



What do rattle quills tell? A morphological analysis of the rattling in the African crested porcupine

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Abstract

Sonations are non-vocal acoustic signals whose production mechanisms have been rarely investigated in mammals. Since sonations are directly tied to specific anatomical characteristics, one issue in acoustic communication studies is estimating the morphological diversity of the structures responsible of sound emission. The nocturnal and social habits of the African crested porcupine make them an ideal model to address this issue. Both sexes bear highly specialised quills on their tail that, by colliding against each other, produce a sound (rattling). We measured the quills of 130 subjects and found that their morphology did not vary in relation to season and sex. Compared to subadults (N = 39) and adults (N = 81), cubs (< 6 months, N = 10) have fewer and stubbier rattle quills that also differ in their length and diameter across the age classes. The passage from the cub to the subadult phase seems to sign the most important changes in the quill development. Although it is unknown when and how often a cub produces rattling, the presence of quills at a very early stage of life indicates that they can potentially be used. Although several hypotheses can explain the potential role of cub rattling, one of the most reasonable is that, when olfactory and/or visual contacts are prevented, this sound can alert adults about potential predation risks on offspring. Matching morphological and acoustic data under different contexts will allow understanding the correlates at the basis of the potential roles of such a peculiar way of communication.

Keywords *Hystrix cristata* · Acoustic communication · Social recognition · Rodents · Sonations

Introduction

Sonations are communicative non-vocal sounds produced without the involvement of the vocal system (Bostwick and Prum 2003). While vocalisations have been studied extensively in many vertebrate taxa, the literature on non-vocal

acoustic communication remains scarce (Garcia et al. 2012; Clark 2016; Wright et al. 2021). However, many different mechanisms of sonation are achieved through various behaviours and/or specialised structures to which a single conceptual overview is not applicable (Clark 2016). Indeed, one issue in acoustic communication studies is understanding the relationship between morphological and acoustic characteristics and their implications on behaviour. Most studies focused on sonations aimed to estimate the variation within species of their acoustic components (e.g., *beak drumming* of great spotted woodpeckers, *Dendrocopos major*; Budka et al. 2018; *chest beating* of mountain gorillas, *Gorilla beringei beringei*; Wright et al. 2021; *beak clattering* of oriental white storks, *Ciconia boyciana*; Eda-Fujiwara et al. 2004). Some studies went a step further by experimentally confirming that sonations can function as alarm signals in crested pigeons (*Ocyphaps lophotes*; Murray et al. 2017) and as a binary recognition cue in banner-tailed kangaroo rats (*Dipodomys spectabilis*; Randall 1994). Only a few studies investigated the morpho-functional aspects linked to such variation. The stridulating organ of streaked tenrecs

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(*Hemicentetes semispinosus*) is formed by differentiated hollow quills that are rubbed together for producing a low-frequency sound (Endo et al. 2010). The sonation produced by the golden-collared manakin (*Manacus vitellinus*) derives from the percussive collision of wings whose radius bone is highly differentiated (Bodony et al. 2016). By manipulating alive individuals of hummingbirds and observing the behaviour of single (and grouped) feathers when interacting with an airflow, Clark and Feo (2008) identified different modes of fluttering, which were influenced by the shape and number of feathers and their orientation in relation to airflow. To describe this sonation, Clark (2014) borrowed the key terms from the Source Filter Theory. The source is the minimum structure that is both necessary and sufficient to produce the sound; the filter is represented by the structures that are not necessary or sufficient to produce the sound but that can modify it. In many species of birds, tonal sounds serve as “acoustic signatures” of flutter, and even minor changes in feather morphology or behaviour can substantially alter the sound (Clark and Prum 2015). Knowing the morphological variation of a sound producing system is pivotal to understand its evolutionary implications and functions (Clark 2016). Sonations likely arise from locomotion induced sounds which may have become the target of selection and thus co-opted (Darwin 1871; Bostwick and Prum 2003), as it has been suggested for bird flutter-induced acoustic signals that have evolved from involuntary avian flight mechanics (Clark and Prum 2015). Sonations can then acquire important functions in a variety of behavioural contexts, being also used in concert with vocalisations (Bostwick and Prum 2003). Still, identifying the function of a sound is not an easy task. Sounds can be considered as *signals* when they elicit a reaction in a receiver, implying that both the sound produced and the behavioural reaction have been selected for that function. But sounds can also be *cues* when only the receiver’s behavioural reaction is selected (Scott-Phillips 2008). Sounds can also be *honest signals* (Fitch and Hauser 2003) when conveying information about the sender such as size, condition, or class (Reby and McComb 2003; Wright et al. 2021).

