


Short Communication

Passive acoustic monitoring of the endangered African Penguin (*Spheniscus demersus*) using autonomous recording units and ecoacoustic indices

LIVIO FAVARO,*^{1,2}  ELEONORA CRESTA,¹

OLIVIER FRIARD,¹ KATRIN LUDYNIA,^{3,4}

NICOLAS MATHEVON,² LORIEN PICHEGRU⁵ 

DAVID REBY²  & MARCO GAMBA¹ 

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

²Equipe de Neuro-Ethologie Sensorielle ENES/CRNL, CNRS UMR5292, INSERM UMR_S 1028, University of Saint-Etienne, Saint-Etienne, France

³Southern African Foundation for the Conservation of Coastal Birds (SANCCOB), Cape Town, South Africa

⁴Department of Biological Sciences, University of Cape Town, Cape Town, South Africa

⁵Institute for Coastal and Marine Research, Nelson Mandela Metropolitan University, Port Elisabeth, South Africa

African Penguins *Spheniscus demersus* are endangered and declining seabirds which make extensive use of vocal signals for intra-specific vocal communication. Accordingly, passive acoustic monitoring tools could be developed as robust population monitoring methods that cause minimal disturbance to the birds. In this study, we collected soundscape recordings at the Stony Point penguin colony (Betty's Bay, South Africa) during the breeding season in 2019 to document the circadian rhythms of vocal activity of this species and to investigate whether the magnitude of variation of three different ecoacoustic indices correlates with the number of ecstatic and mutual display songs counted in recordings, which might inform on the breeding activity of the colony. Indeed, whereas ecstatic display songs are produced

by males during intersexual competition and territorial defence, mutual display songs are given by parents returning to the nest after foraging trips. We found that the vast majority of the display songs (> 80%) occurred between 04:00–08:00 and 17:30–21:30 h. We also found that the Acoustic Entropy Index was a good predictor of the number of penguins' songs within a recording. Overall, our study shows that African Penguins vocalizations have the potential to assist the monitoring of this species while minimizing disturbance.

Keywords: bioacoustics, ecoacoustics, penguins, seabirds, soundscape, *Spheniscus*.

Passive acoustic monitoring using autonomous recorders offers a modern, powerful and non-invasive alternative to traditional methods for studying wildlife presence, activity and distribution (Gibb *et al.* 2019). Automated analysis of environmental recordings has been shown to be particularly useful in the case of remote and endangered seabird colonies (Arneill *et al.* 2019) because it minimizes the costs and the disturbance to the animals (Buxton & Jones, 2012, Borker *et al.* 2014, Oppel *et al.* 2014), while increasing the scale and efficacy of the detections (Borker *et al.* 2015).

Several ecoacoustic indices have been developed to extract and analyse the biophonic component (i.e. animal vocalizations, mostly occurring within the frequency range 0.1–8 kHz) from large datasets of soundscape recordings (Sueur *et al.* 2014). Among these, the Acoustic Complexity Index (ACI; Pieretti *et al.* 2011), the Acoustic Entropy Index (HI; Sueur *et al.* 2008) and the Acoustic Richness Index (ARI; Depaetere *et al.* 2012) have been shown to be particularly sensitive to environmental recordings dominated by bird calls and thus have become the method of choice in a variety of studies investigating avian diversity and distribution over space and time (Machado *et al.* 2017, Borker *et al.* 2020, Brownlie *et al.* 2020). In particular, the ACI measures the average absolute fractional change in signal amplitude from one frame to the next through a recording. This index characterizes the acoustic environments dominated by bird songs. The HI relies on the calculation of the total entropy of time waves, while the ARI relies on the temporal entropy of the sound, also taking into account the overall amplitude. Importantly, recent experimental evidence suggests that the combined use of multiple indices allows a far better understanding of the differences among acoustic scenes, as the relative magnitude of the variance of the different indices is far more informative than absolute values (Bradfer-Lawrence *et al.* 2019).

The African Penguin *Spheniscus demersus* is the only penguin species endemic to the African continent, with

*Corresponding author.
Email: livio.favaro@unito.it

Twitter: @LivioF_80

27 extant colonies breeding between Namibia and South Africa (Borboroglu & Boersma 2013). The species has been recently identified as one of the most critical in need of conservation among penguins (Boersma *et al.* 2019), as the global population is nowadays estimated at under 21 000 breeding pairs, down from over 1.5 million pairs in the early 1900s (Crawford *et al.* 2011). In this context, monitoring of population trends and activity is crucial to, *inter alia*, measure the success of management actions and keep track of the species population dynamics overall. However, the *African Penguin Management Plan* (DEA 2013) recommends that strict minimal disturbance must be ensured to limit the impacts of monitoring methods and researchers on this threatened species.

