PHILOSOPHICAL TRANSACTIONS B

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Research

Cite this article: Morandi I, Zanoli A, Tenneriello C, Terranova F, Balestra F, Cadman M, Ludynia K, Favaro L. 2025 Nonlinear vocal phenomena in African penguin begging calls: occurrence, significance and potential applications. *Phil. Trans. R. Soc. B* **380**: 20240019.
https://doi.org/10.1098/rstb.2024.0019

Received: 6 May 2024
Accepted: 23 July 2024

One contribution of 22 to a theme issue 'Nonlinear phenomena in vertebrate vocalizations: mechanisms and communicative functions'.

Subject Areas:
behaviour

Keywords:
bird syrinx, deterministic chaos, sidebands, *Spheniscus demersus*, subharmonics

Author for correspondence:
Livio Favaro
e-mail: livio.favaro@unito.it

†Ilaria Morandi and Anna Zanoli are joint first authors.

THE ROYAL SOCIETY PUBLISHING

Nonlinear vocal phenomena in African penguin begging calls: occurrence, significance and potential applications

Ilaria Morandi[1,†], Anna Zanoli[1,†], Chiara Tenneriello[1], Francesca Terranova[1], Flavia Balestra[1], Melissa Cadman[2], Katrin Ludynia[2,3] and Livio Favaro[1,4]

[1]Department of Life Sciences and Systems Biology, University of Turin, Turin 10121, Italy
[2]Southern African Foundation for the Conservation of Coastal Birds (SANCCOB), Cape Town, South Africa
[3]Department of Biodiversity & Conservation Biology, University of the Western Cape, Bellville, Cape Town, South Africa
[4]Stazione Zoologica Anton Dohrn, Naples, Italy

IM, 0009-0006-4298-2542; AZ, 0000-0002-9402-5617; CT, 0009-0001-8731-9908; FT, 0000-0003-1060-3756; FB, 0009-0003-8772-6866; MC, 0009-0005-8558-7211; KL, 0000-0002-0353-1929; LF, 0000-0002-8698-472X

African penguins (*Spheniscus demersus*) extensively use high-frequency food solicitation signals (begging calls) to request food from parents. We studied the occurrence of nonlinear vocal phenomena (NLP) in begging calls in 91 hand-reared penguin chicks at the Southern African Foundation for the Conservation of Coastal Birds. For each chick, we recorded the begging calls daily, from the hatching of wild abandoned eggs to the release of the chicks into the wild approximately three months later. We found that most (70%) of begging calls contain NLP. The most frequently observed are sidebands (54.1%) and deterministic chaos (71.4%), and these phenomena often coexist (26.5%). We suggest that the aperiodic chaotic features of begging calls assist in increasing adults' attention and avoiding habituation. The occurrence of NLP also depends on the penguins' age, with older chicks producing more NLP in their calls. Moreover, we found that NLP significantly increased in chicks after contracting a respiratory disease (for example, bacterial infections or aspergillosis). Such findings might be useful for the timely diagnosis of penguins needing veterinary treatment, contributing to conservation efforts for this endangered species.

This article is part of the theme issue 'Nonlinear phenomena in vertebrate vocalizations: mechanisms and communicative functions'.

1. Introduction

Vertebrate vocalizations often show perceptually harsh-sounding and chaotic vocal features, called nonlinear phenomena (NLP; [1–6]). In mammals and in other terrestrial vertebrates where the larynx is involved in sound production [7], these nonlinear dynamics in vocalizations have been distinguished into four primary types: frequency jumps, subharmonics, sidebands and deterministic chaos (see [4]). Frequency jumps manifest as abrupt alterations in vocal fold vibration [8]. Among the several possible mechanisms, subharmonics can emerge when one vocal fold vibrates at a frequency corresponding to a fractional value of the second vocal fold's frequency (e.g. 1 : 2, 2 : 3; [9]). Meanwhile, sidebands, resulting from biphonation, stem from the independent vibration of two sound sources (such as vocal folds vibrating at two distinct frequencies; [4]). Last, deterministic chaos, commonly known as chaos, typically arises when vocal folds vibrate asynchronously in non-periodic patterns [3].

