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Research article

Calls of Manx shearwater *Puffinus puffinus* contain individual signatures

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Vocalisations are widely used to signal behavioural intention in animal communication, but may also carry acoustic signatures unique to the calling individual. Here, we used acoustic analysis to confirm that Manx shearwater *Puffinus puffinus* calls carry individual signatures, and discerned which features made the calls individual. Manx shearwater are nocturnal seabirds that breed in dense colonies, where they must recognize and locate mates among thousands of conspecifics calling in the dark. There is evidence for mate vocal recognition in two shearwater species, but quantitative data on the vocalisations are lacking. We elicited vocal responses to playback of conspecific calls in Manx shearwaters, and measured spectral and temporal parameters of the calls. We then applied linear discriminant analysis with leave-one-out cross-validation and could confirm the presence of individual vocal signatures. We then calculated among-individual repeatability of 34 features describing the vocalisation to determine the extent to which these features may contribute to individual signature coding. We found that calls cluster by individual in both temporal and spectral characteristics, suggesting these traits are contributing to Manx shearwaters' unique call signatures.

Keywords: communication, individuality, Manx shearwater, vocalisation

Introduction

Individual recognition is an integral aspect of animal social behaviour, and the means by which individuals are identified by conspecifics varies between species (Beer 1971, Carlson et al. 2020). Animals may use multiple cues to discriminate between individuals, using a range of sensory modalities (Yorzinski 2017). Acoustic cues are important where recognition must take place, in particular in situations where visual or chemical cues may not be effective, such as in the dark, in large crowds, or across larger distances (Partan 2017). Individual acoustic signatures have evolved as a mechanism for individual recognition in many taxa that have life history traits involving situations

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where individuals must find each other amongst large crowds of similar conspecifics (Beecher 1989, Seyfarth and Cheney 2014, Thiebault et al. 2016). One such example is the dense breeding colonies of many seabirds, where individuals exist in close spatial proximity, with a need to correctly identify mates or offspring amongst potentially thousands of others (Danchin and Wagner 1997, Carlson et al. 2020). Thus, many colonial seabirds use individual vocal signatures to identify conspecifics, for example, penguins Spheniscidae (Lengagne et al. 1999, Aubin and Jouventin 2002) and two Procellariidae species (Cure et al. 2009, 2011).

Despite a clear role for individual vocal recognition in colonial seabirds, the extent of the trait is poorly understood, as are the acoustic aspects of the calls that provide the unique signifiers necessary for individual vocal recognition in these species. Selection for individual signatures would be expected to lead to a highly developed acoustic recognition system in nocturnally-active colonial species such as shearwaters (Procellariidae), which often arrive in their breeding colonies in complete darkness, and thus are presumed to rely on vocal signals to find their partners (Brooke 1990). A study on Yelkouan *Puffinus yelkouan* and Cory's *Calonectris borealis* shearwaters found that vocalisations serve a role in locating reproductive partners using both sex-specific and individual recognition (Cure et al. 2009).

Shearwaters, and indeed all birds, may encode individual identity in their vocal signals through variation in the repertoire, usage, or sequential organisation of different syllables. A syllable in animal vocalisations can be defined as a single utterance that makes up one sub-section of a longer song or complex vocalisation (Catchpole and Slater 2008). Variation in syllable repertoire between individuals may be the result of behavioral plasticity, wherein individuals have many syllables in their repertoire and choose to combine them in individual ways. Such individual identity encoded in avian vocalisations can be predicted to be most common in birds that are vocal learners, such as oscine songbirds. Alternatively, variation in syllable repertoire between individuals may also reflect heritable or developmental differences, in which case vocalisations are predicted to remain the same over the lifetime of an individual, but different individuals each have unique patterns of temporal and spectral modulation that identifies their calls.

An additional mechanism by which individual vocal identity may be encoded is through differences in the animal's voice resulting from individual morphological differences in body size, vocal organ and vocal tract (source-filter theory, for example see Fant et al. 1963). The vibratory masses within the syrinx, the vocal organ of birds, are set into vibration by airflow moving from the lungs (in expiratory phonation), producing a sound wave, which is further modified as it travels from the syrinx through the trachea and oropharyngeal cavity before being emitted (Suthers and Zollinger 2008). As with any other aspect of body size and shape, in any species, individuals vary in the size and shape of their vocal apparatus (e.g. the individual and sex differences in syrinx morphology of European starling (*Sturnus vulgaris*) Prince et al. 2011). In addition, as the shape and size of the supra-syringeal vocal tract varies between individuals, even an identical sound produced at the source (the syrinx) can be emitted with different spectral properties from different individuals (Suthers and Zollinger 2004, Nelson et al. 2005, Fletcher et al. 2006).

