) and the number of complete amplitude modulation cycles per second (AM rate) were calculated (not indicated in the spectrogram). Finally, we calculated the average frequencies for each of the first four formants (F_1 – F_4). (c) Correlation matrix obtained performing a principal components analysis (PCA) on the 14 acoustic parameters (electronic supplementary material, table S4). We extracted four principal components (PCs; PC1 (pink): fundamental frequency; PC2 (yellow): formant frequency; PC3 (blue): frequency modulation; PC4 (purple): amplitude modulation rate and duration). Dot colour: black = positive correlation; white = negative correlation. Dot size: larger = stronger correlation. (d) Vocal distance calculated for the four PCs between penguins belonging to the same (S) colony or different colonies (D). (e) Vocal distance calculated for the four PCs across 2017 and 2020 within the Zoomarine Roma colony. (f) Vocal distances between partners and non-partners within the Zoomarine Roma colony. Superscript ¹ is non-significant based on strict p -value interpretation after applying a Bonferroni correction. Box plots: horizontal lines = median; black squares = mean; boxes extend from lower to upper quartile and whiskers indicate interquartile range above the upper quartile (max) or below the lower quartile (min). Each open circle in (d) and (e) represents the vocal distance between pairs of penguins, and in (f) represents the average vocal distance between penguins (Methods). (Online version in colour.)

(e) Acoustic analysis

Audio segments containing contact calls were visually selected by inspection of their spectrograms (view range = 0–8000 Hz, window length 0.02 s, dynamic range = 50 dB) in PRAAT v. 6.1.16 [25]. Overall, we selected 2985 contact calls showing a good signal-to-noise ratio. In total, 1907 and 349 contact calls were selected from 2017 and 2020, respectively, from 13 adult penguins at the Zoomarine Roma colony. We recorded 330 contact calls from 11 adult penguins at the Zoom Torino and 399 contact calls from 10 adult penguins at the Zoological Garden of Pistoia (electronic supplementary material, table S1). For each vocalization, we measured 14 source and filter related acoustic parameters using a custom-built script [26] in PRAAT [25]. See the electronic supplementary material for acoustic analyses details and table S3 for the description of the parameters extracted.

(f) Statistical analysis

A principal component analysis (PCA) using an orthogonal varimax rotation was carried out on all 14 acoustic parameters extracted (z -score normalization) from the 2985 selected contact calls. The PCA reduced the original set of acoustic measurements to a new set of uncorrelated principal components (PCs). We retained only the PCs with eigenvalues greater than 1 (Kaiser's criterion, electronic supplementary material). For each PC separately, we calculated the Euclidean distance between each pair of penguins' PC values, obtaining a vocal similarity matrix for different years (Zoomarine Roma), and across all three colonies for the cross-colony comparison. We also rescaled the initial matrices using the following formula: $\text{matrices}_x / \max(\text{matrices}_x)$. The values of the rescaled matrices range from 0 (indicating maximum similarity) to 1 (maximum dissimilarity) improving the visualization and interpretation of the vocal distances between each pair of penguins.

For an across-year comparison within the same colony (Zoomarine Roma), we ran four independent generalized linear mixed models (GLMMs), each of which included a single PC as the response variable and a two-level time variable referring to either 2017 or 2020, as a fixed factor. Penguin identity was included as a random factor. For a within-colony versus across-colony comparison, we performed four independent GLMMs, each of which included the vocal distance of a single PC between pairs of penguins (logarithmic transformation to give the data a normal distribution) as the response variable, with colony set as a fixed factor. Penguin identity was included as a random factor. All GLMMs were built with the lme4 package [27] in R 3.6.1. The significance of the full model was established by comparing this model with the model that included only the random factor (null model) using the likelihood ratio test. The model fit and overdispersion were checked using the R-package DHARMA 0.3.3.0 [28]. For a comparison between partners and non-partners, we used a Wilcoxon rank sum test to compare the calls of penguins in the Zoomarine Roma colony. For each PC separately, we calculate the vocal distance between each pair of partners. In addition, for each penguin, we calculated the average vocal distance between that penguin and all other colony members, excluding that penguin's partner. For analysis of our behavioural experiment, we applied a Mantel matrix correlation test (R package 'ape' 5.5) for each PC and the DSI matrices of each behaviour (proximity, affiliative and agonistic). A Bonferroni correction was used to reduce the probability of committing a Type I error: because four PCs were separately tested, all p -values were compared to a significance level of 0.012 ($\alpha = 0.05/4$).