Outside the African continent, crested porcupines (*Hystrix cristata* Linnaeus, 1758) are distributed only in Italy (Mori et al. 2013). They are semi-fossorial, primarily nocturnal rodents that live in family groups comprising a reproductive pair, that mates for life, and their offspring (Santini 1983; Felicioli et al. 1997; Amori et al. 2009; Mori et al. 2016). Males and females show similar body sizes (Felicioli et al. 1997; Mori and Lovari 2014), cooperate in rearing offspring, and form stable pairs also outside the reproductive period (Mori et al. 2016). Copulations occur independently of the female oestrus cycle (Mori et al. 2016; Coppola and Felicioli 2021) and are preceded by a complex courtship of affiliative behaviours such as grooming and sniffing

(Felicioli et al. 1997). The youngsters can stay with their parents for up to a year and help rear the younger siblings (Coppola and Felicioli 2021). Family members typically spend the night foraging together, but also show daytime activity (e.g., sunbathing) (Coppola et al. 2019). In the wild, the family groups seem to tolerate each other, with aggression occurring only if one family closely approaches the den of another family (Coppola et al. 2022).

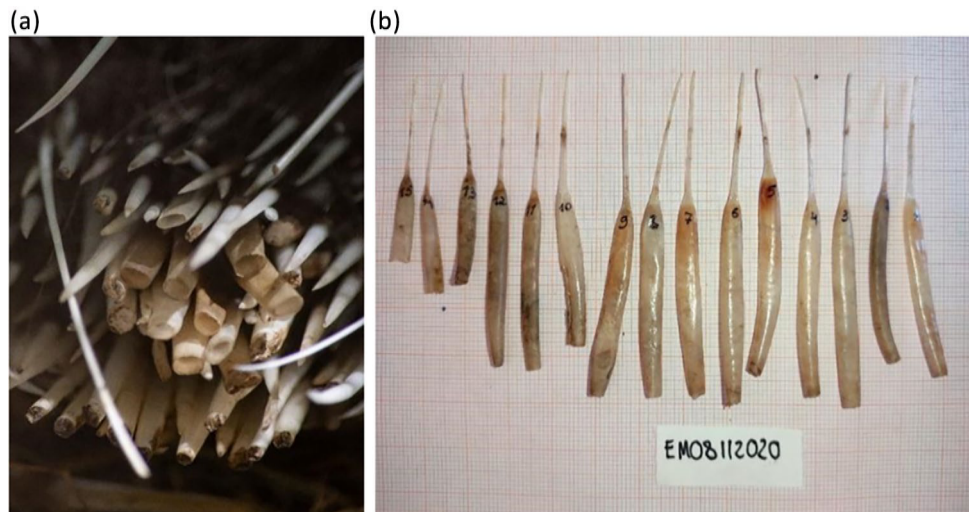
Due to their nocturnal habits, intra-specific communication in porcupines mainly relies on olfactory and acoustic signals. Olfactory communication seems to be involved in individual recognition (Massolo et al. 2009) and in resource defence with animals marking their feeding sites by depositing perianal gland secretions (De Villiers et al. 1994). Mori et al. (2014) reported the production of acoustic signals, involving both vocalizations and sonations, in coincidence with the presence of hunting dogs.

All 11 species of the Hystricidae family possess long quills covering most of their body with 10 species, the most derived ones (Rovie-Ryan et al. 2017), showing specialised quills clustered on their tail (Fig. 1). These “rattle quills” are enlarged, hollow, and open at one end, allowing the production of the rattling sound when the tail is shaken (Mohr 1965; Amori et al. 2009; Mori et al. 2014). Newborns possess rattle quills, although these are softer and closed at the tip, which open and wear away later in life. Adults sometimes show closed, undeveloped rattle quills, suggesting a possible periodic renovation of these structures, but the rate at which this occurs is unknown (Mohr 1965). Rattling is a typical defence display of the species, used as advertisement to prevent dangerous fights with potential predators and competitors that may have learned to associate the sound with pain (Mori et al. 2014). In *Hystrix* spp. the younger individuals, and particularly cubs, are mostly subjected to predatory events (Mills and Shenk 1992; Monetti et al. 2005). In Central Africa, common predators are terrestrial carnivores such as lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), and African wild painted dogs (*Lycaon pictus*) (Breuer 2005). In Italy, *H. cristata* seems to be predominantly hunted by red foxes (*Vulpes vulpes*; Lucherini et al. 1995) and domestic dogs (*Canis familiaris*; Monetti et al. 2005). These predators can rely on acoustic cues, also to locate their preys especially under conditions of limited visibility (Österholm 1964; Faragó et al. 2010; Webster et al. 2010, 2012).