Vocal repertoires in seabirds are not as complex as in most passerine songbirds (Kumar 2003), and the degree of behavioral vocal plasticity seabirds exhibit remains largely unexplored. While a lack of vocal complexity may limit the potential for syllable usage-based individuality in their calls, the use of vocalisation for mate identification have been found in other species of colonial nesting seabirds, including black-legged kittiwake *Rissa tridactyla* (Aubin et al. 2007), two species of burrowing petrels *Halobaena caerulea* and *Pachyptila desolata* (Gémard et al. 2019), and notably, Cory's and Yelkouan shearwaters (Cure et al. 2009, 2011).

However, although these studies concluded that vocal identity was encoded by acoustic cues, we do not know whether certain acoustic features are more important than the others or even critical for encoding individual identity, or whether differences in the acoustic features were due to variation in syllable repertoire and or presumptive morphological differences. Earlier work with Manx shearwaters *P. puffinus* used experimental call playback to demonstrate that they show a behavioural ability to discriminate between males and females, and between mates and unfamiliar individuals by voice (Brooke 1978). Further, in playback studies, females were more likely to respond to playback of their mate (13/24 responded) than to the calls of strange males (0/26 responded). In contrast, incubating male shearwaters were not significantly more likely to respond to the call of their own mate than that of an unknown female (Brooke 1978). One explanation offered for this difference in response is that male calls contain more cues to individual recognition, as male calls contain more complex spectro-temporal structure than the calls of females, which means that males cannot recognize the call of their mate from the call of any other female. However, given that the evidence for individual recognition was based on behavioural responses, and no detailed spectral analysis was done to test whether female calls do have fewer cues available for individual vocal recognition, this hypothesis remains untested.

Understanding acoustic features needed for individual identification of shearwaters (or any vocal species) is not only relevant for understanding shearwater behaviour, but can also have applied conservation benefits (Pollard et al. 2010). Acoustic censusing methods can be a particularly valuable tool for species such as shearwaters that present logistical challenges for population estimates due to their nocturnal activity and burrow-nesting habits. The first steps towards developing an applied censusing protocol are to determine if calls differ between individuals, and then to quantify the degree to which different acoustic parameters contribute to an ability to statistically separate calls of each individual.

Here, we collected calls from 13 Manx shearwaters on Lundy Island, UK and used acoustic analysis to identify whether distinct acoustic signatures can be consistently linked to signaler identity. We then determine which specific acoustic features may be important in encoding individual identity.

Material and methods

Study species

Manx shearwaters are pelagic seabirds that nest exclusively in burrows on the rocky shores of islands in the North Atlantic (Brooke 1990, Lee et al. 2020). During the breeding season, Manx shearwaters assemble at sea (Richards et al. 2019) before returning to breeding colonies after dark (Brooke 1990). Upon arriving to the colony, both sexes emit loud, prolonged rasping calls, in flight or from the ground. While calls are sometimes made from the surface, others are emitted from inside the subterranean nesting burrows (James 1985, Brooke 1990), or from the entrance leading into a burrow (Sun et al. 2022). This loud display call is the primary vocal signal described for this species (Brooke 1990), although they also make quiet short range calls within the burrow between parent and offspring or between the breeding pair (pers. obs.; Brooke 1990). As Manx shearwaters retain the same mate year after year, individuals may use calls to localize each other, and re-establish a pair-bond at the start of the new breeding season (Brooke 1978). They likely also use vocalisations to navigate to their own nesting burrow in the dark (James 1985), as they have poor night vision (Martin and Brooke 1991). Brooke (1978) suggested that, when presented with playback of conspecific calls, incubating females called exclusively in response to playback of their own mate's call. In contrast, male Manx shearwater were equally likely to call in response to playback of their partner as to that of an unknown female (Brooke 1978). These experiments show that behaviourally, at least for male calls, shearwater vocalisations convey some information on the identity of the individual. Human participants successfully matched 10 individual Manx shearwater's calls to 29 printed sonograms of those calls (Brooke 1978), supporting the idea of Manx' vocalisations containing sufficient variation for individual signatures. However, no study to date has quantitatively demonstrated the existence of individual vocal signatures in Manx shearwaters from an acoustic perspective, nor explored how such signatures were encoded acoustically.

