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Short Communication

Acoustic cues to development of African Penguins (*Spheniscus demersus*) begging calls

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Avian begging calls mediate parent–offspring conflict and direct parental care to genetically related progeny. We found that the fundamental frequency of begging calls of African Penguins *Spheniscus demersus* decreases as the penguins age and gain mass, before reaching a lower plateau when the chick reaches about 1 kg. Our results suggest that the food solicitation signals of this species may inform parents of the offspring's body mass. Our results may also lead to the development of non-invasive tools for facilitating censusing chick growth in wild colonies.

Keywords: food solicitation signals, *banded penguins*, vocal ontogeny, vocal signalling.

Avian begging calls can mediate direct parental care to genetically related progeny (Caro *et al.* 2016, Davis *et al.* 2019) by advertising the chicks' motivation to obtain food, possibly honestly reflecting their feeding needs (Klenova 2015, Corney & Barber 2018). However, in the context of sibling competition, these food solicitation calls can also be exaggerated and so partially dishonest (Johnstone & Grafen 1993, Budden & Wright 2001, Caro *et al.* 2016). Understanding how 'honest' information about identity, developmental advancement and body dimension is encoded in offspring calls is an important research objective in avian vocal communication (Royle *et al.* 2002) and can enhance our understanding of parent–offspring conflict. Moreover, it can also lead to the development of non-invasive methods to monitor age-class composition and chick growth within wild populations.

African Penguins *Spheniscus demersus* are a monogamous species, with a strong breeding locality fidelity, and a *k*-selected reproductive strategy (MacArthur & Wilson 2001), characterized by heavy investment in each offspring (Borboroglu & Boersma 2015). In particular, the clutch of the African Penguin usually comprises only two eggs, differing in size (but see Crawford *et al.* 1999). However, the eggs show clear hatching asynchrony (mean hatching interval 2.1 days, range 1–4 days; Seddon & Heezik 1991), and the chick hatching from the bigger egg has a heavier body mass (range 0–12 g; Seddon & Heezik 1991). Previous studies showed that in the case of abundant food resources, both chicks have equal probability of fledging at 90 days with a weight of approximately 3 kg (Seddon & Heezik 1991). However, when food is scarce, parents must decide which sibling to invest in to maximize their genetic inheritance. In this context, from 42 to 90 days of life, the smaller and later-hatched chicks most often starve (Seddon & Heezik 1991). This strategy, known as the brood-reduction hypothesis (Lack 1947), is thought to be advantageous in environments with unpredictable fluctuations in food resources (Lack 1954). Although this strategy is common in penguins, the proximate causes guiding parents' decisions on which sibling to invest in remain unknown.

African Penguin begging calls are produced by the syrinx (King 1989), where the rate of vibration of the syringeal membranes leads to a source signal characterized by a fundamental frequency (f_o, Titze *et al.* 2015) responsible for the perceived pitch of the call (Favaro *et al.* 2014, 2015; Terranova *et al.* 2023). The dimension of the syrinx is likely to be allometrically constrained. Because larger and heavier oscillators tend to vibrate at lower frequencies (Gaunt & Gaunt 1985), source-related acoustic features may contain information about caller size. Accordingly, previous studies have demonstrated that in adult penguins, larger individuals produce lower-pitch calls (Favaro *et al.* 2017). Here, we investigated whether acoustic/size allometric relationships were also present during development when the emitters

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undergo a fast and considerable increase in body size and organ maturation (Miller *et al.* 2007, Lubbe *et al.* 2014, de Reus *et al.* 2022). Specifically, we investigated relationships between chick age, body mass and f_o descriptors in calls from 105 chicks aged between 1 and 66 days being hand-reared at a wildlife rescue centre. We assumed non-linear relationships between mass, age and acoustic parameters because structural and linguistic growth trajectories often show non-linear trends (Gould 1966, Cornec *et al.* 2022). We predicted that frequency components of the begging calls would negatively correlate with increases in body mass as the age of the animals increased.