African Penguins make extensive use of vocal signals for intra-specific vocal communication (Favaro *et al.* 2016, McInnes *et al.* 2020). The vocal repertoire of adult African Penguins is made up of two discrete call types and two display songs (Favaro *et al.* 2014). Calls are single-unit vocalizations used to mediate agonistic interactions (agonistic calls) and or maintain acoustic contact (contact calls) among group members at sea (Jouventin 1982, Favaro *et al.* 2014). Display songs are complex sequences of short vocal units called 'syllables', given at land and characterizing the breeding season (Favaro *et al.* 2014, 2015). Display songs can be further divided into ecstatic display songs (vocalized mostly by males to attract females and territorial defence) and mutual display songs (vocalized by established pairs within their nest, primarily for recognition when joining after one of the members comes back from a foraging trip at sea) (Jouventin 1982, Favaro *et al.* 2014). Ecstatic and mutual display songs are acoustically distinct vocalizations (Favaro *et al.* 2014) and can be readily identified by visual inspection of spectrograms (Fig. S1).

By analysing a dataset of environmental recordings collected in a wild African Penguin colony using an autonomous recording system, we aimed to provide the first quantitative description of the diurnal variation in vocal activity of this species during the breeding season. Moreover, we aimed to investigate the extent to which three ecoacoustic indices correlate with the observed vocal activity of the penguins. We expected that the temporal variation of the ecoacoustic indices derived from the recordings should follow the temporal variation in the number of songs spectrographically identified. We also investigated whether the variation of the indices could be a useful predictor of the number of ecstatic display songs, which are an indicator of the number of active breeding males or the number of mutual display songs, and also peak as the birds return to the colony after foraging trips. If its reliability were to be confirmed, the analysis of the soundscape of African Penguin colonies through ecoacoustic indices could be used to develop a non-invasive and cost-effective passive

acoustic monitoring tool to assist the monitoring of this endangered species.

METHODS

Study site and acoustic recordings

The study site was the Stony Point penguin colony in Betty's Bay, South Africa (Appendix S1). Stony Point is one of the five main African Penguin breeding colonies in the Western Cape, along with Dassen Island, Robben Island, Simon's Town (Boulders Beach) and Dyer Island. Nowadays, the colony supports more than 1700 breeding pairs and is considered a site of national as well as international significance for the conservation of this species (Sherley *et al.* 2020).

We collected the acoustic recordings in 2019, over 55 days during the peak of the African Penguin breeding season (early March to late May), with a Song Meter 4 (SM4; Wildlife Acoustics, Inc.) mounted 1 m high on a fixed pole support in the centre of the penguin colony. The SM4 was equipped with two built-in omnidirectional microphones (flat frequency response 60–8 kHz \pm 2 dB; sensitivity -35 ± 4 dB re: 0 dB = 1 V/pa @ 1 kHz; pre-amplifier gain set to 26 dB). The gain of the recorder was 16 dB as a default setting, which is recommended to maintain the fidelity of weaker (far) vocalizations while maximizing dynamic range to handle louder (close) calls. The audio signal from each microphone was digitalized at a sampling rate of 44.1 kHz and saved into an internal Secure Digital memory card as a .WAV file (16-bit amplitude resolution). The recorder was scheduled with a duty cycle of 15 min of recording, followed by 15 min of sleep.

The total number of files recorded during the recording period was 2424. However, since the area of the Cape Peninsula is affected by strong wind gusts, we had to exclude 803 recordings showing evident waveform distortion (clipping), which would make unreliable both the counting of the vocalizations and the calculation of the ecoacoustic indices (Depraetere *et al.* 2012). Overall, the data sorting left us with a total of 1621 files, corresponding to 405 h of audio recordings.

Calculation of ecoacoustic indices and counting of vocalizations

For each file, the Fast Fourier Transform spectrogram was generated in PRAAT (v. 6.0.33) (Boersma 2001) (Gaussian window shape, view range = 0–8 kHz, window length = 0.02 s, dynamic range = 50 dB) and author E.C. counted the number of ecstatic display songs ($n_{\text{tot}} = 24\,041$; mean per file \pm sd = 14.84 ± 26.02) and mutual display songs ($n_{\text{tot}} = 7053$; 4.35 ± 7.84). Subsequently, 5% of the audio files were randomly chosen to

be inspected by a second blind observer with previous expertise in African Penguin vocalizations. The interobserver reliability for the number of display songs counted in each file was extremely high (Cohen's κ coefficient > 0.95 for both vocal types).

The audio files were then transferred to the OCCAM SuperComputer (Aldinucci *et al.* 2017) at the Competence Centre for Scientific Computing of the University of Turin for the calculation of the Acoustic Entropy, Acoustic Complexity and Acoustic Richness indices using the 'soundecology' (Villanueva-Rivera & Pijanowski 2018) and 'seewave' (Sueur *et al.* 2008) packages in R (R Core Team 2017). For the ACI, we set frequency limits of 0.2–8 kHz, corresponding to the frequency range in which display song components were detectable. All other parameters were left as default values.

Statistical analyses

To investigate whether the number of penguin vocal displays has an effect on the ecoacoustic indices, we built a series of generalized linear mixed effect models (GLMMs) using the 'lmer' package (Bates *et al.* 2014) in R v. 4.0.0 (R Core Team 2017). In turn, we included the values of the indices as the response variable and the number of ecstatic display songs (hereafter EDS) and mutual display songs (hereafter MDS) as fixed factors. We included the day and the hour of the day as random effects to control for repeated measurements. We used the timestamps to group recordings in 30-min bins (e.g. all recordings between 00:00 and 00:30 h were grouped in time bin 1, recordings between 00:31 and 01:00 h in time bin 2). Before running the models, we confirmed the absence of collinearity among predictors by examining the variance inflation factors (*vif* package, Fox & Weisberg 2011). We also looked at the distribution of the residuals plotted against the fitted values and a *qq-plot* to check the assumptions that the model residuals were normally distributed and homogeneous. Finally, using a likelihood ratio test (Dobson 2002), we tested the significance of a 'full model' comprising both the fixed and the random factors, against a 'null model'

comprising the random factor exclusively (Estienne *et al.* 2017, Gamba *et al.* 2017) (Table 1). We calculated the α -value for the predictor using the R-function 'drop1' (Barr *et al.* 2013).