Study location

We conducted our study on Lundy Island (51°10′N, 4°41′W), United Kingdom, where an estimated 5504 Manx shearwater pairs bred in 2018 (Booker et al. 2019). This accounts for ~2% of the global population (BirdLife International 2015). Our study site was located on a grassy slope on the southwestern side of the island where the population is at its greatest density (Booker et al. 2019).

Eliciting and recording calls

During daytime, Manx shearwater are silent in the colony, rarely calling (field observation). However, a bird that has occupied a burrow may call at invaders as a territorial defense behaviour (Brooke 1990), therefore the calls can be elicited and recorded in response to playback of conspecific calls at the burrow opening (Brooke 1978, Perkins et al. 2017). We collected such calls during the incubation period between 4 and 9 July 2021, when we expected there to be at least one parent present on the nest in the burrow at all times (Brooke 1990). The playback file we used contained three different Manx shearwater calls (sex unknown) on two sound files downloaded from the xeno-canto bird sound archive (no. 591932, no. 591934), recorded on Skokholm Island, Pembrokeshire, Wales, in May 2016. The playback stimuli consisted of six discrete calls (three each from two burrows). We played one discrete call at a time from the playback stimuli, and played no more than six calls per day to any individual burrow, with a 20–40 second silent interval between playback of each call to reduce disturbance. We then terminated the playback and began recording when birds started to call back, using a handheld recorder (ZOOM, H4n Pro. Sampling frequency: 48 kHz, dynamic: 24 bit) connected to an external omnidirectional microphone (Wildtronics, Micro Mic XLR Frequency response: 20 Hz–20 kHz), fitted with a furry windscreen. We collected all the recordings during daytime (8:00–18:00) in calm weather (wind speed < 8 mph, no rain). The recorder's settings were kept consistent throughout.

Acoustic analysis of individual vocal signature

In shearwaters, vocalisations are produced during both the inhalant and the exhalant parts of the respiratory cycle (Cure et al. 2009), which appears to be true for Manx shearwaters as well (Sun et al. 2022). During inspiration, vocalisations are produced as air is drawn over the vibratory masses in the syrinx into the posterior air sacs (Schmidt and Wild 2014). A typical Manx shearwater call consists of a succession of motifs (a series of syllables with a brief silent interval between each) with similar patterns (Fig. 1a–b). This type of call is observed when a Manx shearwater explores a burrow (Sun et al. 2022) or responds to vocalisations of conspecifics (Brooke 1978, 1990). For each motif, we assume based on our field observations, that the ending syllable, which has a distinct interval between it and previous syllables, is the inhalant vocalisation, and the rest of the syllables are exhalant vocalisations (Fig. 1c–d) (Sun et al. 2022).

All recordings were high-pass filtered at 200 Hz before measurement to remove low frequency background (generally wind) noise. We took each motif as an observation, and measured 34 acoustic features describing the motif using the automatic acoustic measurement tools in Avisoft SASLab Pro ver. 5.2.14 (Avisoft Bioacoustics). The feature space contains five temporal features (duration of the motif, interval between motifs, duration of inhalant syllable, ratio of duration of inhalant syllable over duration of the whole motif, interval between exhalant syllable and inhalant syllable) and 28 frequency features which include 14 features describing the exhalant syllables and 14 features describing the inhalant syllable. We have separate measures for exhalant and inhalant syllables to test if there is a difference in the contribution of the two types of syllable to coding individual signatures. The frequency features describe the syllables from two aspects, one is the holistic