3. Results

To determine if shared social environment causes any changes to the vocal structure of individual penguins, we

compared 14 acoustic parameters of contact calls between penguins across time and within and across different colonies (figure 1*b*). Using a PCA, we reduced the dimensionality of our dataset to four orthogonal PCs (PC1: most correlated with fundamental frequency; PC2: formant frequency; PC3: frequency modulation; PC4: amplitude modulation rate and duration; figure 1*c*; electronic supplementary material, table S4). We then determined how similar the calls were between pairs of penguins, i.e. their vocal distance. To do this, for each pair of penguins, we calculated the difference between each of their respective PCs (electronic supplementary material). If their calls are susceptible to social accommodation, as penguins spend more time together, and as a natural result experience more of each other's vocalizations, penguins' calls should become more similar.

We first investigated whether the vocal distance between calls of penguins within and across distinct colonies differed. As a natural consequence of physical distance, penguins in the same colony will experience their colony mates' calls frequently, whereas they never hear the calls of a distant colony. The effect of these differences will have accumulated over many years, providing that colony membership is relatively stable. Therefore, if social accommodation occurs, the calls of penguins within the same colony should be more similar to each other than the calls of penguins that belong to different colonies. To test this, we compared the calls of penguins from three different colonies (Methods). The PC1 and PC2 differences in the same colony were no different than between penguins from different colonies (PC1 same colony (S) = 0.23 ± 0.01 , different colony (D) = 0.25 ± 0.01 ; full versus null GLMM $\chi^2_1 = 3.61$, $p = 0.057$; PC2 S = 0.27 ± 0.01 , D = 0.29 ± 0.01 ; full versus null GLMM $\chi^2_1 = 0.97$, $p = 0.32$; figure 1*d*). However, penguins from the same colony had smaller PC3 and PC4 differences than penguins from different colonies (PC3: figure 1*d*; S = 0.25 ± 0.01 , D = 0.31 ± 0.01 ; full versus null GLMM $\chi^2_1 = 28.21$, $p = 1.084 \times 10^{-7}$, mean % difference 21.4%; PC4: figure 1*d*; S = 0.17 ± 0.01 , D = 0.19 ± 0.009 ; full versus null GLMM $\chi^2_1 = 6.48$, $p = 0.010$, mean % difference 11.1%). These results suggest that while certain parameters of penguins' contact calls are relatively constrained and vary less, other parameters can be and are modified subtly in response to their social environment over long periods of time.

If penguins' calls are amenable to their social environment, then we should also see evidence of this when comparing calls of penguins within the same colony over long enough period of time. To test this, we compared contact calls that were recorded 3 years apart (Methods). Similar to the results of our cross-colony comparison, both PC1 and PC2 differences between pairs of penguins remained similar over 3 years (PC1: 2017 = 0.32 ± 0.02 , 2020 = 0.31 ± 0.02 ; full versus null GLMM $\chi^2_1 = 0.15$, $p = 0.69$, figure 1*e*; PC2: 2017 = 0.32 ± 0.02 , 2020 = 0.33 ± 0.02 ; full versus null GLMM $\chi^2_1 = 0.02$, $p = 0.87$; figure 1*e*). However, the penguins' PC3 differences increased (2017 = 0.19 ± 0.01 , 2020 = 0.31 ± 0.02 ; full versus null GLMM $\chi^2_1 = 16.86$, $p = 4.013 \times 10^{-5}$, mean % difference 48%; figure 1*e*), while their PC4 differences decreased over 3 years (2017 = 0.34 ± 0.02 , 2020 = 0.21 ± 0.01 ; full versus null GLMM $\chi^2_1 = 15.25$, $p = 9.381 \times 10^{-5}$, mean % difference 47.2%; figure 1*e*). These results suggest that certain parameters of penguins' vocalizations are modified by the cumulative number of social interactions that occur, but also that the way they are modified will be partially

determined by the stability of colony membership over time. We discuss this in more depth below.