RESULTS

Figure 1 shows an overview of the soundscape of the Stony Point penguin colony at different time scales. We found that the vocal activity of the penguin colony during the breeding season is mostly concentrated in two temporal windows (Fig. 2, see also Table S1). More specifically, we recorded 49% of the EDS and 35% of the MDS between 04:00 and 08:00 h, and 39% of the EDS and 47% of the MDS between 17:30 and 21:30 h. We also found that EDS are the vocalizations more frequently observed within the recordings, with a ratio between MDS and EDS of 1 : 3.4.

The GLMMs showed a statistically significant effect of the number of penguin songs within a recording on the magnitude of variance of the Acoustic Entropy Index (H, *full* vs. *null*: $\chi^2 = 180.94$, $df = 2$, $P < 0.001$) and the Acoustic Complexity Index (ACI, *full* vs. *null*: $\chi^2 = 213.54$, $df = 2$, $P < 0.001$), but not the Acoustic Richness Index (ARI, *full* vs. *null*: $\chi^2 = 5.10$, $df = 2$, $P = 0.078$). However, when looking more specifically at the effect of each single predictor on the response variable, we found a positive relationship between the H index variation and the number of EDS (estimate = 0.001, $se < 0.001$, $t = 9.82$, $P < 0.001$) and MDS (estimate = 0.001, $se < 0.001$, $t = 3.85$, $P < 0.001$), but a negative relationship between the ACI and the number of EDS (estimate = -0.001, $se < 0.001$, $t = -9.821$, $P < 0.001$) and MDS (estimate = -0.002, $se < 0.001$, $t = -4.526$, $P < 0.001$). To investigate this result further, we plotted the average variation of the HI, ACI and ADI over 24 h along with the average number of EDS and MDS recorded (Fig. 2). The visual representation reveals how the number of penguin songs strongly correlates with the daily fluctuation of the HI. Conversely, the highest values of the ACI occur between 09:00 and 16:00 h, when the penguin colony is mostly vocally inactive.

Table 1. Summary of the full vs. null generalized linear mixed effect models.

Ecoacoustic index	Model type	GLMM
Acoustic Entropy (H)	<i>full</i>	H ~ EDS + MDS + (1 timebins) + (1 day), family = gaussian
	<i>null</i>	H ~ (1 timebins) + (1 day), family = gaussian
Acoustic Complexity (ACI)	<i>full</i>	ACI ~ EDS + MDS + (1 timebins) + (1 day), family = gaussian
	<i>null</i>	ACI ~ (1 timebins) + (1 day), family = gaussian
Acoustic Richness (AR)	<i>full</i>	AR ~ EDS + MDS + (1 timebins) + (1 day), family = gaussian
	<i>null</i>	AR ~ (1 timebins) + (1 day), family = gaussian