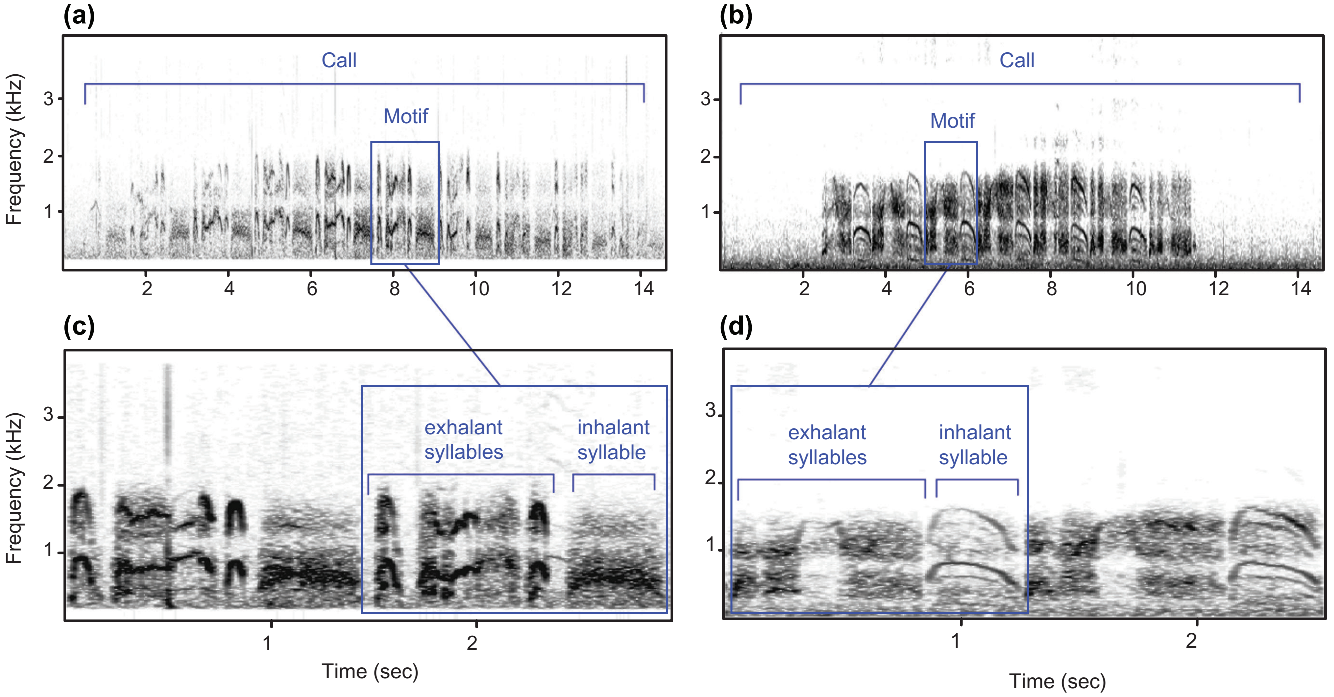

Figure 1. Spectrograms of Manx shearwater calls from two individuals (individual 1: a, c; individual 2: b, d) showing typical call structure. Calls are made up of a series of repeated motifs, which consist of 1–6 exhalant syllables and 1 inhalant syllable (boxes in a, b, and zoomed in to show acoustic details in c, d). Birds varied in the number of exhalant syllables in motifs among and within individuals. All recordings were high-pass filtered at 200 Hz. Spectrogram 1024 point FFT, window overlap 98%, Hamming window.

characteristics of the entire syllable, derived from the mean spectrum of all analysis windows across the syllable; the other is the characteristics of the climax of the syllable, derived at the maximum amplitude. For a full list of the 34 features and their annotations, Supporting information. Notably, because the birds called from inside their burrows, it was not possible to determine the distance from the caller to the microphone, thus we did not include any amplitude features in this study. We avoided the first and the last motifs in each call as they were often produced with less consistency, or were incomplete (Fig. 1a–b), likely resulting from incitation of the vocal and respiratory apparatus and depletion of respiratory air, respectively (Sun et al. 2022). After these motifs were eliminated, only individuals with ≥ 4 motifs remaining for measurement were included in the analysis, they are 13 birds, each has 12 ± 8 motifs (168 motifs in total).

To test whether calls are individually distinct, we performed Linear Discriminant Analysis (LDA) on the motifs, with leave-one-out cross-validation for more robust output. The process is as follows: each time we used all but one motifs to build an LDA model, then applied the model on the one motif left out of the model to predict which individual the motif belonged to, then saved the prediction. We repeated this process for n times where n = total number of motifs. Then we calculated how many motifs were correctly classified to the individual they belonged to (Percent of Correct Classification, PCC), this indicates the degree of individualization. Finally, we performed a binomial test on the correct classification to test against chance.

Then, to determine which features may code for individual identity, we computed the repeatability for each feature among individuals using Markov chain Monte Carlo Sampler for multivariate generalized linear mixed models (MCMCglmm) (Hadfield 2010). Repeatability is a value between 1 (all variation explained by among-individual differences) and 0. The higher the repeatability is, the more different are individuals among each other, and the more similar are individuals within themselves, and thus the more likely the feature encodes individual vocal signatures.

Our analytical method on motifs is stated as above. However, in order to determine whether the features of individual syllables, for example, the duration of each syllable and the interval between syllables (Fig. 1c–d), also contribute to encoding individual signatures, we also applied the same analytical method to syllables. This needed to be tested because the effects of individual syllables were not reflected in the analyses on motifs. LDA with leave-one-out cross-validation and repeatability computation were both performed in the same way, the only difference was the analytical units were syllables instead of motifs.