To our knowledge, the only study investigating the morphological variation of rattle quills in the Hystricidae family was conducted by Corbet and Jones (1965). The researchers discovered notable distinction between various species and individuals of the same species, especially in the length of the hollow part of the quill and the diameter of the opening.

Given that porcupines’ nocturnal and social habits require acoustic-oriented communication, the species

Fig. 1 **a** Close up of an adult female's tail, with the rattle quills clustered in the center; **b** Rattle quills collected from one adult individual (Credit: V. Schianini). These quills are translucent and are made by an enlarged and hollow portion and a peduncle that is embedded in the skin. During the tail vibration, the emitted sound is produced when these structures hit against each other and/or against normal quills



is a valuable model for exploring sonations in rodents. Although we do not know how rattle quill variability affects the sound production, we aim to analyse the morphology of quills to estimate intra-species variation in populations of crested porcupines in Central Italy.

As a first step, we hypothesise that the morphology of the quills is related to physical characteristics of the individual engaging in rattling. Since porcupines show softer and closed at the tip quills at birth, we predict that along the development these structures can undergo further changes along the development, with cubs, subadults, and adults varying in the morphology and number of rattle quills (*Prediction 1*).

We do not expect differences in the morphology and number of rattle quills according to the sex for both anatomical and functional reasons (*Prediction 2*). Since the species lacks sexual dimorphism, there is no reason to suppose that males and females can differ in their sonation apparatus. Moreover, if the sonations are involved in the defence of offspring that is an activity executed by both parents, both males and females need similar sonation structures.

The data about reproductive seasonality of wild crested porcupines in Italy are still unclear. It seems that births can occur throughout the year (Santini 1980, 1983; Mori et al. 2016; Coppola and Felicioli 2021), however a higher number of reproductive pairs having litters has been recorded in February and the maximum number of twins and triplets are reported in October (Mori et al. 2016). If the reproductive seasonality in term of number of offspring reflects the necessity to increase the redundancy of the sonations, we would expect that the number and morphology of rattle quills in adults may change throughout the year and being larger and/or in higher number around October (*Prediction 3*).

Methods

Data were collected from 130 subjects (adults, N = 39; subadults, N = 81; cubs, N = 10) that were found dead in the provinces of Grosseto and Siena (Central Italy) between 1993 and 2021 (one of the frequent causes of mortality in this species is car collisions; Amori and Capizzi 2002). Only corpses that were intact in all their body parts were sampled. For each individual, we collected information about sex and date of collection. The age class of each porcupine was estimated by examining their maxillary teeth eruption/replacement (Van Arde 1985; Pigozzi 1987). Each subject was assigned to either a cub (up to 6 months old), subadult (between 6 and 18 months old), or adult class (> 18 months old). We collected, counted and measured all the rattle quills for each individual. By using a Manual Vernier Caliper (0–100 mm), we took data on the length and diameter of the intact rattle quills and calculated the mean values by using the cm as unit of measurement. We also evaluated the Standard Error (\pm SE). The operators (N = 6) counted and measured the quills three times each, and reported the mean value calculated on the three measurements. As for the number of quills, the dataset included entries from photographs of five captive live subjects rescued by the “Centro Recupero Animali Selvatici della Maremma” (Semproniano, Grosseto).

We utilised Generalised Linear Mixed Models (GLMMs) to predict rattle quills' number and morphological features. The variables sex, age class, and climate seasons for temperate environments (spring/summer/fall/winter) were included as fixed factors. Individual identity of the operators was included as the random factor to control the potential variability deriving from the different operators. Our response variables were the number of