METHODS

Penguin chicks and acoustic recordings

We recorded the begging calls of 125 immature African Penguins housed at the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) in Cape Town, South Africa, from February to April 2022. These birds were part of the Chick Bolstering Project (https://sanccob.co.za/projects/chick-bolstering-project/) and were hosted at the SANCCOB from egg hatching until release into the wild. Vocalizations were collected every day in the early morning (5:00–6:00 AM) after the daily routine of the birds' weighing. A staff member or volunteer placed the penguins on an electronic balance (mod. Ohaus CS 2000) on a table separate from the rest of the brood and weighed to the nearest 0.001 g. Each operation lasted 30 s to 1 min. To limit disturbance to the chicks, it was not possible to determine the sex of individuals or collect body size measurements.

Acoustic recordings were collected at a 44.1-kHz sampling rate using a RØDE NTG-4+ shotgun microphone connected to a ZOOM H5 digital recorder or a Zoom SGH-6 microphone connected to a Zoom-F1-LP audio recorder. The acoustic sensor was placed on a fixed tripod at approximately 1 m from the focal individuals.

To avoid sampling bias, we excluded from the final dataset penguins that died during the 3 months of data collection (n = 10), those diagnosed with respiratory or cachectic diseases (n = 6) and instances where it was not possible to record the body mass of the vocalizer (n = 4). This led to a final sample size of 105 individuals.

Acoustic analyses

We discarded from the analysis all the begging calls that showed excessive background noise (i.e. signal-to-noise ratio < 10 dB) or overlap with other birds vocalizing in the background. To avoid pseudoreplication, for the analyses, we selected only the first and the last begging calls of a sequence for each daily session per penguin recorded. Overall, the preliminary spectrographic inspection allowed us to select 529 begging calls (6.40 ± 3.91 sd calls per chick, 1.6 ± 0.42 sd calls per chick/day, 5.48 ± 3.01 sd days recorded per chick). We edited segments containing begging calls using Praat 6.3.10 (Boersma & Weenink 2023; spectrogram setting: view range, 0–10 000 Hz; window length, 0.02 s; time steps, 1000; frequency steps, 250; Gaussian window shape, dynamic range, 60 dB). Finally, using a custom-built script in Praat, we selected and extracted the fundamental frequency (f_o) contour of each call and measured the following acoustic parameters: f_o mean, Δf_o and Max f_o (described in Table S1).

Statistical analyses

Using R v. 4.3.1 (R Core Team 2021), we first tested for a correlation between the body mass and age of penguin chicks. As neither mass nor age had a normal distribution (checked with the Shapiro–Wilk normality test, 'shapiro.test' function) for the correlation, we used the Spearman rank correlation coefficient ('cor.test' function, method – Spearman). Then, we investigated the potential nonlinear association between penguins' mass, age and acoustic parameters using Generalized Additive Models (GAMs) and segmented regression techniques. The GAMs allowed for a more efficient consideration of nonlinear relationships, making it advantageous for modelling acoustic allometry through smooth functions instead of linear terms (MacLeod 2010, Holland *et al.* 2014, Winter & Wieling 2016, Gomez-Rubio 2018). To further test whether GAMs with segmented regression explained the association between penguins' mass, age and acoustic parameters better than linear models, we created Linear Mixed Models (LMMs, *lme4*; Bates *et al.* 2014) using the same dataset. We ran six LMMs by setting the acoustic parameters as the response variables, the mass or the age as fixed effects, and the chicks' identity as random factors. For each model, we checked the Gaussian distribution of the response variables (*fitdistrplus*; Delignette-Muller & Dutang 2015) and model residuals (*diagnostic.plot*; Estienne *et al.* 2017). We used a likelihood ratio test (*Anova* – 'Chisq' test argument; Dobson 2002) to test the significance of the models, comparing it against a null model comprising only the random factor (Forstmeier & Schielzeth 2011) and to estimate the P values of each predictor (*drop1*; Barr *et al.* 2013). Then, we constructed GAMs in R (R Core Team 2021) using the 'gam' function from the mgcv package (Wood 2011) and applied restricted maximum likelihood estimation. Secondly, we used segmented regression models (SRMs) to detect breakpoints indicating changes in acoustic