While mostly documented among larynx-phonating vertebrates and particularly mammals [3,10], NLP have also been identified in several

terrestrial bird species (e.g. [2,11–13]), where the vocal organ is the syrinx [14], which does not appear to be homologous to the larynx at any structural level [15]. However, the vibrating median and lateral labia [16] of the syrinx also comprise a nonlinear physical system [2,17], where myoelastic-aerodynamics is the primary mechanism for sound production [18]. Accordingly, documented syringeal NLP also include low-dimensional chaos arising from oscillatory dynamics [2], as well as frequency jumps [19], subharmonics [20] and biphonation [21].

Penguins (Order *Sphenisciformes*) are flightless birds adapted to marine life [22]. The penguin lineage diverged approximately 60 million years ago (Mya) in Zealandia, with further speciation events driven by changes in global climate and extensive radiations and dispersals to South America and Antarctica via the Antarctic Circumpolar Current [23–25]. Extant penguin species are grouped into 1 family (Spheniscidae), 6 genera and 18 recognized species ([22]; but see [26]) distributed in the Southern Hemisphere from polar to tropical environments [22]. All penguin species exhibit a relatively conserved vocal repertoire that can be divided into two broad categories: 'calls' and 'display calls' (or 'display songs'; [27–29]). Calls are simple single-element vocalizations produced by both sexes throughout the year, which mediate agonistic interactions (agonistic calls; [28]) or allow cohesion and recruitment between group members at sea (contact calls; [30–32]). Display songs tend to be longer and more complex multi-syllable vocalizations [27,33] that are produced in the breeding season, with a characteristic circadian rhythm [34]. Display songs allow individual recognition [35–37] and mediate intersexual competition, male attraction and territorial defence [28,38–40]. Finally, penguin chicks and juveniles extensively use high-frequency food solicitation signals (begging calls) to request food from parents [28,41]. These signals play a crucial role in mediating the parent–offspring conflict (POC; [42]) and can inform parents about offspring condition and growth rate, thus facilitating adequate food allocation [41].

To the best of our knowledge, the presence and occurrence of NLP in penguins' vocalizations have never previously been documented nor systematically investigated. The spectral composition of penguins' vocalizations (both calls and display songs) is often described as periodic, with a harmonic series [28,31,36,43,44], where harmonics are positive integer multiples of the fundamental frequency (f_0). In several penguin species, the f_0 and its modulation over time, as well as the energy distribution through the harmonics that result from the natural resonances of the vocal tracts (formants; [45,46]), are known to encode species identity (e.g. [31]), individual identity (e.g. [37,44]) and body size information [40,43]. Previous studies have also examined the presence of the 'two-voice system' (a biphonation mechanism) in the display songs of the penguin species belonging to the genus *Aptenodytes* (i.e. the emperor penguin and the king penguin; [47,48]). The evolution of this signal has been explained as an extreme adaptation of these non-nesting species to a breeding ecology where individuals have few, if any, landmarks to meet. Indeed, the beat generated by the interaction of two fundamental frequency components encodes a robust individual signature while propagating efficiently in a noisy and crowded environment [48,49]. Recently, evidence for two-voice phonation has also been found in at-sea surface calls of African penguins, *Spheniscus demersus* [32]. However, because the tracheobronchial syrinx of penguins contains two distinct and independent sound sources located on the internal side of each primary bronchus [50], two-voice phonation in penguins is likely to result from coordination between the syrinx and respiratory system rather than passive dynamic vibratory properties of the oscillators (labia) on each side of the syrinx, contrasting with the mechanism of biphonation observed in mammals.

Several adaptive functions have been proposed for NLP in animal vocalizations, including the possibility to increase vocal complexity without complex neural control [2], assist individual recognition [51], encode arousal or distress in vocalizations [52,53] and avoid habituation to certain call types (i.e. 'unpredictability hypothesis'; [4,54]). Another suggested function is providing an honest or deceptive cue regarding size. Subharmonics can reduce the perceived frequency, potentially creating a misleading impression of size [3,4]. Alternatively, deterministic chaos reveals formant structure in vocalizations [4], accurately conveying body size information in many mammals [55–57]. Moreover, the intricate signals produced through NLP can increase vocal diversity among individuals, potentially influencing sexual selection in songbirds [2,13,21]. Emerging at the threshold of acoustic stability within the vocal tract, NLP may reflect an individual's fitness [58], supported by their increased occurrence in individuals with poorer health [3,59]. Previous studies have also suggested that NLP occurrences are more frequent in the vocalizations of juveniles and subordinate individuals, potentially indicating age or arousal status [3,4,60,61]. Finally, in humans and other mammals, dysphonia and other vocal disorders caused by irregularities in vocal fold vibration are characterized by the presence of NLP [59,62]. Therefore, in recent years, there has been increasing attention on the identification and analysis of these phenomena in pathological human voices, as this approach promises to develop early and non-invasive diagnostic methods for laryngeal pathologies [63–65].