All statistical analysis in this project was performed in R ver. 4.0.3 (www.r-project.org).

Results

Among 168 motifs, 83.3% were correctly classified by the LDA ($p < 0.001$) (Fig. 2), suggesting that Manx shearwater calls are individually distinct and could be used for individual recognition. The among-individual repeatability of each feature is shown in Fig. 3, sorted from the largest to the smallest. We found 30 features with repeatabilities significantly different from 0, which suggests that they all may contribute to individual identity coding. The features with the highest repeatability describe either the call's temporal properties or 25% quartile of the spectrum. Quartiles are frequencies that split off the distribution of energy across the spectrum to a specified percentage. For example, a 25% quartile is a frequency where 25% of the total energy of the sound is located below this frequency. Quartiles provide us with information of how the power of a syllable is distributed across frequency. We also found that features describing the mean spectrum ('mean', parameters derived from the mean spectrum of all analysis windows across the element selected) have higher individual repeatability than features describing the max spectrum ('max', parameters derived from the maximum, or peak spectrum across the entire element selected). This means that the holistic features of the syllables may be more reliable for individual recognition than the features of the climax of the syllables. There is no obvious difference in repeatability between features of exhalant syllables and inhalant syllables.

When we performed LDA on syllables, the PCC was down to 37.2%. This shows that the features of entire motifs are more reliable in predicting individual identity than those of syllables. Features describing 25% quartile are still of high repeatability, which is consistent with what we found in motifs, while temporal features of individual syllables (i.e. duration and interval) did not show high repeatability (Fig. 4).

Discussion

With modern acoustic and statistical analysis we confirmed that the calls of Manx shearwater contain unique acoustic signatures and thus likely serve a function in individual recognition, as has been shown in other Procellariiformes (Cure et al. 2009, Gémard et al. 2019). We found that temporal features (specifically, the duration of the motif, interval between motifs, duration of inhalant syllable) and the low frequency components of the call can be especially important for individual signature coding. The importance of features in temporal domain has been reported frequently in previous studies in other seabirds (e.g. in Yelkouan shearwaters and Cory's shearwaters (Cure et al. 2009, 2011), black-legged kittiwakes (Aubin et al. 2007), blue petrels *H. caerulea* and Antarctic prions (*P. desolata*, Gémard et al. 2019)). We suggest that the temporal features of shearwater vocalisations have a function in vocal recognition, likely present in more seabird species.

Another apparently important aspect of shearwater vocalisations is the distribution of acoustic power across frequency. In our analysis we examined acoustic power distribution divided across quartile ranges. In Manx shearwater calls, although we found good repeatability in the 25% quartiles in exhalant and inhalant syllables, the 50% and 75% quartiles

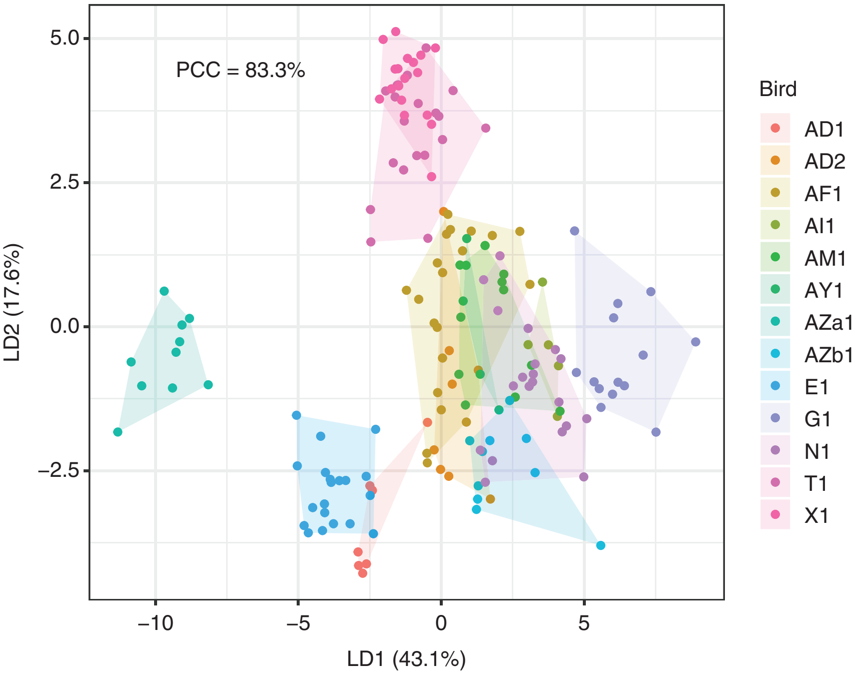

Figure 2. Manx shearwater calls show repeatable individual acoustic differences. More than 83% of the motifs are classified to the correct individual ($p < 0.001$) by a linear discriminant analysis (LDA) with leave-one-out cross-validation. Each dot corresponds to a motif ($n = 168$), while colour denotes individuals. PCC: Percent of Correct Classification. For PCCs for each individual respectively, Supporting information. LD: Linear Discriminant.