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parameters' trajectories. We initially developed linear models for each acoustic parameter using the 'lm' function and then estimated breakpoints using the 'segmented' function from the segmented package (Muggeo 2008). We instructed each model, including mass and age, to estimate a single breakpoint at 1 kg and 30 days, respectively. These measures approximately correspond to a plateau in the growth of flipper length and foot length, the earliest skeletal structures to reach the final adult size (Lubbe *et al.* 2014). We employed six GAMs and six SRMs. Model diagnostics, convergence and power of the models were investigated by examining residuals and using the 'gam.check' function from the mgcv package (Wood 2011) and are presented in Appendix S1. In each model, the response variable was the acoustic parameter, the predictor variable was the penguins' mass or age, and the random variable was the individual penguin's identity. As the Spearman coefficient showed a strong positive correlation between penguins' mass and age ($\rho = 0.99$, $n = 529$, $P < 0.0011$; Fig. S1), we could not include the two variables as predictors in the same model but used them in separate GAMs. Finally, we calculated the Akaike Information Criterion for all the models and compared them following the rule of thumb according to which a two-unit difference in AICs ($\Delta AIC = 2$) is moderate evidence of a difference in the models and more than four units ($\Delta AIC > 4$) is strong evidence of a difference (Burnham & Anderson 2002).

RESULTS

The GAMs provided a better fit than the LMMs, as indicated by lower AIC values across all analyses (Appendix S2). We found that the f_o descriptors exhibited highly nonlinear relationships with body mass (Table 1). The results of SRMs mirrored patterns observed in GAMs for f_o mean, Δf_o and Max f_o (Table 1). For f_o mean, Δf_o and Max f_o, immature penguins exhibited breakpoints at 1222.43 g, 1129.38 g and 1220 g, respectively (Table 1). SRMs indicated a decrease in these acoustic parameters to approximately 1 kg (Fig. 1), after which values for f_o mean, Δf_o and Max f_o reached a plateau (Fig. 2a–c). Appendix S1 shows the convergence and power of each model in detail.

We found that the f_o descriptors exhibited highly nonlinear relationships with age (Table 2). The results of SRMs mirrored patterns observed in GAMs for f_o mean, Δf_o and Max f_o (Table 2). For f_o mean, Δf_o and Max f_o, immature penguins exhibited breakpoints at 38.86 days, 35.32 days and 37.53 days, respectively (Table 2). SRMs indicated a decrease in these acoustic parameters with increasing chick age until approximately 30 days (Fig. 1), after which values for f_o mean, Δf_o and Max f_o reached a plateau (Fig. 2d–f).

DISCUSSION

This study investigated the relationships between body mass, age and the fundamental frequency of food solicitation calls of African Penguin chicks. Our results revealed relationships between mass, age and the acoustic parameters examined, up to a body mass of approximately 1.1–1.2 kg and an age of 35–40 days. A breakpoint was reached at this stage, and weight, age and acoustic parameters became more weakly correlated. In African Penguins, some skeletal structures (i.e. flipper length and foot length) reach adult size by 30 days, eventually weighing approximately 1 kg (Lubbe *et al.* 2014). Our results show that the chicks' development may be reflected in the acoustic characteristics of the begging calls. This suggests that, up to this specific limit, begging calls may constitute honest signals of the chicks' age and body mass.