Here, we present the first quantitative investigation of NLP occurrence and its possible function in penguins. Specifically, we investigated the presence of NLP in the begging calls of the African penguin. In line with the previously proposed adaptive functions of NLP, we expected to find the occurrence of NLP in a high percentage of chicks' begging calls to make the signal difficult for parents to ignore. We also predicted that NLP should increase in chicks contracting a respiratory disease (for example, bacterial infections or aspergillosis) that could affect the vibration dynamics of the oscillators (syringeal membranes) in the vocal organ.

2. Material and methods

We recorded begging calls from African penguin chicks aged between 1 and 63 days, hosted at the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB, Cape Town, South Africa). We collected vocalizations during the 2022 and 2023 breeding seasons using a focal animal sampling method [66]. We recorded the birds using a Zoom SGH-6 hypercardioid microphone (flat frequency response 20 Hz–20 kHz) placed approximately 1 m from the vocalizing individuals to capture good signal-to-noise vocal sequences. We also confirmed the identity of the emitter using a simultaneous video recording. The

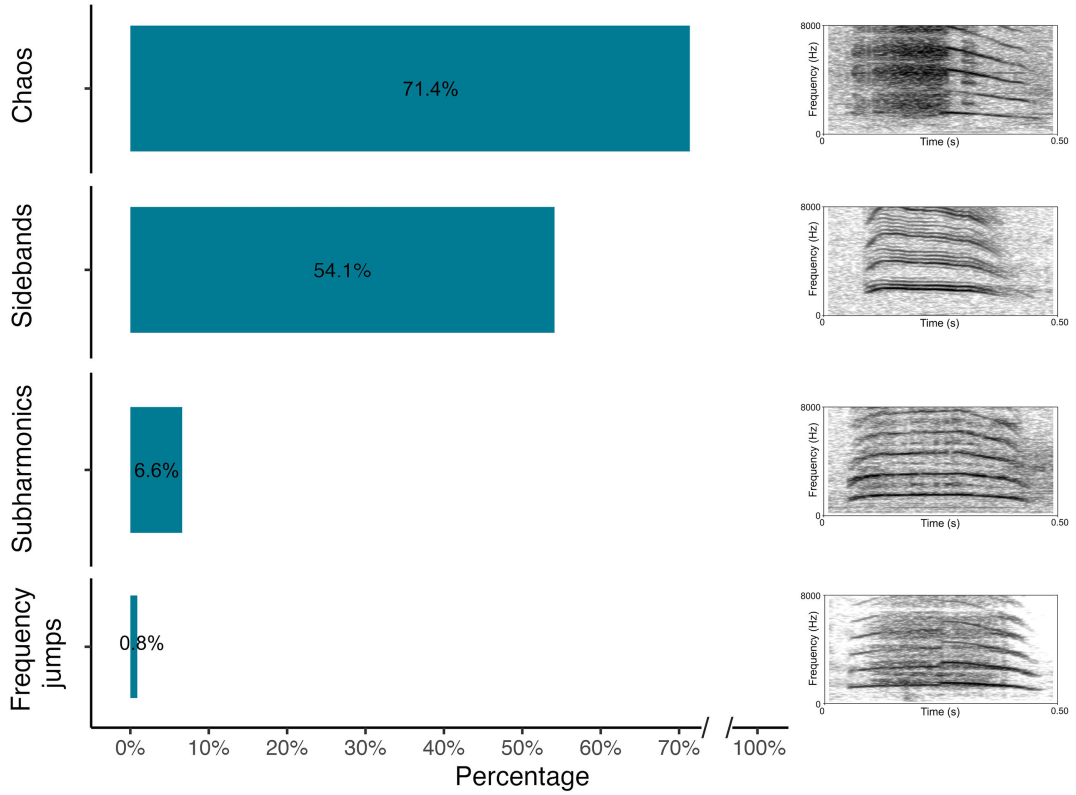

Figure 1. Barplot showing the percentages at which each category of nonlinear vocal phenomena (NLP) was found in the begging calls. Spectrograms of a begging call containing the respective NLP category are depicted on the right side of each bar. Spectrograms were generated in Praat v.6.3.09 [69] with the spectrogram settings used for the acoustic analyses (view range (Hz): 0–8000; window length (s):0.02; dynamic range (dB): 60).

microphone output signal was digitized using a Zoom F1 professional recorder at a 44.1 kHz sampling rate and saved into an internal Secure Digital High Capacity (SDHC) memory card (30 MB s^{-1} write speed) in a Waveform Audio File Format (WAV) with 16-bit amplitude resolution.

Each penguin was categorized as either 'Healthy' or 'Sick', and its vocalizations were recorded only in its respective health status: healthy chicks were those that exhibited no signs of avian influenza or respiratory diseases throughout the data collection period, whereas sick chicks were identified by displaying symptoms of respiratory diseases, such as crackling noises when breathing or difficulties breathing. These birds were treated by placing them in nebulizer stations where they inhaled diluted veterinary disinfectant solutions for extended periods of time [67]. Then, we selected three random recording sessions on different days for each penguin. For