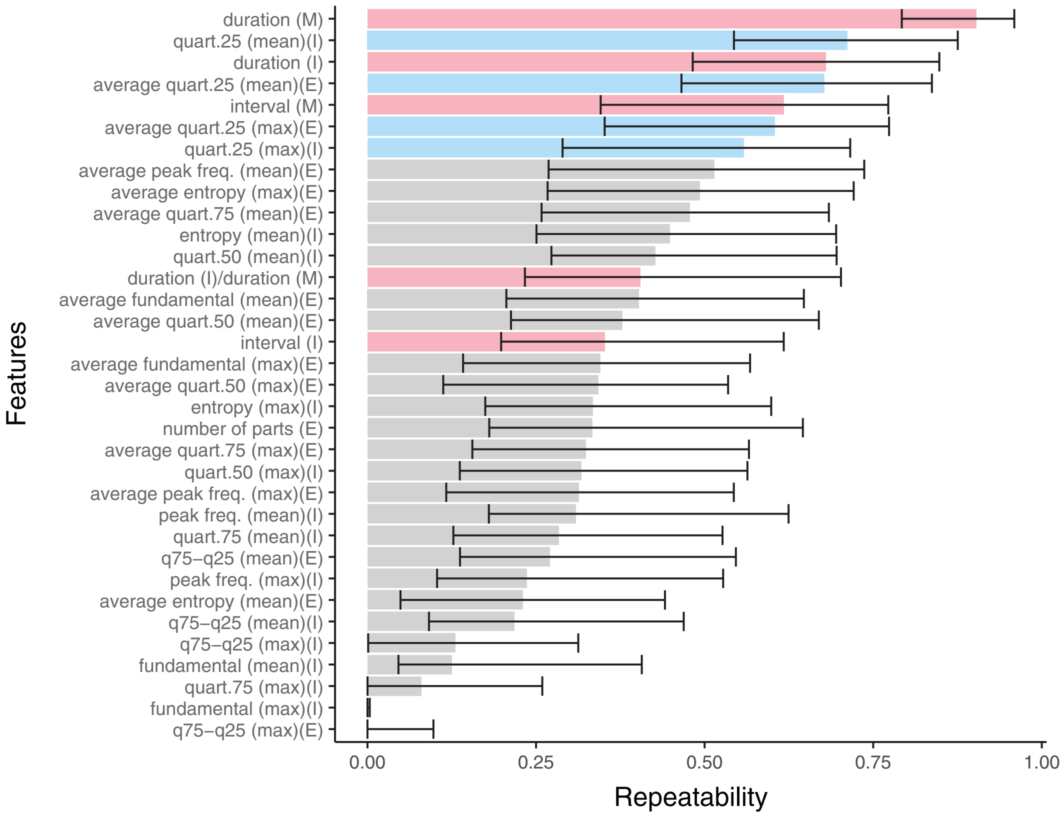

Figure 3. Among-individual repeatabilities with 95% confidence intervals for 34 acoustic features describing motifs of Manx shearwater calls, sorted from the largest to the smallest. Temporal features (red) and features describing 25% quartile of the spectrum (blue) are of high repeatability. Annotations: M = entire motif, I = inhalant syllable, E = exhalant syllables; quart. 25/50/75 = 25%/50%/75% quartile, fundamental = fundamental frequency; mean = of mean spectrum, max = at maximum amplitude. For a more detailed description of the features Supporting information.