Within a colony, most African penguins form long-lasting monogamous-pair relationships. These partners perform various types of calls only with each other. For example, mutual display songs are produced only between two partnered birds in synchrony, usually when one partner returns to the nest [19]. Penguins experience some of their partner's vocalizations at a much higher intensity, because they are simply very close to each other, and in different emotional states than they probably would while hearing non-partner's calls. Therefore, we hypothesized that the special relationship between partners might manifest in greater similarity between their calls than between non-partners. To test this, we compared the calls between partners and between non-partners in the same colony. We found that the PC1 distance between a penguin and their partner was consistently smaller than the average distance from their non-partners (PC1, 2020, partner = 0.15 ± 0.05 , non-partner = 0.30 ± 0.02 ; Wilcoxon rank sum test $W=43$, $p=0.03$, mean difference 66.6%; figure 1f). No differences were found between comparisons of the other PCs (electronic supplementary material, table S5). We discuss the significance of these findings and their comparison with our other results below.

So far, our findings suggest that the more social interactions penguins have with each other, the more similar certain aspects of their vocalizations become. Another way to test this is to look at how often pairs of penguins are near each other. Given the results of our partner versus non-partner comparison, we might expect that the more often penguins are in close proximity, the more they experience each other's calls, and therefore are more susceptible to vocal accommodation. To test this, we recorded a snapshot of which penguins were within one body width of one another over a period of 19 days. To assess the quality of penguins' social relationship with one another, each day we also recorded the instances of affiliative and agonistic behaviours (Methods). We then examined whether any of these measurements correlated with the vocal distance between penguins' calls for each of the four PCs (Methods). We expected that the more often two penguins were seen in close proximity and/or engaging in affiliative and agonistic behaviours, the shorter the vocal distance should be between those penguins. However, we found no correlation between proximity, affiliative or agonistic behaviours and any of the PC differences (electronic supplementary material, table S6). We discuss why we might actually expect these results below.

4. Discussion

We investigated the role of shared social environment on potential modifications of African penguin's contact calls. We found that frequency modulation (PC3) and amplitude modulation rate and duration (PC4) of calls were more similar between penguins of the same colony than between penguins of different colonies. We also found that amplitude modulation rate and duration (PC4) of calls of individuals within the same colony became more similar to each other over a 3-year period. Taken together, these results suggest that vocal accommodation does occur in this taxon. The fact that amplitude modulation rate and duration were found to be affected by social environment in both analyses is not

surprising given that these vocal aspects are likely to be the most amenable [1,3].

The increased distance found between frequency modulations (PC3) of penguins within the same colony over 3 years may at first seem contradictory to our overall results. However, we should expect that because of physiological constraints, any changes in vocalization will be very subtle. Our cross-colony analysis compares penguins that have interacted with each other over many years compared to penguins that have not interacted at all. The fact that PC3 distance changed in just 3 years shows that it is amenable. It is rare that biological changes occur in one direction monotonically over time. Divergences may very well happen intermittently owing to changes in colony membership over a short period of time (e.g. new penguins being added to or hatched into the colony). Indeed, in the Zoomarine Roma colony, between the recording collected in 2017 and 2020, one penguin had passed away, and three chicks were hatched. Our cross-colony comparison results suggest that given longer time frames and relative stability in colony membership these parameters will eventually become closer.

The proximate mechanism underlying vocal accommodation can be the automatic relationship between vocal perception and production which has been assumed to enhance communication between individuals [29]. This seems to be a fundamental response of vocal organs and neurocircuitry—acoustic information is received and processed by the brains of communicators and their voices change over time to become more similar to each other. Recent studies suggest that integration in the sensorimotor area is responsible for vocal accommodation of vocal output in response to acoustic input [29–31]. These studies support the idea that vocal convergence represents a form of implicit motor learning common to both non-human animals and humans [10].

This implicit motor learning mechanism of vocal convergence may explain our results between partners. Although overall significance did not survive the applied Bonferroni correction, the fundamental frequency (PC1) of a penguin was consistently more similar to their partner than to their average distance from all non-partners, and the mean difference was substantial (66%; figure 1f). It may be that no true difference in PC1 exists between these groups. However, a true difference may be hidden within the small size of our colony. Analysis of a much larger colony may help reveal any true difference. If the PC1 difference is true, it may not be the consequence of simply a greater number of interactions between partners, but instead have more to do with the strong bond between partners. Partners may often be in a heightened state of arousal when and where they hear their partner's calls. Emotions have been found to affect learning of all types in a myriad of ways [32]. We suggest that a partner-induced emotional state may similarly affect how the vocal input they receive from their partner can implicitly modify their vocal output. If this PC1 difference is not true, the non-significant differences between partners and non-partners for all PCs are not surprising. In fact, we would only expect greater similarities in even the PCs most susceptible to change (PC3 and PC4) for partners compared to non-partners if partners heard their own calls significantly more than all other colony members. However, within the confines of a colony, especially those that are smaller and in captivity, the calls of all colony mates will be heard by each penguin simply because they are often not that far away. In addition,