In birds, parents do not deliver food to broods at a fixed rate, but at a rate determined by the characteristics of the begging calls (Bengtsson & Rydén 1981). Accordingly, in penguins, food allocation by parents returning from foraging trips is known to be influenced by sibling competition (Davis & McCaffrey 1989). Indeed, parents' breeding success, especially during scarcity of resources, is determined by their ability to determine which chick to invest in, when to invest in them and how much to invest. Our study provides the first evidence that 'honest' cues to body mass and age are encoded in the spectrotemporal features of food solicitation signals of the African Penguin. These vocalizations may inform parents about offspring's body mass and/or age, and so facilitate adequate food allocation, with obvious implications for their fitness. Moreover, African Penguins are burrow-nesting species, and during the breeding season, parents often stand in vigilance outside their nest, lacking visual contact with their chicks (Borboroglu & Boersma 2015). In this context, we can imagine that acoustic cues to body size could also complement visual cues in a cross-modal perception of the offspring (Baciadonna *et al.* 2021).

Although in some avian species the fundamental frequency of begging calls remains relatively stable from hatching until fledging (e.g. Red-crowned Crane *Grus japonensis* (Klenova *et al.* 2007, Klenova *et al.* 2010); Slender-billed Prion *Pachyptila belcheri* (Duckworth *et al.* 2009); Alcidae sp. (Klenova & Kolesnikov 2013)), our results align well with observations in species where the fundamental frequency decreases as development progresses (e.g. Anseriformes (Würdinger 1970, ten Thoren & Bergmann 1986, 1987, Engländer & Bergmann 1990); Charadriiformes (Adret 2012); Otidiformes (Cornec *et al.* 2022)). However, it is important to emphasize that the f_o values we observed are characterized by a high dispersion (Fig. 2) from the early days

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Table 1. Generalized Additive Models (GAM), Segmented Regression Model (SRM) and Estimated Breakpoint (EB) assessing non-linear associations of acoustic parameters with immature penguins' mass (g).

GAM					SRM							EB	
	edf	Ref.df	F	*P*-value	Est. S1	se S1	*t* value S1	Est. S2	se S2	*t* value S2	Pr(>|*t*|)	Est.	se
f_o mean	5.739	6.814	90.783	<0.001	−0.569	0.038	−14.77	0.044	0.097	−4.312	<0.001	1222.43	91.223
Δf_o	7.999	8.681	33.78	<0.001	−0.577	0.049	−11.57	0.096	0.12	−1.967	<0.001	1129.38	97.226
Max f_o	6.327	7.398	85.283	<0.001	−0.701	0.045	−15.42	0.084	0.114	−3.734	<0.001	1.22	84.121

The slope before and after the estimated breakpoint is provided in the SRM as S1 and S2, in which the *P*-values indicate that the two slopes are statistically different.