the sick penguins, we randomly chose sessions between days when the penguins were undergoing medical treatment. This approach ensured a balanced representation of calls for each penguin while accounting for potential variations in vocal behaviour across different time points. We further refined our 'full dataset' within each recording session by randomly choosing 20 vocalizations per penguin. This methodological framework aimed to enhance the robustness and reliability of our analysis by promoting diversity in both temporal and call-specific dimensions. Furthermore, we constructed a 'health dataset' to determine whether the presence of NLP was associated with respiratory disease or baseline morphological variability among individual chicks. This dataset included begging calls from the periods of illness and at least 8 days before any symptom onset when the chicks were considered healthy. We chose the 8 day period as it aligns with the upper limit of the incubation period for avian respiratory infections like aspergillosis [68]. The selection of calls for this dataset followed the same criteria as those used for the 'full dataset'. At the end of the call selection, the 'full dataset' consisted of 1781 begging calls from 91 chicks (*N* healthy chicks = 74, *N* calls = 1442; *N* sick chicks = 17, *N* calls = 339). Besides, the 'health dataset' consisted of 120 begging calls from 6 chicks. Each chick was represented with 10 calls emitted in the healthy condition and 10 calls emitted in the diseased condition, respectively.

(a) Acoustic analysis

For both datasets, we extracted the randomly selected begging calls from the original WAV files, including 0.25 s before and after the call for background noise assessment. Subsequently, we visually inspected the spectrogram of each call in Praat v.6.3.09 [69] to detect the presence of NLPs with standardized spectrogram settings (view range (Hz): 0–8000; window length (s): 0.02; dynamic range (dB): 60). Since visual analysis of spectrograms can be subjective, mainly when conducted by multiple observers, we assessed the inter-rater agreement between two observers (I.M. and C.T.) regarding their annotations on 10% (i.e. 195 calls) of the dataset before proceeding to analyse the entire dataset. The agreement was quantified using the unweighted kappa statistic, yielding a kappa value of 0.985 ($z = 13.9$, p-value < 0.001), indicating an almost perfect level of agreement [70]. Subsequently, the observers proceeded to analyse the entire dataset, annotating the presence of NLP and categorizing it into

Table 1. Generalized linear mixed models used for the analyses. NLP, nonlinear vocal phenomena.