during the breeding season when penguins forage in the water they form small foraging groups [29] of non-partner colony mates while their partners stay at the nest. These natural occurrences would predict that penguins experience the calls of many penguins relatively equally and varied over time.

We had initially expected that the greater the number of behavioural interactions (proximity, affiliative and agonistic) between penguins, the greater their vocal similarity would be. However, we found no correlation between any of the behavioural interactions measured and any single PC. In the light of the results of our other analyses, we actually should have expected such a result. At any single point in time, penguins will be more likely to have greater vocal similarity to any one of their many non-partner colony mates than to their single partner, simply based on chance. Moreover, there is no reason to suspect that two penguins become partners based on their vocal similarity.

Vocal production can potentially be influenced by genetic inheritance and (as just highlighted) acoustic similarity can result from simply having vocal apparatuses of similar morphology [7]. Because we were unable to obtain genetic information of penguins, we cannot entirely rule out some effect from genetic similarity that may account for the observed cross-colony results (figure 1*d*). However, the genetic diversity across colonies should not be any greater than within colonies because of the efforts to reduce inbreeding within colonies, because all African penguins in zoos come from wild penguins put in captivity less than a century ago, and because the three colonies used in this study are equally unrelated [33]. In addition, those parameters that are more susceptible to vocal accommodation in response to social interactions were those that we observed to change and become more similar over long periods of time (amplitude modulation rate and duration (PC4), frequency modulation (PC3), and fundamental frequency (PC1)). By contrast, parameters that are known to be much more genetically constrained to the anatomy of the supra-syringeal vocal tract (formants (PC2); [20,26]) were not found to change in any of the analyses. Importantly, genetic similarities cannot explain the vocal changes observed in the comparison of penguins in the same colony across different years (figure 1*e*). Indeed, their genetic makeup did not change significantly because only three chicks hatched into the colony from 2017 to 2020 and all came from different parents.

Vocal accommodation as a consequence of social interactions has been proposed to enhance members' recognition,

group cohesion and social bonds between individuals [34]. Evidence of socially caused vocal accommodation in penguins suggests similar arguments. Ecological pressures of colony life pushes for vocal accommodation to help identify and discriminate colony mates from penguins outside the colony [35]. We speculate that, similar to what has been found in monkeys [16], vocal accommodation may help clusters of penguins within the same colony identify each other. However, evaluating this will require extended research efforts which can identify and track social and vocal interactions over long time periods and large areas.

Our results support recent evidence suggesting that acoustic accommodation is possible even in species where the majority of their vocal repertoire is genetically constrained [16,36,37]. Our findings suggest that vocal accommodation as a result of social interaction may be phylogenetically old and widespread. We speculate that it may be driven by the ecological pressures found in large vocal groups and is a result of implicit sensory-motor integration present in many animals. Our results highlight the importance of and provide a template for evaluating all aspects of an animal's vocalizations when investigating vocal flexibility.

Ethics. All procedures were conducted in accordance with the guidelines of the Association for the Study of Animal Behaviour for the care and the use of animals for research activities [38] and were approved by the Ethics Committee of the University of Turin (approval no. 280324).

Data accessibility. The data and associated code for analysis are provided in the Figshare repository (https://figshare.com/projects/Vocal_accommodation_in_penguins_Spheniscus_demersus_as_a_result_of_social_environment/139756).

Electronic supplementary material is available online [39].

Authors' contributions. L.B.: conceptualization, data curation, formal analysis, methodology, writing—review and editing; C.S.: formal analysis, writing—original draft; F.d.V.: data curation; D.B.: data curation; F.B.: data curation; V.I.: data curation; L.F.: conceptualization, data curation, formal analysis, writing—review and editing; C.P.: data curation; M.G.: formal analysis, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. L.B. was supported by the University of Turin through a MIUR postdoctoral fellowship. C.S. was supported by a Templeton World Charity Foundation project grant (no. TWCF0539).