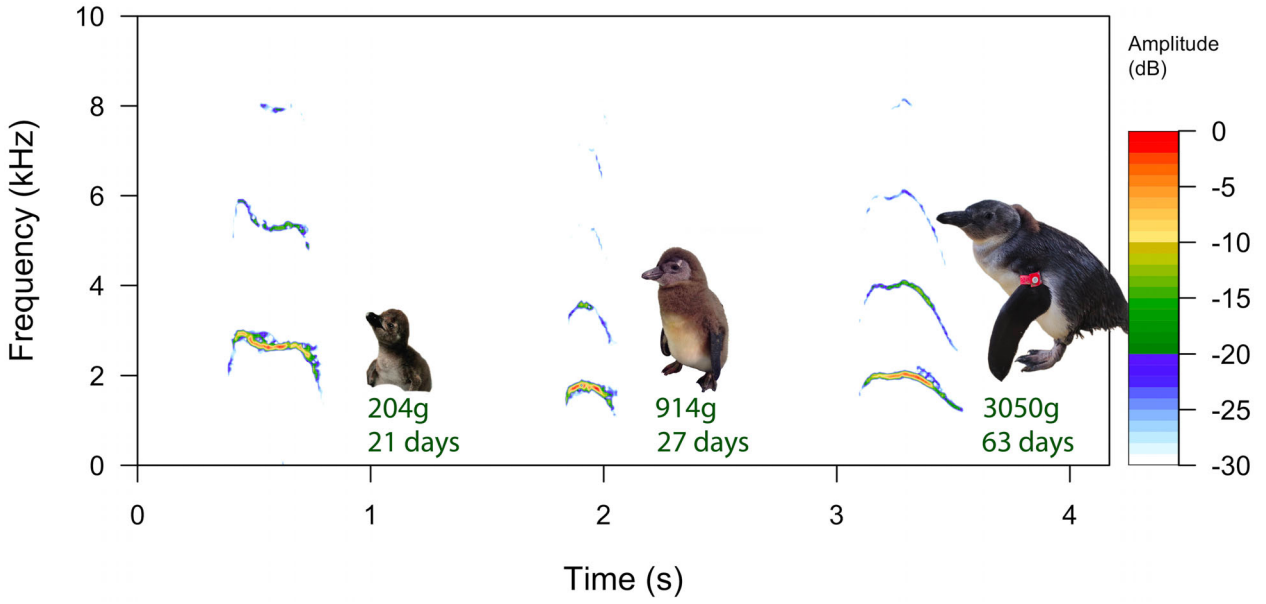

Figure 1. Example of fundamental frequency variation as a function of body mass and age in African Penguin chick AP078. The spectrogram was generated using the 'spectro' function of the Seewave R-package (Sueur *et al.* 2008). Fourier transform parameters included a sampling frequency of 44.1 kHz, a window length of 1024 and overlap between two successive windows of 50. Colour scale indicates the amplitude (dB) of calls.

after the chicks hatched. The experimental setting under which we collected vocalizations at SANCCOB did not allow us to study the potential effect of chick arousal and fatigue on variability of call acoustics. Yet, these may partially explain the observed f_o fluctuations. Future studies, using playback experiments, should investigate whether the breakpoint we found in the acoustic allometry of begging calls has a role in regulating the feeding by parents. Moreover, anatomical investigations correlating the size and thickness of syrinx membranes with fundamental frequency values would be necessary to determine whether and which anatomical constrictions limit the acoustic signal's fundamental frequency (particularly Max f_o). In several bird species, during ontogeny, the vocal apparatus of chicks and fledglings undergoes continuous changes in size and development, directly influencing the acoustic parameters of their vocalizations (Volodin *et al.* 2007). These modifications in the vocal organ are expected to be reflected in the acoustic characteristics of juveniles' calls until they eventually reach adult vocal patterns.

In penguins, adult vocalizations (and particularly display songs) have been shown to provide acoustic cues to the emitter's body size. For instance, in the Little Penguin *Eudyptula minor* and the Adélie Penguin *Pygoscelis adeliae*, adult male skeletal size negatively correlates