	response variable	fixed factors	random factors	dataset
model$_1$	NLP (presence/absence)	status (healthy/sick)	chicks' identity	full ($n = 1781$)
		age (days)	sequences' identity	
model$_2$	NLP (presence/absence)	status (healthy/sick)	chicks' identity	health ($n = 120$)
			age (days)	
model$_3$	chaos (presence/absence)	status (healthy/sick)	chicks' identity	reduced (only the begging calls that contain NLP; $n = 1240$)
			sequences' identity	
model$_4$	sidebands (presence/absence)	status (healthy/sick)	chicks' identity	reduced (only the begging calls that contain NLP; $n = 1240$)
			sequences' identity	
model$_5$	subharmonics or frequency jumps (presence/absence)	status (healthy/sick)	chicks' identity	reduced (only the begging calls containing NLP; $n = 1240$)
			sequences' identity	
model$_6$	duration of the NLP normalized on the call duration	status (healthy/sick)	chicks' identity	reduced (only the begging calls containing NLP chaos, sidebands and subharmonics: $n = 1230$)
			sequences' identity	

chaos, subharmonics, sidebands or frequency jumps. The observers also measured the call duration, the duration of chaos, subharmonics and sidebands and they calculated the normalized duration of NLP for each call.

(b) Statistical analysis

To investigate which factors could influence the occurrence of NLP in begging calls, we ran on the 'full dataset' a generalized linear mixed model (GLMM; *glmmTMB* R-package; [71]) in R v. 4.3.1 [72] with the binomial factor presence/absence of NLP as the response variable (model$_1$). We used the health status (healthy/sick) and chicks' age in days as fixed factors. The chicks' and the sequences' identities were the nested random factors. Then, to check whether the presence of NLP was associated with the presence of respiratory disease or with the baseline inter-individual morphological variability of the chicks, we ran a second GLMM on the 'health dataset', using the binomial factor presence/absence of NLP as the response variable (model$_2$). The health status (healthy/sick) was the fixed factor, while chicks' age in days and their identities were the nested random factors. Finally, to understand whether the status of the chicks could be predicted by the general presence of NLP, by one of the most present types of NLP (chaos and sidebands) or by the other NLP categories, we built three other GLMMs on a 'reduced dataset' comprising only the begging calls containing NLP (n = 1 240). As the response variables, we used the presence/absence of each NLP category (model$_3$, model$_4$ and model$_5$), respectively. Finally, in model$_6$ we tested whether the NPL duration could predict the chicks' status, and we further reduced the dataset by including only the NLP categories with a measurable duration (chaos, sidebands and subharmonics; n = 1230). The duration of the NLP normalized on the call duration was the response variable (model$_6$). In the cases where there was more than one NLP present in the call, we calculated the sum of the NLP durations and normalized this measure based on the duration of the call. In each model, the health status of the chicks was the fixed factor, while the individuals and sequence identities were the nested random factors. In table 1, we summarized the structure of the six models built for the analysis. Importantly, no collinearity has been found in the models between the fixed factors (VIF_{min} = 1.00; VIF_{max} = 1.41; *check_collinearity* R-function; *performance* R-package; [73]). For the first two models, we used the likelihood ratio test (analysis of variance with argument test 'Chisq'; [74]) to verify the significance of each full model against a null model comprising only the random factors [75]. For the last four models, we verified the significance of each full model by comparing it against a control model comprising age as a fixed factor and the random factors [75]. Then, the p-values for the individual predictors were calculated based on the likelihood ratio tests between the full and null models using the R-function *drop1* [76].

3. Results

We found the presence of NLP in a significant proportion of the begging calls, with NLP being identified in 70% of the recorded instances. Within this subset, chaos was observed in 71.4% of cases, sidebands in 54.1%, subharmonics in 6.6% and frequency jumps in 0.8% (figure 1). In 32.3% of cases, we observed that begging calls encompass multiple categories of NLP. Notably, deterministic chaos and sidebands emerge as the two most prevalent categories of NLP and they frequently co-occur within the same begging calls, representing 26.5% of the total occurrences. Further statistical analysis elucidated various factors that influence the occurrence of NLP. Notably, a comparison between the model$_1$ and the null model revealed a significant difference between them (χ^2 = 14.636; d.f. = 2; p-value < 0.001), suggesting that sick penguins exhibited a higher frequency of NLP compared with their healthy counterparts (figure 2). Additionally, older chicks tended to produce more instances of NLP than younger chicks (figure 2). Detailed estimates, standard errors (s.e.), odds ratios, z-values and corresponding p-values can be found in table 2.