Acknowledgements. We are grateful to Chiara Calcari, Eleonora Cresta and Eleonora Fumagalli for helping with the recording of the penguin vocalizations.

References

- Cate C. 2021 Re-evaluating vocal production learning in non-oscine birds. *Phil. Trans. R. Soc. B* **376**, 20200249. (doi:10.1098/rstb.2020.0249)
- Hauser MD, Chomsky N, Fitch WT. 2002 The faculty of language: what is it, who has it, and how did it evolve? *Science* **298**, 1569–1579. (doi:10.1126/science.298.5598.1569)
- Janik VM, Slater PJB. 2000 The different roles of social learning in vocal communication. *Anim. Behav.* **60**, 1–11. (doi:10.1006/anbe.2000.1410)
- Nowicki S, Searcy WA. 2014 The evolution of vocal learning. *Curr. Opin. Neurobiol.* **28**, 48–53. (doi:10.1016/j.conb.2014.06.007)
- Tyack PL. 2019 A taxonomy for vocal learning. *Phil. Trans. R. Soc. B* **375**, 20180406. (doi:10.1098/rstb.2018.0406)
- Fischer J. 2021 Primate vocal communication and the evolution of speech. *Curr. Dir. Psychol. Sci.* **30**, 55–60. (doi:10.1177/0963721420979580)
- Hammerschmidt K, Fischer J. 2008 Constraints in primate vocal production. In *The evolution of communicative creativity: from fixed signals to contextual flexibility* (eds K Oller, U Griebel), pp. 93–119. Cambridge, MA: MIT Press.
- De Gregorio C, Valente D, Raimondi T, Torti V, Miarctsoa L, Friard O, Giacomini C, Ravignani A, Gamba M. 2021 Categorical rhythms in a singing primate. *Curr. Biol.* **31**, R1379–R1380. (doi:10.1016/j.cub.2021.09.032)