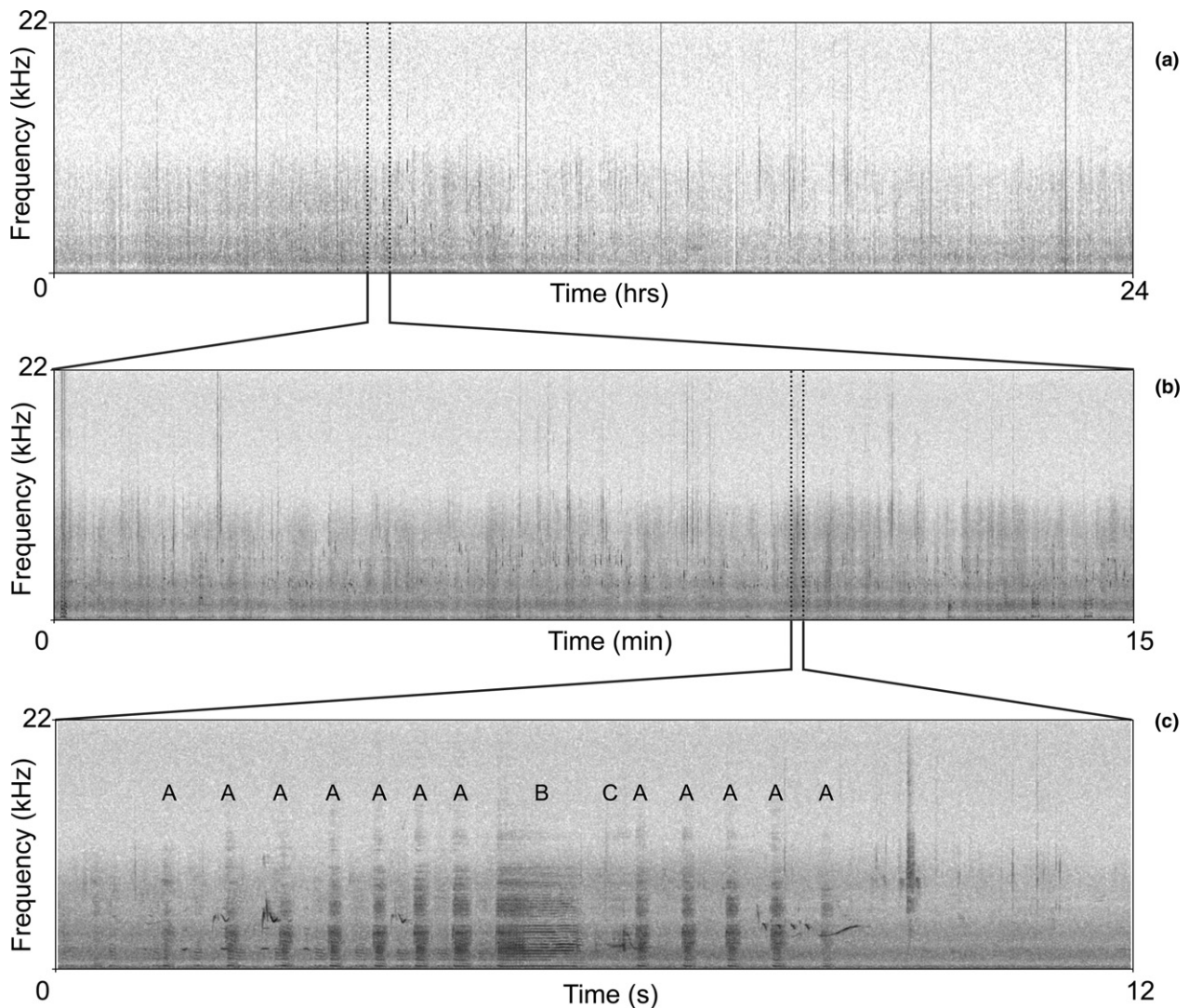


Figure 1. Daily packed spectrogram (a) of the Stony Point penguin colony (Betty's Bay, South Africa) on 23 April 2019. Recordings were collected with a duty cycle of 15 min (48 frames/day), x-axis 24 h, y-axis 22.05 kHz. Spectrogram (b) shows one single recording of 15 min that occurred between 07:30 and 07:45 h. Spectrogram (c) shows a focus on 12 s of sound where it is possible to observe an ecstatic display song emitted by an adult male African Penguin. Capital letters indicate the three syllable types constituting the song (for more details on the syllabic structure, see Favaro *et al.* 2014).

DISCUSSION

We report the first application of passive acoustic monitoring techniques to an extant wild African Penguin colony, based on the analysis of environmental recordings collected using an autonomous recording unit. We found that, during the breeding season, within a day African Penguins are mostly vocally active between 4:00–8:00 and 17:30–21:30 h. This is the first description of the pattern in frequency of vocalizations given by this species at a breeding site. We also observed that most of

the ecstatic display songs are given in the first window, while mutual displays are more abundant in the second one. We explain these circadian differences in penguin vocal behaviour as a result of the turnover of their breeding and foraging activities. African Penguins are diurnal foragers (Wilson 1985) and return to their colony at the end of the day until late at night (Wilson *et al.* 1988, Wilson & Wilson 1990), hence their mutual songs when re-joining the partner on the nest. Male-calling in the morning before departure could be related to a territorial display (Williams 1995).

Our findings show that the African Penguin peak in vocal activity in the day does not match those of other territorial and burrowing seabirds. For example, the acoustic activity of petrels (order Procellariiformes) is relatively constant overnight, with peaks of vocalizations dependent on the lunar phases and associated risk of predation rather than sunset–sunrise or specific hours of the day (Mougeot & Bretagnolle 2000). Audubon's Shearwaters *Puffinus lherminieri* exhibit a single daily peak of vocal activity, occurring 50–120 min after sunset and corresponding to the return of breeders from their foraging trips to their burrows (Bretagnolle *et al.* 2000). These findings have strategic implications for future applications of passive acoustic monitoring to the African Penguin, as they allow sampling (recording) to be concentrated on these specific hours to optimize the energy consumption and data storage on recording devices.

We then assessed the validity of several ecoacoustic indices against visual inspection of spectrograms. Confirming our expectations, we found that the magnitude of variation of the HI is influenced by the number of display songs occurring within a recording. This index relies on the combined calculation of both the temporal entropy and the spectral entropy of the sound (Sueur *et al.* 2008), and does not take into account the overall amplitude of the signal (Depraetere *et al.* 2012). From a practical standpoint, the values of the HI can vary between 0 and 1, with low values indicating an acoustic scene characterized by pure tones (or noise) and high values a scene dominated by harmonics, where the acoustic energy is apportioned across frequency bands (Sueur *et al.* 2014). Accordingly, we suggest that the acoustic structure of the African Penguin display songs (Favaro *et al.* 2014, 2015, 2020), with many harmonic frequencies covering a broad portion of the spectrum (0.2–8 kHz; Favaro *et al.* 2014), explains the effect of the number of vocalizations we observed within recordings and the increase of the HI values. Most importantly, our results demonstrate for the first time that the acoustic entropy can be used as a reliable indicator of the number of ecstatic display songs produced within a colony, which might reflect the number of reproductive males (Jouventin 1982, Favaro *et al.* 2014). We further suggest that acoustic entropy is suitable for estimating the relative number of mutual display songs and thus quantifying the foraging efficiency of pairs (Jouventin 1982), which determines their chick-rearing efficiency. Earlier return of the birds to the colony, detected via the timing of the peak in mutual display songs, could be

used as an indicator for shorter foraging trip duration, which can be an important indicator for better food availability (Petersen *et al.* 2006, Pichegru *et al.* 2010).