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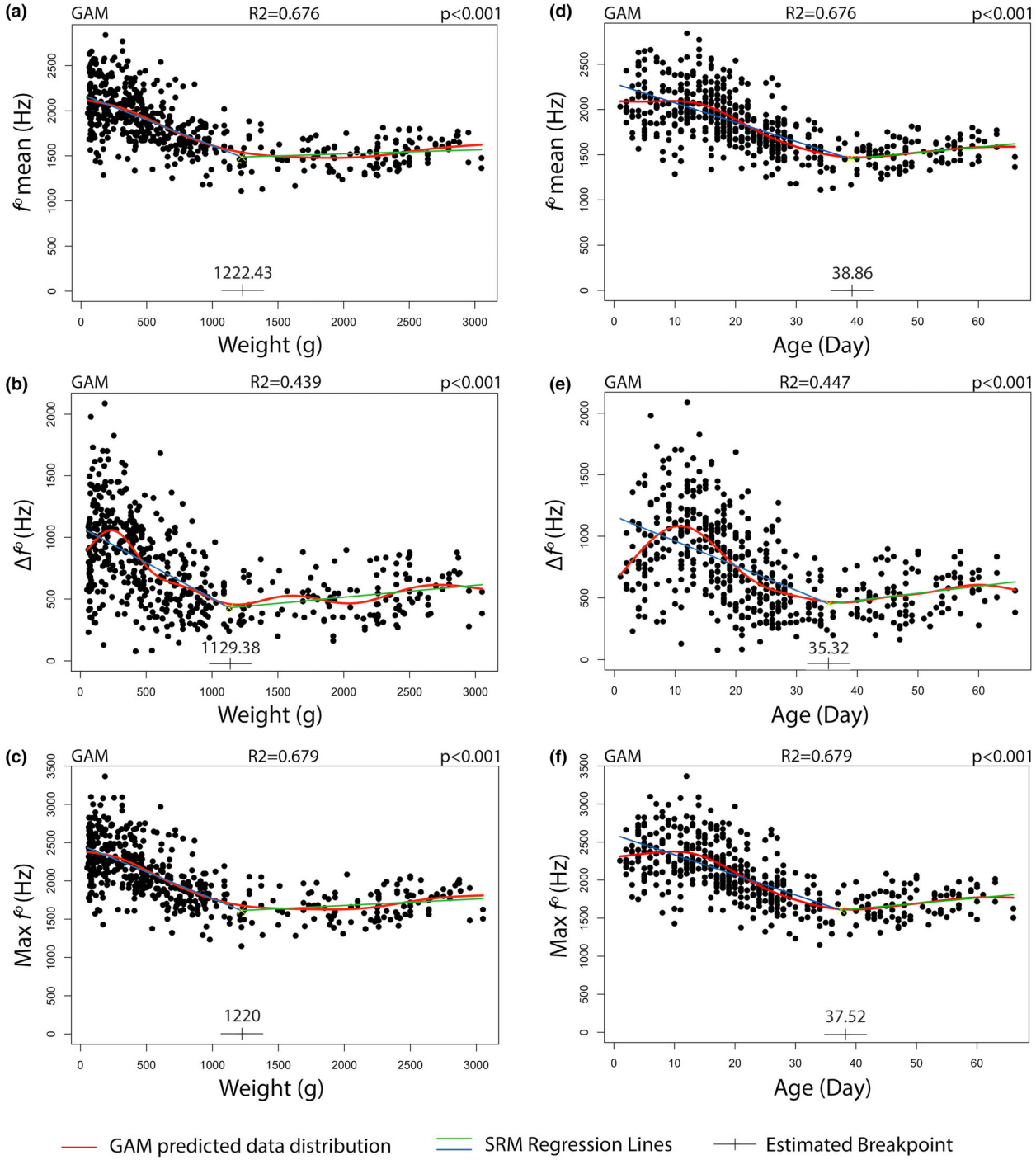

Figure 2. Relationship between acoustic parameters and body mass and age. Estimated functional relationship between (a) f_o mean, (b) Δf_o, (c) Max f_o and weight using Generalized Additive Models (GAMs). Estimated functional relationship between (d) f_o mean, (e) Δf_o, (f) Max f_o and age using GAMs. In each plot, points represent the real data distribution. The red line shows the GAM-predicted data distribution. Green and blue lines represent the slope found with the Segmented Regression Model with the relative estimated breakpoint (yellow cross). Estimates for both slopes are given in Tables 1 and 2.

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Table 2. Generalized Additive Models (GAM), Segmented Regression Model (SRM) and Estimated Breakpoint (EB) assessing non-linear associations of acoustic parameters with immature penguins' age (days).