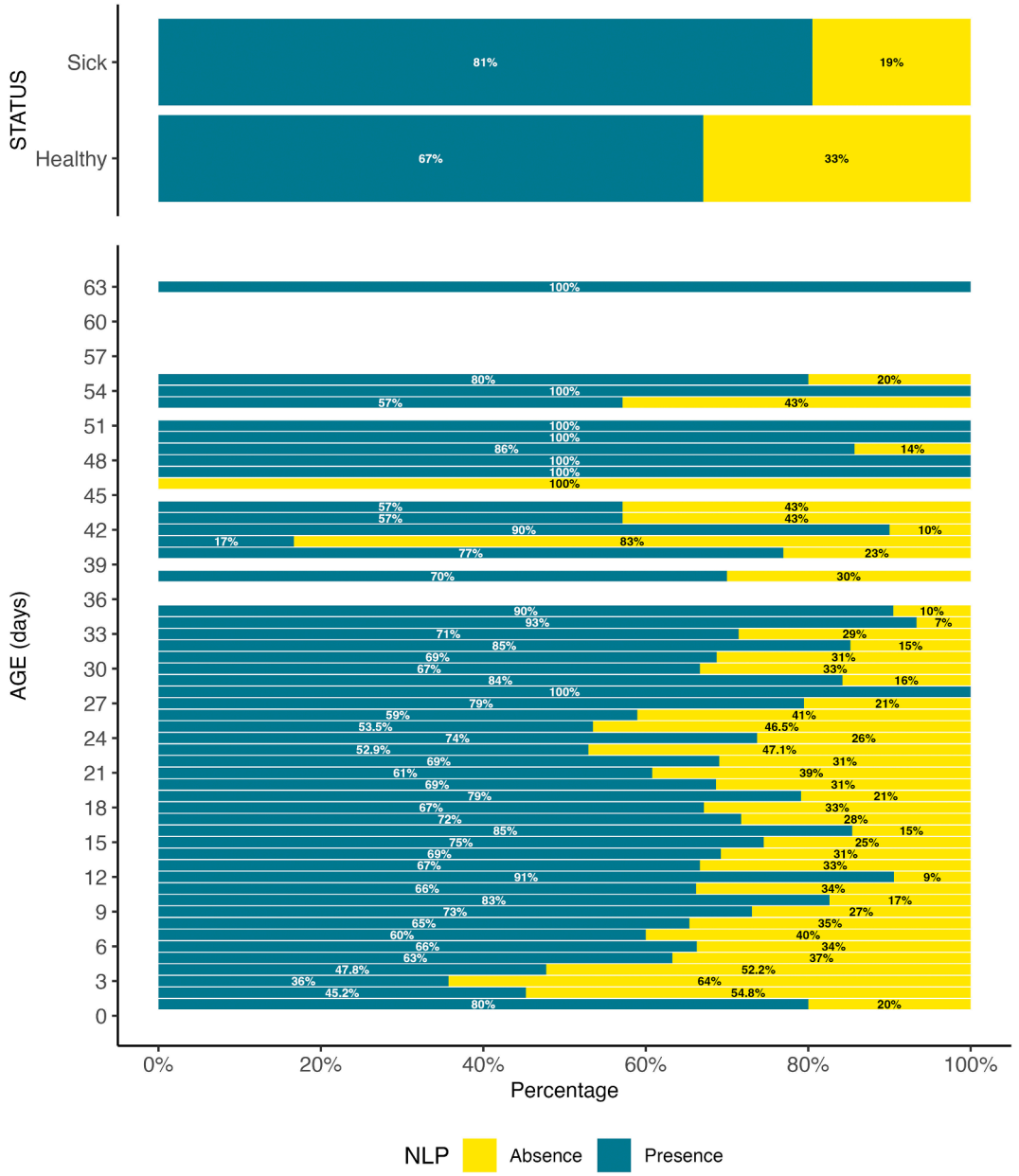

Figure 2. *(a)* Barplot showing the percentages of presence and absence of nonlinear vocal phenomena (NLP) in the begging calls of sick and healthy chicks. *(b)* Barplot showing the percentages of presence and absence of NLP across the age (days) of the chicks. In each plot, the presence of NLP is depicted in blue, while the absence is in yellow.