rattle quills (Poisson distribution), mean total length, mean total diameter, and the ratio between length and diameter means (Gaussian distribution). We ran all analyses in R, version 2024.04.1 (R Core Team 2024) using the *glm-tMB* package (Brooks et al. 2017). We inspected the Variance Inflation Factor (*performance* package, Lüdtke et al. 2021) to check for collinearity among predictors. In all the models, the variables showed negligible collinearity (number rattle quills: $VIF_{MIN} = 1.03$; $VIF_{MAX} = 1.06$; mean total length, $VIF_{MIN} = 1.04$; $VIF_{MAX} = 1.14$; mean total diameter, $VIF_{MIN} = 1.02$; $VIF_{MAX} = 1.14$; the ratio between length and diameter, $VIF_{MIN} = 1.03$; $VIF_{MAX} = 1.14$). For each model, we evaluated the distribution of the residuals with the *DHARMA* package (Hartig 2022). Then, each full model was compared to a null model including only the random factor via the *anova* function (Chambers and Hasties 1992). We then computed the significance of the single fixed factors for each model with a likelihood ratio test using the *drop1* function (Chambers 1992). Lastly, we used a Tukey–Kramer test to calculate differences between groups of significant predictors (*emmeans* package, Lenth 2024).

Results

We collected a total of 130 cases. The mean for quill number was $13.93 (\pm 0.41 \text{ SE})$, for the total mean length $3.80 (\pm 0.09 \text{ SE})$, for total mean diameter $0.38 (\pm 0.01 \text{ SE})$, for the total mean diameter/total mean length ratio (D/L) $0.10 (\pm 0.003 \text{ SE})$.

All the full models significantly differed from the null models (GLMMs: quill number, $\chi^2 = 41.20$, $p < 0.001$, number of cases = 130; total mean length, $\chi^2 = 43.62$, $p < 0.001$, number of cases = 92; total mean diameter, $\chi^2 = 19.44$, $p = 0.003$; D/L model, number of cases = 91, $\chi^2 = 17.10$, $p = 0.009$, number of cases = 90). Sex and season did not significantly affect any of the response variables (Table 1). However, the age class had a significant effect on all the response variables. In particular, cubs showed a lower number of quills (mean $7.70 \pm 1.14 \text{ SE}$) than subadult (mean $13.46 \pm 0.57 \text{ SE}$) and adult individuals (mean $14.93 \pm 0.51 \text{ SE}$). The quills were shorter in cubs (cms) (mean $2.06 \pm 0.14 \text{ SE}$) than in subadults and adults and in subadults (mean $3.72 \pm 0.11 \text{ SE}$) than in adults (mean $4.07 \pm 0.10 \text{ SE}$).

The quill diameter differed between cubs (cms) (mean $0.27 \pm 0.02 \text{ SE}$) and adults (mean $0.41 \pm 0.01 \text{ SE}$), with subadults (mean $0.36 \pm 0.02 \text{ SE}$) not showing any significant difference between the two other age classes scoring values in between. The diameter/length ratio was significantly higher in cubs (mean $0.13 \pm 0.01 \text{ SE}$) than in subadults (mean $0.10 \pm 5 \times 10^{-3} \text{ SE}$) and adults (mean $0.10 \pm 3 \times 10^{-3} \text{ SE}$) that did not differ significantly between each other. By the Tukey–Kramer post-hoc test we calculated differences between groups of significant predictors (see Fig. 2 for the results).

Discussion

The study of sonations in rodents is in its infancy and represents a challenge in the study of acoustic communication that deserves more attention. We studied the variability of rattle quills in African crested porcupines in Central Italy trying to address some issues on the possible function of sonations by analysing the acoustic apparatus producing sounds. Obviously, this is a preliminary step that needs to be further expanded through experimental and naturalistic observations. Our findings show that the passage from the cub to the subadult phase signs the most important changes in the development of quills which seem to occur around the first 6 months of life (Fig. 3). Overall, cubs have fewer (Fig. 2a) and stubbier rattle quills (Fig. 2d) compared to the other two age classes. Quills differed in their length across the three age classes (Fig. 2b), resulting in a quill length gradient. Finally, the diameter significantly differed between cubs and adults, with subadults falling in-between (Fig. 2c).

As predicted, our results indicate no difference between males and females in any of the rattle quill parameters considered. These data are in agreement with the lack of sexual dimorphism of *Hystrix cristata*. Finally, we also found that the season did not influence the morphology of rattle quills thus confirming the stability over time of these structures once they reach a complete development.