9. De Gregorio C, Zanoli A, Valente D, Torti V, Bonadonna G, Randrianarison RM, Giacoma C, Gamba M. 2018 Female indris determine the rhythmic structure of the song and sustain a higher cost when the chorus size increases. *Curr. Zool.* **65**, 89–97. (doi:10.1093/cz/zoy058)
10. Ruch H, Zürcher Y, Burkart JM. 2018 The function and mechanism of vocal accommodation in humans and other primates. *Biol. Rev.* **93**, 996–1013. (doi:10.1111/brv.12382)
11. Brumm H, Zollinger SA. 2011 The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour* **148**, 1173–1198. (doi:10.1163/000579511X605759)
12. Vernes SC, Wilkinson GS. 2019 Behaviour, biology and evolution of vocal learning in bats. *Phil. Trans. R. Soc. B* **375**, 20190061. (doi:10.1098/rstb.2019.0061)
13. Favaro L, Neves S, Furlati S, Pessani D, Martin V, Janik VM. 2016 Evidence suggests vocal production learning in a cross-fostered Risso's dolphin (*Grampus griseus*). *Anim. Cogn.* **19**, 847–853. (doi:10.1007/s10071-016-0961-x)
14. Poole JH, Tyack PL, Stoeger-Horwath AS, Watwood S. 2005 Elephants are capable of vocal learning. *Nature* **434**, 455–456. (doi:10.1038/434455a)
15. Elowson AM, Snowdon CT. 1994 Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Anim. Behav.* **47**, 1267–1277. (doi:10.1006/anbe.1994.1175)
16. Fischer J, Wegdell F, Trede F, Dal Pesco F, Hammerschmidt K. 2020 Vocal convergence in a multi-level primate society: insights into the evolution of vocal learning. *Proc. R. Soc. B* **287**, 20202531. (doi:10.1098/rspb.2020.2531)
17. Levréro F, Carrete-Vega G, Herbert A, Lawabi I, Courtiol A, Willaume E, Kappeler PM, Charpentier MJE. 2015 Social shaping of voices does not impair phenotype matching of kinship in mandrills. *Nat. Commun.* **6**, 7609. (doi:10.1038/ncomms8609)
18. Prum RO, Berv JS, Dornburg A, Field DJ, Townsend JP, Lemmon EM, Lemmon AR. 2015 A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**, 569–573. (doi:10.1038/nature15697)
19. Favaro L, Ozella L, Pessani D. 2014 The vocal repertoire of the African penguin (*Spheniscus demersus*): structure and function of calls. *PLoS ONE* **9**, e103460. (doi:10.1371/journal.pone.0103460)
20. Favaro L, Gili C, Da Rugna C, Gnone G, Fissore C, Sanchez D, McElligott AG, Gamba M, Pessani D. 2016 Vocal individuality and species divergence in the contact calls of banded penguins. *Behav. Processes* **128**, 83–88. (doi:10.1016/j.beproc.2016.04.010)
21. Eggleton P, Siegfried WR. 1979 Display of the jskcass penguin. *J. African Ornithol.* **50**, 139–167. (doi:10.1080/00306525.1979.9634105)
22. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267. (doi:10.1163/156853974X00534)
23. Dal Pesco F, Trede F, Zinner D, Fischer J. 2021 Kin bias and male pair-bond status shape male-male relationships in a multilevel primate society. *Behav. Ecol. Sociobiol.* **75**, 24. (doi:10.1007/s00265-020-02960-8)
24. Silk JB, Altmann J, Alberts SC. 2006 Social relationships among adult female baboons (*Papio cynocephalus*): variation in the strength of social bonds. *Behav. Ecol. Sociobiol.* **61**, 183–195. (doi:10.1007/s00265-006-0249-2)
25. Boersma P, Weenink D. 2009 Praat: doing phonetics by computer. See <http://www.praat.org/>.
26. Favaro L, Gamba M, Alfieri C, Pessani D, McElligott AG. 2015 Vocal individuality cues in the African penguin (*Spheniscus demersus*): a source-filter theory approach. *Sci. Rep.* **5**, 17255. (doi:10.1038/srep17255)
27. Bates D, Mächler M, Bolker BM, Walker SC. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
28. Harting F. 2020 DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. See <https://CRAN-r-project.org/package=DHARMA>.
29. Pickering MJ, Garrod S. 2013 An integrated theory of language production and comprehension. *Behav. Brain Sci.* **36**, 329–347. (doi:10.1017/S0140525X12001495)
30. Pickering MJ, Garrod S. 2004 Toward a mechanistic psychology of dialogue. *Behav. Brain Sci.* **27**, 169–190. (doi:10.1017/S0140525X04000056)
31. Tyack PL. 2016 Vocal learning and auditory-vocal feedback. In *Vertebrate sound production and acoustic communication* (eds RA Suthers, WT Fitch, RR Fay, AN Popper), pp. 261–295. Cham, Switzerland: Springer.
32. Tyng CM, Amin HU, Saad MNM, Malik AS. 2017 The influences of emotion on learning and memory. *Front. Psychol.* **8**, 1454. (doi:10.3389/fpsyg.2017.01454)
33. Bos C, Schad K, Fienieg E. 2016 Long-term management plan for the African penguin (*Spheniscus demersus*) European Endangered Species Programme (EEP). *Artis R. Zoo.*
34. Tyack P. 2008 Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. *J. Comp. Psychol.* **122**, 319–331. (doi:10.1037/a0013087)
35. Aubin T, Jouventin P, Hildebrand C. 2000 Penguins use the two-voice system to recognize each other. *Proc. R. Soc. Lond. B* **267**, 1081–1087. (doi:10.1098/rspb.2000.1112)
36. Jouventin P, Dobson F. 2018 *Why penguins communicate: the evolution of visual and vocal signals*. New York, NY: Academic Press.
37. Lemasson A, Ouattara K, Petit EJ, Zuberbühler K. 2011 Social learning of vocal structure in a nonhuman primate? *BMC Evol. Biol.* **11**, 362. (doi:10.1186/1471-2148-11-362)
38. Association for the Study of Animal Behaviour. 2021 Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.* **171**, 1–XI. (doi:10.1016/S0003-3472(20)30373-0)
39. Baciadonna L, Solvi C, del Vecchio F, Pilenga C, Baracchi D, Bandoli F, Isaja V, Gamba M, Favaro L. 2022 Vocal accommodation in penguins (*Spheniscus demersus*) as a result of social environment. Figshare. (doi:10.6084/m9.figshare.c.6070394)