show lower repeatabilities. This implies that the information about individual identity may be mainly carried by the low-frequency component in the calls, which contains the fundamental frequency for the harmonic portions of the call. The fundamental frequency (the lowest frequency of a periodic sound) in birds, as in mammals, it is determined by the oscillation rate of pairs of vibratory tissue masses within the vocal organ, set into vibration by respiratory air pressure (Elemans et al. 2015). In some mammals, it has been shown that fundamental frequency is vital for vocal individual recognition (Sousa-Lima et al. 2002, Volodina et al. 2006). However, in this study, while we included fundamental frequencies in our feature space we did not find high repeatability. A possible reason is that some portions of calls are high in entropy and thus are not periodic enough to extract a fundamental frequency. Yet there is evidence that some birds can rely on other frequency features for individual recognition even when fundamental frequency is experimentally modified, although with decreased success (Lengagne et al. 1999, Vignal et al. 2008). The reason why the low-frequency component in Manx shearwater calls is important for individual discrimination remains to be explored, although a similar pattern has been shown in king penguins (*Aptenodytes patagonicus*) (Lengagne et al. 1999). Note that these do not mean that features other than temporal and 25% quartile are not important. We found thirty features with among-individual repeatability significantly different from zero, meaning that they all possibly carry information about individual identity. It is likely that the birds use multi-dimensional features in their vocalisations as cues for individual recognition because this enables larger variability, allowing better potential for individual recognition in large colonies.

We also found that the features describing motifs are more reliable in predicting which individual the vocalisation belongs to than the features describing syllables. This is also reflected in the spectrograms: for the same individual, sometimes the exhalant part consists of one or two long syllables, while at other times these long syllables are broken into several short pieces divided by brief silences, resulting in syllables shorter in duration but greater in quantity. Therefore, features describing syllables are less repeatable compared with the features of the motif as a whole, since for motifs the variation in temporal features of individual syllables is ignored. Thus, motifs were a more stable unit of comparison within individual birds than syllables. As far as we are aware, this characteristic whereby syllables are sometimes vocalised in smaller parts has not been previously described in non-vocal learning birds. For example, although Cory's and Yelkouan shearwater calls also contain inhalant and exhalant parts like Manx shearwater calls do, unlike Manx shearwaters, their motifs

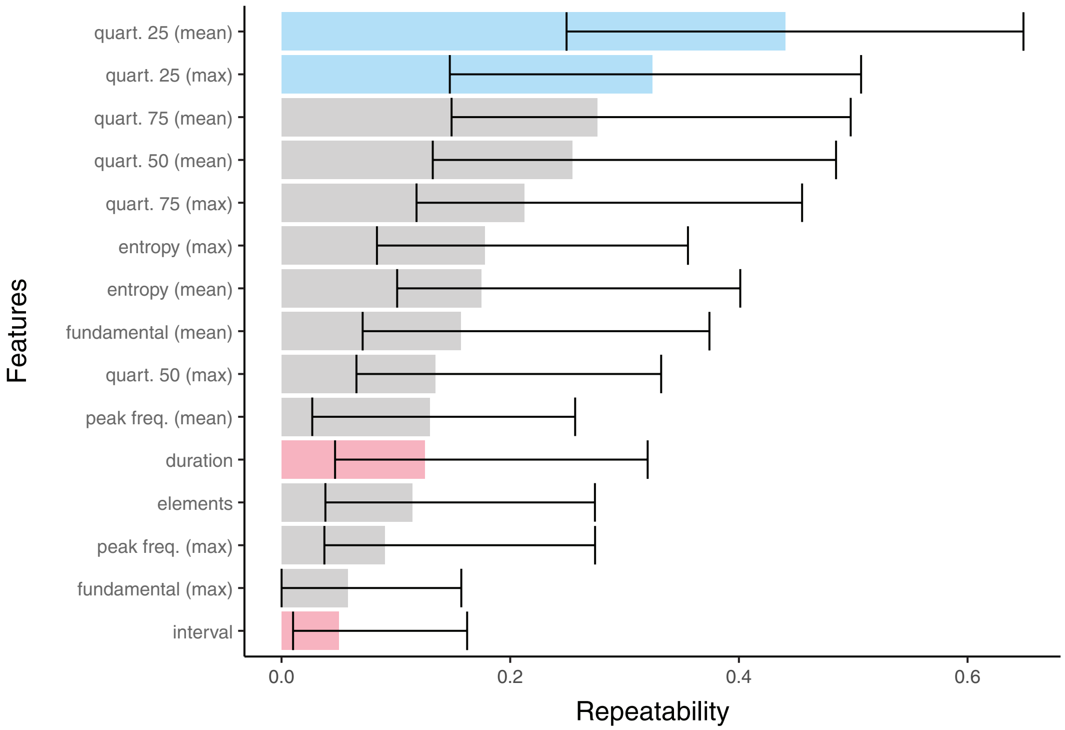

Figure 4. Among-individual repeatabilities with 95% confidence intervals for 15 acoustic features describing syllables of Manx shearwater calls, sorted from the largest to the smallest. Features describing 25% quartile of the spectrum (blue) are of high repeatability, while temporal features (red) do not. Annotations: quart. 25/50/75 = 25%/50%/75% quartile, fundamental = fundamental frequency; mean = of mean spectrum, max = at maximum amplitude.

are constituted by a certain number of syllables (Cure et al. 2009). This uniqueness of Manx shearwater vocalisation may be interesting for future studies.