Although it is still uncertain whether the morphological differences observed in porcupines translate into acoustic differences, our data satisfies the two conditions that enable a trait to be used as a recognition cue (Sherman et al. 1997; Dale et al. 2001; Tibbetts and Dale 2007). The trait must be distinctive between different categories (e.g., age class) and

Table 1 Results of likelihood ratio tests for each model. LRT value and p-values for each predictor are shown

	Quill number		Tot. mean length		Tot. mean diameter		D/L	
	LRT	p-value	LRT	p-value	LRT	p-value	LRT	p-value
Season	0.602	0.896	5.429	0.335	5.751	0.124	7.253	0.064
Sex	1.609	0.205	1.013	0.724	0.277	0.599	0.914	0.339
Age class	35.099	<0.001	38.252	<0.001	10.909	0.004	11.378	0.003

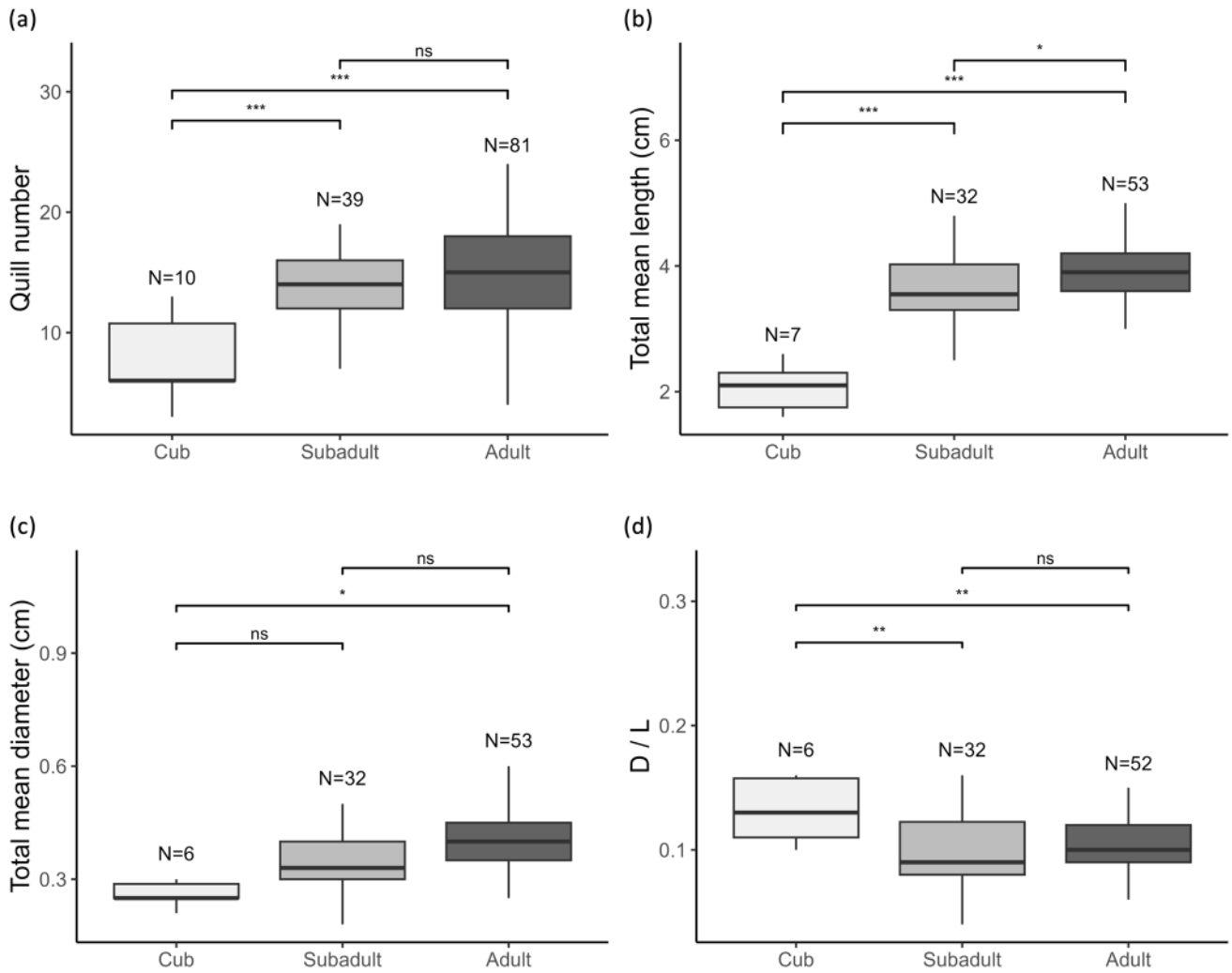


Fig. 2 Distribution of quills' **a** number, **b** total mean length, **c** total mean diameter and **d** mean diameter/total mean length ratio (D/L) across the three age classes. The number of observations for each group is reported on the x-axis. The thick line in each box corresponds to the median, while the upper and lower limits of the boxes

delimit the interquartile range. Significance levels of p-values calculated with the Tukey–Kramer tests comparing age class groups are shown in the upper part of each plot (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). The number of observations is reported above each

Fig. 3 **a** Close ups of a cub's and **b** an adult's tail, with (at least) 6 and 10 rattle quills, respectively. (Credits: V. Schi-
ani)



remain stable over time (e.g., seasons). Acoustic analyses associated with playback experiments are needed to clarify whether animals are able to produce different sonations and use them as recognition cues. We can only speculate about the linkage of quill morphology and the production of the rattling sounds in porcupines' communication.