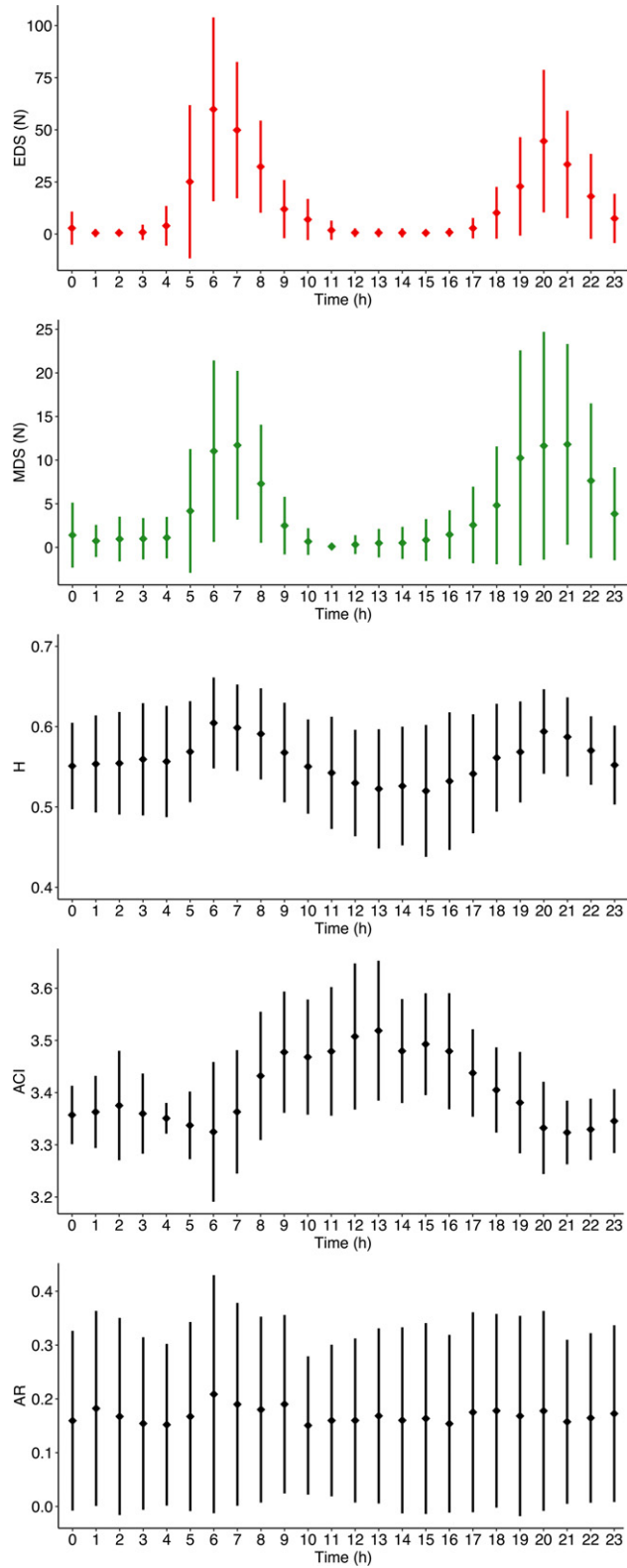
We recognize that one limitation of our study lies in the fact that every single male or couple may have uttered more than one display song in a temporal window corresponding to the duration of an acoustic recording (i.e. 10 min). Nevertheless, as penguin display songs encode acoustic cues to the individual identity of the emitter (Aubin & Jouventin 2002, Jouventin & Aubin 2002, Jouventin & Dobson 2017), further research effort should be directed toward estimating the relative abundance of the vocalizing individuals within a colony using individual spectral signatures.

Contrary to our expectations, we observed an inverse relationship between the daily variation of the ACI and the vocal activity of the penguins. According to Pieretti *et al.* (2011), the ACI is sensitive to rapid variations of intensity in each single frequency bin, a condition that is emphasized by the high-pitched bird songs. Therefore, we explain the higher values recorded for the ACI between 09:00 and 16:00 h as the result of the vocal activity of the variety of other birds observed in the surroundings of the colony. These include, but are not limited to, Egyptian Goose *Alopothen aegyptiaca*, Hadedda Ibis *Bostrychia hagedash*, Helmeted Guineafowl *Numida meleagris*, African Black Oystercatcher *Haematopus moquini*, Laughing Dove *Spilopelia senegalensis*, gulls (*Larus* spp.) and other birds (CapeNature pers. comm; Southern African Bird Atlas <http://sabap2.birdmap.africa>). In contrast, *Spheniscus* penguin display songs are low-pitched (Favaro *et al.* 2014, 2017) and characterized by a constant intensity, which results in a negligible variation of the ACI values. For these reasons, our results indicate that the ACI cannot be considered a reliable indicator of the vocal activity of wild African Penguins, at least where colonies are associated with a significant presence of other bird species.