We were unable to sex the birds in our study, however we believe that the performance of calls emitted by the 13 random individuals shows the potential of individual identity coding of calls in both sexes, because it is statistically unlikely that our recordings of birds in burrows happened to all be of a single sex. Although we do not have evidence for whether the possibilities of being present in the burrow for two sexes are equal, the parents take turns in incubation (Brooke 1990), and the time each parent spent on the sea for feeding is unlikely to differ significantly, and so we assumed that parents are equally likely to spend time on the nest. Manx shearwaters are considered to be sexual dimorphic in vocalisation (James 1985, Brooke 1990), although in earlier behavioural studies only the calls of males were recognised individually by their mates. While we were unable to genetically groundtruth sex, we determined three female type calls (based on the descriptions by Brooke 1978) in our sample. These three individuals were clearly discriminated by our analysis, suggesting that female-type calls also contain individual vocal signatures.

Our finding that calls of both sexes are individually distinct raises the question of why, if both male and female calls carry information on the identity of the individual, females behaviourally discriminate male calls while males do not discriminate female calls (Brooke 1978)? The same behaviour was found in a closely-related species, Yelkouan shearwaters, where both male and female calls were shown to be acoustically identifiable (Cure et al. 2009), but only females responded exclusively to their mate (Cure et al. 2009, 2011). One hypothesis is that the males do recognize their mate's call but choose to respond the same way to any female's calls. This kind of behaviour is often related to extra-pair copulation in monogamous animals (reviewed by Griffith et al. 2002). A second, perhaps less likely hypothesis is that males do not have the ability to discriminate different female calls, despite the calls of both sexes carrying individual call signatures. Both hypotheses might benefit from further behavioural studies.

Using passive acoustic monitoring (PAM), and algorithms for individual identification may allow for an a more accurate estimate of the number of birds in an area as has been demonstrated in an increasing number of species (Terry and McGregor 2002, Adi et al. 2010, Wijers et al. 2021, Trapanotto et al. 2022). Studies on the application of PAM in ecology research have been quickly growing in the past thirty years and are extending from marine ecology to terrestrial ecology (Sugai et al. 2019). Researchers have started to explore using PAM to obtain individual information for conservation purpose in dolphins *Tursiops truncatus* (Kershenbaum et al. 2013) and gibbons *Hylobates funereus* (Clink and Klinck 2021). PAM is a particularly important tool when monitoring vocal species that are cryptical, nocturnal, and/or endangered (Sugai et al 2019, Clink and Klinck 2021). While Manx shearwater holds healthy global population, there are many related species that are critically endangered and call for effective monitoring, e.g. Balearic shearwater *Puffinus mauretanicus*, Townsend's shearwater *Puffinus auricularis*, Rapa shearwater *Puffinus myrtae*, etc. (IUCN 2021). The current method of censusing Manx shearwaters involves using call playback at burrows, and counting the individuals that respond by calling from inside the burrow (Perrins et al. 2020). Despite improvements to this method (Perkins et al. 2017, Perrins et al. 2020), the unreliability of shearwaters in responding to playback means that the population estimates are prone to large errors. Call-back experiments on shearwaters are not only error-prone, but also time-intensive and so PAM, in conjunction with individual identification, could allow for detection of vocalisations from many burrows simultaneously, and thus facilitate better monitoring of endangered species (Clink and Klinck 2021).

In conclusion, we found Manx shearwater vocalisations contain individual signatures which can be potentially used as individual recognition cues by conspecifics. Vocal individual signatures are encoded by a wide range of acoustic features from both temporal and frequency domains, among which temporal features and frequencies within the lower 25% quartile of the spectrum are especially important. We hypothesize that the unique life-history of these nocturnally-active, colonially-breeding, long-lived, monogamous seabirds has driven selection in the family Procellariidae for individual vocal signatures and increased vocal complexity.

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Author contributions

Yuheng Sun: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Jamie Dunning**: Investigation (supporting); Writing – review and editing (equal). **Tony Taylor**: Conceptualization (supporting); Investigation (supporting). **Julia Schroeder**: Project administration (lead); Methodology (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Sue Anne Zollinger**: Conceptualization (lead); Methodology (equal); Resources (supporting); Supervision (equal); Visualization (supporting); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hdr7sqvm6 (Sun et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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