GAM					SRM							EB	
	edf	Ref.df	F	*P*-value	Est. S1	se S1	*t*-value S1	Est. S2	se S2	*t* value S2	Pr(>|*t*|)	Est.	se
f_o mean	6.071	7.151	86.721	<0.001	−21.38	1.387	−15.409	6.081	5.201	−8.209	<0.001	38.86	2.008
Δf_o	7.042	8.008	37.721	<0.001	−20.078	1.796	−11.181	5.752	6.146	−5.244	<0.001	35.322	2.716
Max f_o	6.339	7.405	85.519	<0.001	−26.435	1.668	−15.848	7.115	6.092	−8.264	<0.001	37.523	1.991

In SRM, S1 and S2 indicate the slope before and after the estimated breakpoint, respectively, and the *P*-values indicate that the two slopes are statistically different.

with dominant frequencies (Miyazaki & Waas 2003, Waas 2006), which also reliably predict the condition and breeding success of the males (Marks *et al.* 2010). In Humboldt *Spheniscus humboldti* and Magellanic *Spheniscus magellanicus* Penguins, heavier males emit longer and low-pitched ecstatic display Songs (Favaro *et al.* 2017). Our results suggest that in the family Spheniscidae, body size indications are encoded in the pitch of the vocalizations from the earliest stages of development but that the honesty of this information is a function of vocal type and age.

The correlation between f_o and body mass in begging calls reported here could allow us to assess the mass and age of wild individuals at early developmental stages (Morten *et al.* 2017) and to improve the rehabilitation outcomes of rescued and hand-reared chicks (Sherley *et al.* 2014, Vanstreels *et al.* 2019), contributing to the overall success of the management practices for this endangered species. One limitation of our study is the lack of skeletal measures collected on the chicks that would allow a calculation of the proportion of the body mass available in the form of metabolizable energy reserves (i.e. body condition). Further research should investigate whether the body condition of African Penguin chicks can be inferred from fundamental frequency parameters in early-hatched chicks and so complement the index of Lubbe *et al.* (2014), currently limited to chicks with head length greater than 75 mm (i.e. approximately 1 kg body weight). Assessing the body condition of hatchlings could have significant practical applications. Rescuing abandoned chicks in low body condition has been identified as an important conservation intervention in the African Penguin Biodiversity Management Plan (Department of Environmental Affairs 2013). In recent years, the body condition of African Penguin fledglings has also been successfully used to investigate whether fishing restrictions positively impact African Penguin populations (Sherley *et al.* 2018). We hope that our study could spark further research in this direction and contribute to developing reliable and non-invasive approaches for managing this endangered species.

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AUTHOR CONTRIBUTIONS

Anna Zanoli: Methodology; software; data curation; investigation; validation; formal analysis; visualization; writing – original draft; writing – review and editing. **Chiara Tenneriello:** Conceptualization; data curation; investigation; writing – review and editing. **Ilaria Morandi:** Conceptualization; data curation; investigation; writing – review and editing. **Francesca Terranova:** Software; data curation; investigation; writing – review and editing. **Melissa Cadman:** Resources; funding acquisition; writing – review and editing. **Katrin Ludynia:** Conceptualization; funding acquisition; resources; writing – review and editing. **Nicolas Mathevon:** Methodology; funding acquisition; supervision; writing – review and editing. **David Reby:** Methodology; supervision; funding acquisition; writing – original draft; writing – review and editing. **Livio Favaro:** Conceptualization; methodology; supervision; funding acquisition; writing – original draft; project administration; writing – review and editing.

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ETHICAL NOTE

The study was approved by the Research and Ethics Committee of the SANCCOB (approval no. REC2020/02).

CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

Data Availability Statement

Detailed data can be obtained from https://zenodo.org/doi/10.5281/zenodo.8398411 upon request.

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SUPPORTING INFORMATION

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Table S1. Acoustic parameters measured on the f_o contour of begging calls.

Figure S1. Scatter plot showing the correlation between penguins' age and weight.

Appendix S1. Details of the convergence and power of each GAM used for the analysis.

Appendix S2. Linear Mixed Model results and AIC comparisons.

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