Finally, we did not find a statistically significant effect of the acoustic activity of the penguins on the ARI. The ARI is based on the temporal entropy and the median amplitude envelope of the signal (Depraetere *et al.* 2012). As observed for the ACI, we suggest that the flat amplitude modulations over time of penguin songs only minimally affect the amplitude envelope of the recordings, and thus have little influence on the ARI.

To date, population monitoring of this species (numbers of breeding or moulting individuals) is still conducted by traditional counts, involving several persons walking carefully around a colony and individually

Figure 2. Ecstatic display songs (EDS) and mutual display songs (MDS) (mean per hour \pm sd) detected over the 24-h cycle at the Stony Point penguin colony along with the average variation of the Acoustic Entropy Index (HI), Acoustic Complexity Index (ACI) and Acoustic Richness Index (ARI). [Colour figure can be viewed at wileyonlinelibrary.com]



counting all nests, potential nests and moulting birds (e.g. Kemper 2009, Pichegru & Oosthuizen 2018). Passive acoustic monitoring could, therefore, further reduce the disturbance induced. Developing automated acoustic survey approaches for the African Penguin could also allow estimating presence, population sizes and mating/breeding activity of the colonies, while still minimizing any disturbance of the individuals. This is in line with the current development of passive monitoring for this species (e.g. McInnes 2016, McInnes *et al.* 2019). In particular, acoustic surveys could complement the currently trialled automated system comprising PIT (Passive Integrated Transponders) readers and weighbridges to assess foraging trip length and foraging success, especially in remote areas which cannot be visited regularly. Such important information might then be instrumental in assisting with decision-making and conservation policies for this species, which is nowadays considered in most critical need of conservation among penguins (Boersma *et al.* 2019). We hope that our study will stimulate further research in this direction.

The study was partially supported by the Regione Lazio (Italy) through a 'Torno Subito' scholarship (no. J86G16000160009) awarded to Eleonora Cresta and by an IDEXLYON fellowship (ANR-16-IDEX-0005) awarded to Prof. David Reby. The University of Turin provided the acoustic recording equipment through a System s.p.a. research grant for bioacoustics (no. PES_D_RIC_N_COMP_16_01). SANCCOB is supported by a wide range of local and international donors, including international zoos and aquaria, foundations and trusts, corporations and individuals. The research was conducted under a permit from CapeNature (permit number no. CN-44-59-6775) and in agreement with the current laws of South Africa and Italy.

AUTHOR CONTRIBUTION

Livio Favaro: Conceptualization (lead); Data curation (supporting); Formal analysis (equal); Funding acquisition (equal); Investigation (supporting); Methodology (lead); Project administration (lead); Resources (equal); Software (equal); Supervision (lead); Visualization (equal); Writing-original draft (lead); Writing-review & editing (equal). **Eleonora Cresta:** Conceptualization (equal); Data curation (lead); Formal analysis (supporting); Funding acquisition (equal); Investigation (lead); Project administration (equal); Validation (supporting); Writing-review & editing (supporting). **Olivier Friard:** Data curation (supporting); Formal analysis (lead); Software (lead); Writing-review & editing (supporting). **Katta Ludinya:** Conceptualization (supporting); Project administration (lead); Supervision (supporting); Visualization (supporting); Writing-review & editing (equal). **Nicolas Mathévon:** Funding acquisition (equal); Project administration (supporting); Resources (equal); Supervision (equal); Writing-review & editing (supporting). **Lorien Pichegru:**

Conceptualization (equal); Funding acquisition (supporting); Project administration (equal); Supervision (equal); Visualization (supporting); Writing-review & editing (equal). **David Reby:** Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Supervision (supporting); Writing-review & editing (lead). **Marco Gamba:** Conceptualization (supporting); Data curation (supporting); Formal analysis (lead); Methodology (equal); Software (lead); Visualization (equal); Writing-review & editing (equal).