We then performed the statistical comparison between $model_2$ and the null model, exploring the potential association between the occurrence of NLP and respiratory disease ($\chi^2 = 4.468$; d.f. = 4; p-value = 0.034). We found that chicks exhibited a higher frequency of NLP during periods of illness compared with their pre-illness state before infection with the respiratory disease (estimate ± s.e. = 1.280 ± 0.613; odds ratio = 3.596; z-value = 2.087; p-value = 0.036). Finally, the health status (i.e. presence of respiratory infections) of the chicks did not appear to influence the occurrence of any specific NLP category in the begging calls (chaos: $model_3$ versus null model: $\chi^2 = 0.020$; d.f. = 5; p-value = 0.887; sidebands: $model_4$ versus null model: $\chi^2 = 0.224$; d.f. = 5; p-value = 0.635; subharmonics and frequency jumps: $model_5$ versus null model: $\chi^2 = 0.629$; d.f. = 5; p-value = 0.427). However, we made a noteworthy observation regarding the duration of NLP in sick penguins ($model_6$ versus null model: $\chi^2 = 3.925$; d.f. = 6; p-value = 0.0475). Indeed, we found that in sick penguins, NLP lasted longer compared with NLP in healthy chicks (estimate ± s.e. = 0.349 ± 0.174; odds ratio = 1.417; z-value = 2.001; p-value = 0.045).

4. Discussion

We investigated the occurrence of NLP in food solicitation signals of African penguin chicks. We found that NLP are widely present in the begging calls of this species (observed in >70% of the calls) but with remarkable differences in the relative presence of each NLP type. Indeed, while we found chaos and sidebands to be predominant, subharmonics were observed in a minority of the calls and frequency jumps were only observed with an incidence of 0.8%. Moreover, we found that more NLP often co-occur in the same call. This scenario appears to differ from the adult vocal repertoire, where calls are not

Table 2. Results of model$_1$ investigating which factors influenced the presence of NLP.

	estimate	s.e.	odds ratio	d.f.	*z*-value	*p*-value
(**intercept**)	0.546	0.216	[a]	[a]	2.531	[a]
status (sick)[b,c]	0.664	0.332	1.942	1	1.998	0.046
age	0.029	0.01	1.029	1	2.768	0.005

[a]Not shown as not having a meaningful interpretation.
[b]Estimate ± s.e. refers to the response difference between the reported level of this categorical predictor and the reference category of the same predictor..
[c]This predictor was dummy-coded, with the 'STATUS (healthy)' being the reference category.

substantially characterized by NLP [28,31,37,77,78]. Overall, our results align with previous studies in mammals, where apart from adult vocalizations [79–81], NLP have been proven to occur in human babies [82], dog pups [61], marmot pups [60], infant giant pandas [83] and infant African elephants [84]. One previous experimental study also documented a higher incidence of nonlinear sounds in zebra finches during song development [20]. According to the 'unpredictability hypothesis' [4], one possible explanation for our observations is that NLP in begging calls of African penguins may serve to increase the attention of adults, as the aperiodic chaotic structure makes them harder to ignore than predictable periodic calls of equal amplitude [54,60]. Indeed, begging has been linked to food intake and weight gain in African penguin chicks. Two-clutch broods show higher begging rates compared with single broods, and smaller B-chicks spend more time begging than larger A-chicks to receive sufficient food from the parents [85]. Together with previous research, these findings also suggest that the adaptive function of NLP in juvenile vocalizations may be ancestral and widespread among tetrapods [4].

Contrary to our expectations, we observed that NLP in begging calls increase with age, with early hatched chicks more frequently uttering vocalizations with a harmonic/periodic structure than older chicks. Penguins undertake a fast growing process to reach adult body size and fledge in approximately 60 days [86]. Although detailed studies about the ontogeny of the African penguin syrinx are not available, one could imagine that rapid and profound changes in the size of the vocal organ follow those observed for the skeletal and body dimensions. Thus, we could expect that the sizes of the syringeal membranes in pre-fledging and fledging chicks resemble those of the adults. However, until fledging, penguin chicks still need to produce high-pitch food solicitation signals to receive food from their parents [85], as food demands peak between 40 and 70 days [87]. Therefore, one possible explanation of our results is that ageing could increase NLP in vocalizations as bigger chicks force larger and thickness syringeal membranes to vibrate at high frequencies ($f_{o\ mean}$ of begging calls = 1851 ± 199 Hz; [28]), while those oscillators are fully grown for producing low-pitched calls of the adults ($f_{o\ mean}$ of the contact calls = 282 ± 25 [28]; 275 ± 22 Hz; [31]).