The specialised morphology of rattle quills and the scarce variability between sexes and between subadults and adults support the hypotheses of the alerting and warning function of rattling. Since both male and female porcupines have similar roles in actively protecting and rearing offspring (Sever and Mendelsohn 1988; Mori et al. 2016; Coppola and Felicioli 2021), this can reflect into the presence of similar anatomical adaptations in the defensive domain. Like the sonation-producing feather modifications in crested pigeons (*Ocyphaps lophotes*), sexually monomorphic structures may produce sonations that are likely alarm signals (Murray et al. 2017). This makes it reasonable to assume that rattle quills have not been subjected to sexual selection, with our current findings providing support to this assumption.

In the light of the Source Filter Theory (sensu Clark 2014), we do not have information about which parts of the quills function as source or as filter in the modulation of the acoustic features of rattling, but our results prompt us to ask further questions. One is whether and how exactly the number, length and diameter of rattle quills can influence the rattling acoustic features. Their hollow and open portion can amplify the sound generated by quills colliding against each other. It is likely that having more, and larger rattle quills can affect the spectral features of the sound emitted. A way to assess how distinct anatomical features influence particular characteristics of the sound is replicating the mechanism of production artificially so that single anatomical parameters can be controlled (Clark 2016). Another possibility to produce different sounds could be due to the motor actions enacted by the subject during rattling: the same instrument can be played in different ways. The association with other sensory cues (e.g., vocalisations, postures) can enrich rattling with other elements that can provide different functions to the sonation (multimodal communication; Bradbury and Vehrencamp 1998).

Although it is unknown when and how often a cub produces rattling, the presence of quills at a very early stage of life indicates that they can be used potentially to emit sounds. Therefore, a crucial question is, what could be the benefit for a cub emitting sonations? The emission of rattling may not be adaptive for young individuals as the sound can be eavesdropped by potential predators (Peake 2005). The fact that porcupine cubs are equipped with morphologically distinct rattle quills does not necessarily imply that they emit rattling. While we know that newborns have softer rattle quills closed at the outer end (Mohr 1965) and that newborns are precocial and emerge relatively early from their burrows

(Coppola and Felicioli 2021), no data are available regarding the ontogeny of porcupines' multi modal defence display. Indeed, the development of porcupines' defence behaviour might be interesting to investigate further.

A limitation of our study resides in the impossibility to determine the uniqueness of the rattle quill morphology among different individuals that would require repeated measurements on the same animal across different age stages. Gathering data on quill morphology of a given subject for an extended period and, simultaneously, collecting behavioural data is the only approach allowing to establish a link between the rattle quill morphological and acoustic characteristics thus understanding whether differences at the individual level remain stable over time. Such an approach is obviously extremely challenging to carry out. Another limitation resides in the restricted number of individuals we were able to sample. Expanding the dataset, both in terms of number of subjects and geographical locations, would allow us to draw a more accurate picture of the variability of rattle quills in the Italian porcupine population.

Since Charles Darwin (1871)'s first reports, the role of bird sonations has been extensively explored. Yet, research on acoustic communication has only recently focused on mammal sonations that probably evolved numerous times independently, and this diversity allows exploring how acoustic communication systems emerged (Clark 2016). Expanding our focus on these numerous and diverse sound production mechanisms could provide a more comprehensive understanding of vertebrate acoustic communication.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42991-024-00454-y>.

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Author contributions Conceptualization and methodology: EM, EP Investigation: VS; Formal Analysis: VS, MG; Supervision: EP; Writing – original draft preparation: VS, EP; Review and editing: VS, MG, EM, EP.

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Data availability Data used for conducting analyses in this study are available in the Supplementary Material.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Ethical approval The data on quills were opportunistically collected on carcasses of animals deceased for accidental causes. Data on alive animals were collected with the aid of a camera without any manipulation of the subjects. The “Centro Recupero Animali Selvatici della Maremma” gave permission to take pictures of animals.

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