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

- Aldinucci, M., Bagnasco, S., Lusso, S., Pasteris, P., Rabellino, S. & Vallero, S.** 2017. OCCAM: a flexible, multi-purpose and extendable HPC cluster. *J. Phys. Conf. Ser.* **898**: 082039.
- Arneill, G.E., Critchley, E.J., Wischnewski, S., Jessopp, M.J. & Quinn, J.L.** 2019. Acoustic activity across a seabird colony reflects patterns of within-colony flight rather than nest density. *Ibis* **162**: 416–428.
- Aubin, T. & Jouventin, P.** 2002. How to vocally identify a kin in a crowd: the penguin model. *Adv. Stud. Behav.* **31**: 243–277.
- Barr, D.J., Levy, R., Scheepers, C. & Tily, H.J.** 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. *J. Mem. Lang.* **68**: 255–278.
- Bates, D., Mächler, M., Bolker, B.M. & Walker, S.C.** 2014. *lme4: linear mixed-effects models using Eigen and S4 R package. Version 11-7.* Available at: <https://cran.r-project.org/web/packages/lme4/> (accessed 10 September 2020).
- Boersma, P.** 2001. Praat, a system for doing phonetics by computer. *Glott. Int.* **5**: 341–345.
- Boersma, P.D., Borboroglu, P.G., Gownaris, N.J., Bost, C.A., Chiaradia, A., Ellis, S., Schneider, T., Seddon, P.J., Simeone, A., Trathan, P.N., Waller, L.J. & Wienecke, B.** 2019. Applying science to pressing conservation needs for penguins. *Conserv. Biol.* **34**: 103–112.
- Borboroglu, P.G. & Boersma, P.D. (eds)** 2013. *Penguins: Natural History and Conservation. A Samuel and Althea Stroum Book.* Seattle, WA: University of Washington Press.
- Borker, A.L., Buxton, R.T., Jones, I.L., Major, H.L., Williams, J.C., Tershy, B.R. & Croll, D.A.** 2020. Do soundscape indices predict landscape-scale restoration outcomes? A comparative study of restored seabird island soundscapes. *Restor. Ecol.* **28**: 252–260.
- Borker, A.L., Halbert, P., Mckown, M.W., Tershy, B.R. & Croll, D.A.** 2015. A comparison of automated and traditional monitoring techniques for Marbled Murrelets using passive acoustic sensors. *Wild. Soc. Bull.* **39**: 813–818.
- Borker, A.L., McKown, M.W., Ackerman, J.T., Eagles-Smith, C.A., Tershy, B.R. & Croll, D.A.** 2014. Vocal activity

- as a low cost and scalable index of seabird colony size. *Conserv. Biol.* **28**: 1100–1108.
- Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G. & Dent, D.H.** 2019. Guidelines for the use of acoustic indices in environmental research. *Methods Ecol. Evol.* **10**: 1796–1807.
- Bretagnolle, V., Attie, C. & Mougeot, F.** 2000. Audubon's Shearwaters *Puffinus lherminieri* on Reunion Island, Indian Ocean: behaviour, census, distribution, biometrics and breeding biology. *Ibis* **142**: 399–412.
- Brownlie, K.C., Monash, R., Geeson, J.J., Fort, J., Bustamante, P. & Arnould, J.P.Y.** 2020. Developing a passive acoustic monitoring technique for Australia's most numerous seabird, the Short-tailed Shearwater (*Ardenna tenuirostris*). *Emu* **120**: 123–134.
- Buxton, R.T. & Jones, I.L.** 2012. Measuring nocturnal seabird activity and status using acoustic recording devices: applications for island restoration. *J. Field Orn.* **83**: 47–60.
- Crawford, R., Altwegg, R., Barham, B.J., Barham, P.J., Durant, J.M., Dyer, B.M., Geldenhuys, D., Makhado, A.B., Pichegru, L., Ryan, P.G., Underhill, L.G., Upfold, L., Visagie, J., Waller, L.J. & Whittington, P.A.** 2011. Collapse of South Africa's penguins in the early 21st century: a consideration of food availability. *Afr. J. Mar. Sci.* **33**: 139–156.
- DEA** 2013. Biodiversity management plan for the African Penguin *Spheniscus demersus*. *Government Gazette*, No. 36966(824): 72.
- Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S. & Sueur, J.** 2012. Monitoring animal diversity using acoustic indices: implementation in a temperate woodland. *Ecol. Indic.* **13**: 46–54.
- Dobson, A.J.** 2002. *An Introduction to Generalized Linear Models*. Boca Raton, FL: CRC Press.
- Estienne, V., Mundry, R., Köhl, H.S. & Boesch, C.** 2017. Exploitation of underground bee nests by three sympatric consumers in Loango National Park, Gabon. *Biotropica* **49**: 101–109.
- Favaro, L., Gamba, M., Alfieri, C., Pessani, D. & McElligott, A.G.** 2015. Vocal individuality cues in the African Penguin (*Spheniscus demersus*): a source-filter theory approach. *Sci. Rep.* **15**: 17255.
- Favaro, L., Gamba, M., Cresta, E., Fumagalli, E., Bandoli, F., Pilenga, C., Isaja, V., Mathevon, N. & Reby, D.** 2020. Do penguins' vocal sequences conform to linguistic laws? *Biol. Lett.* **16**: 20190589.
- Favaro, L., Gamba, M., Gili, C. & Pessani, D.** 2017. Acoustic correlates of body size and individual identity in Banded Penguins. *PLoS One* **12**: e0170001.
- Favaro, L., Gili, C., Da Rugna, C., Gnone, G., Fissore, C., Sanchez, D., McElligott, A.G., Gamba, M. & Pessani, D.** 2016. Vocal individuality and species divergence in the contact calls of Banded Penguins. *Behav. Process.* **128**: 83–88.
- 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.
- Fox, J. & Weisberg, S.** 2011. *An R Companion to Applied Regression*, 2nd edn. Thousand Oaks, CA: SAGE Publications.
- Gamba, M., Favaro, L., Araldi, A., Matteucci, V., Giacomini, C. & Friard, O.** 2017. Modeling individual vocal differences in group-living lemurs using vocal tract morphology. *Curr. Zool.* **63**: 467–475.
- Gibb, R., Browning, E., Glover-Kapfer, P. & Jones, K.E.** 2019. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods Ecol. Evol.* **10**: 169–185.
- Jouventin, P.** 1982. Visual and vocal signals in penguins, their evolution and adaptive characters. *Adv. Ethol.* **58**(S24): 3–148.
- Jouventin, P. & Aubin, T.** 2002. Acoustic systems are adapted to breeding ecologies: individual recognition in nesting penguins. *Anim Behav.* **64**: 747–757.
- Jouventin, P. & Dobson, F.S.** 2017. *Why Penguins Communicate: The Evolution of Visual and Vocal Signals*: 315. London: Academic Press.
- Kemper, J.** 2009. Annex 3: Monitoring seabirds in the BCLME: Data collection manual. In Kirkman, S.P. (ed) *Final Report of the BCLME (Benguela Large Marine Ecosystem) Project on top Predators as Biological Indicators of Ecosystem Change in the BCLME*. Cape Town: Avian Demography Unit.
- Machado, R.B., Aguiar, L. & Jones, G.** 2017. Do acoustic indices reflect the characteristics of bird communities in the savannas of Central Brazil? *Landsc. Urban Plan.* **162**: 36–43.
- McInnes, A.** 2016. *At-sea behavioural responses of African Penguins in relation to small-scale variability in prey distribution: implications for Marine Protected Areas*. PhD thesis. University of Cape Town.
- McInnes, A.M., Lacerda, M., Ryan, P.G. & Pichegru, L.** 2019. Targeted prey fields determine foraging effort thresholds of a marine diver: important cues for the sustainable management of fisheries. *J. Appl. Ecol.* **56**: 2206–2215.
- McInnes, A.M., Thiebault, A., Cloete, T., Pichegru, L., Aubin, T., McGeorge, C. & Pistorius, P.A.** 2020. Social context and prey composition are associated with calling behaviour in a diving seabird. *Ibis* **162**: 1047–1059.
- Mougeot, F. & Bretagnolle, V.** 2000. Predation risk and moonlight avoidance in nocturnal seabirds. *J. Avian Biol.* **31**: 376–386.
- Oppel, S., Hervias, S., Oliveira, N., Pipa, T., Silva, C., Geraldes, P., Goh, M., Immler, E. & McKown, M.W.** 2014. Estimating population size of a nocturnal burrow-nesting seabird using acoustic monitoring and habitat mapping. *Nat. Conserv.* **7**: 1–13.
- Petersen, S.L., Ryan, P.G.E. & Gremillet, D.** 2006. Is food availability limiting African Penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* **148**: 14–26.
- Pichegru, L., Gremillet, D., Crawford, R.J.M. & Ryan, P.G.** 2010. Marine no-take zone rapidly benefits threatened penguin. *Biol. Lett.* **6**: 498–501.
- Pichegru, L. & Oosthuizen, A.** 2018. African Penguin monitoring plan for Addo ENP, Algoa Bay. SANparks.
- Pieretti, N., Farina, A. & Morri, D.** 2011. A new methodology to infer the singing activity of an avian community: the Acoustic Complexity Index (ACI). *Ecol. Ind.* **11**: 868–873.
- R Core Team** 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>