We found a significant increase in NLP when African penguin chicks are affected by respiratory illnesses while controlling for the age of the birds. We also observed that NLP lasted longer in infected chicks compared with chicks in healthy condition. In mammals, laryngeal nodules and polyps are known to affect the vocal folds' vibration pattern, resulting in pitch and amplitude perturbation (e.g. [88]). Bacterial infections causing oedema of the larynx mucosa are also known to cause dysphonia [89,90]. Similarly, a recent study in birds showed increasing chaos and subharmonics occurrence in the vocalizations of broiler chickens affected by bronchitis and paramyxovirus infections show increasing chaos and growing subharmonics occurrence in their vocalizations [91]. In the African penguin, severe fungal infections may cause nodules in the trachea, and bacterial infections generally cause respiratory distress in African penguin chicks (A. Snyman 2023, personal observation). Moreover, a herpesvirus-like infection in African penguins at SANCCOB was confirmed by identifying viral inclusions in the tracheal epithelium, but it remains unclear how many cases of respiratory disease can be attributed to this virus because several other diseases possibly affecting penguins can lead to signs of respiratory diseases [92,93]. Overall, our results provide further experimental evidence that bird calls can be used as a biomarker of health status, particularly for respiratory infections [94,95].

Most penguin species are currently declining and 11 species are threatened, according to the International Union for Conservation of Nature [96]. Among these, the African penguin is considered as one of the three most threatened penguin species in urgent need of conservation actions [97] and it might soon become the first penguin species to be classified as Critically Endangered by the IUCN [98]. The rehabilitation of oiled, injured and abandoned African penguins has been shown to be successful in bolstering the wild population [92,99,100]. SANCCOB's hand-rearing programme has released more than 9000 African penguin chicks back into the wild over the past decade [101], an action also listed in the African Penguin Biodiversity Management Plan [102] to halt the decline of the species. Between 2010 and 2013, about 40% of all deceased African penguin chicks at SANCCOB were judged to have died from respiratory diseases [103]. However, this rate has declined to about 20% between 2020 and 2023 owing to improved treatment (SANCCOB unpubl. data). The early detection of respiratory diseases in hand-reared chicks via the intensification of NLP could further improve rehabilitation success and thus the conservation efforts urgently needed to save the species from extinction.

Ethics. The Research and Ethics Committee of The Southern African Foundation for the Conservation of Coastal Birds provided ethical approval (no.REC2020/02) for recording the penguin chicks.

Data accessibility. The datasets used in this study are available from the open-access repository Zenodo [104].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. I.M.: conceptualization, formal analysis, funding acquisition, investigation, validation, writing—review and editing; A.Z.: conceptualization, formal analysis, methodology, software, supervision, visualization, writing—original draft; C.T.: formal analysis, investigation, validation, writing—review and editing; F.T.: data curation, methodology, supervision, validation, writing—review and editing;

F.B.: formal analysis, investigation, writing—review and editing; M.C.: project administration, supervision, writing—review and editing; K.L.: funding acquisition, project administration, resources, supervision, writing—review and editing; L.F.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—original draft.

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. This project was partly funded by the PADI Foundation grant n°68538 awarded to Livio Favaro. Francesca Terranova was supported by The University of Turin through a PON PhD scholarship n°DOT21BX3F7-8. During the writing of this manuscript, Anna Zanoli was supported by the EMBRC-UP project n°IR0000035, CUP C63C22000570001 entitled 'Unlocking the Potential for health and food from the seas' and Ilaria Morandi was supported by the 'Paolo Brancaccio 2023' memorial fellowship. SANCCOB is supported by a large variety of funders.

Acknowledgements. We acknowledge the support and expertise of the SANCCOB staff and volunteers during data collection, particularly Albert Snyman and David Roberts. We thank the Guest Editor and the three referees for their valuable comments on the manuscript.

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