- Sherley, R.B., Crawford, R.J.M., de Blocq, A.D., Dyer, B.M., Geldenhuys, D., Hagen, C., Kemper, J., Makhado, A.B., Pichegru, L., Tom, D., Upfold, L., Visagie, J., Waller, L.J. & Winker, H. 2020. The conservation status and population decline of the African Penguin deconstructed in space and time. *Ecol. Evol.* **10**: 8506–8516.
- Sueur, J., Aubin, T. & Simonis, C. 2008. Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics* **18**: 213–226.
- Sueur, J., Farina, A., Gasc, A., Pieretti, N. & Pavoine, S. 2014. Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acust. United Acust.* **100**: 772–781.
- Villanueva-Rivera, L.J. & Pijanowski, B.C. 2018. *Soundecology: Soundscape Ecology. R package version 1.3.3*. Available at: <http://lrvillanueva.github.io/soundecology/> (accessed 10 June 2020).
- Williams, T.D. 1995. *The Penguins*: 295. Oxford: Oxford University Press.
- Wilson, R.P. 1985. Diurnal foraging behaviour of the Jackass Penguin, *Spheniscus demersus*. *Ostrich* **56**: 212–214.
- Wilson, R.P. & Wilson, M.P.T. 1990. Foraging ecology of breeding *Spheniscus* penguins. In Davis, L.S. & Darby, J.T. (eds) *Penguin Biology*: 181–206. San Diego, CA: Academic Press.
- Wilson, R.P., Wilson, M.P.T. & Duffy, D.C. 1988. Contemporary and historical patterns of African Penguins *Spheniscus demersus* distribution at sea. *Est. Coastal Shelf Sci.* **26**: 447–458.

Received 13 November 2020;
Revision 7 April 2021;
revision accepted 25 April 2021.
Associate Editor: Stuart Sharp.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Spectrograms of ecstatic display song and mutual display song uttered by adult African Penguins.

Appendix S1. Stony Point Nature Reserve (Betty's Bay, South Africa).

Table S1. Descriptive statistics for the number of ecstatic display songs and mutual display songs detected in each time bin.