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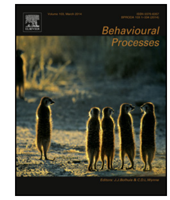

Vocal development during postnatal growth and ear morphology in a shrew that generates seismic vibrations, *Diplomesodon pulchellum*

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ABSTRACT

The ability of adult and subadult piebald shrews (*Diplomesodon pulchellum*) to produce 160 Hz seismic waves is potentially reflected in their vocal ontogeny and ear morphology. In this study, the ontogeny of call variables and body traits was examined in 11 litters of piebald shrews, in two-day intervals from birth to 22 days (subadult), and ear structure was investigated in two specimens using micro-computed tomography (micro-CT). Across ages, the call fundamental frequency (f0) was stable in squeaks and clicks and increased steadily in screeches, representing an unusual, non-descending ontogenetic pathway of f0. The rate of the deep sinusoidal modulation (pulse rate) of screeches increased from 75 Hz at 3–4 days to 138 Hz at 21–22 days, probably relating to ontogenetic changes in contraction rates of the same muscles which are responsible for generating seismic vibrations. The ear reconstructions revealed that the morphologies of the middle and inner ears of the piebald shrew are very similar to those of the common shrew (*Sorex araneus*) and the lesser white-toothed shrew (*Crocidura suaveolens*), which are not known to produce seismic signals. These results suggest that piebald shrews use a mechanism other than hearing for perceiving seismic vibrations.

1. Introduction

Some small mammals, such as golden moles (Afrosoricida: Chrysochloridae) and spalacid mole-rats (Rodentia: Spalacidae), appear to respond both to airborne sound and to seismic vibrations; the interrelationships between these sensory modalities and their potential use in communication have been of research interest for over two decades (Burda et al., 1990; Willi et al., 2006b; Mason and Narins, 2010; Bednářová et al., 2013). Shrews (Soricomorpha: Soricidae) are less well-studied, but recent investigations of the piebald shrew (*Diplomesodon pulchellum*) have revealed interesting bioacoustic parallels. Captive adult and subadult piebald shrews may vibrate the entire body when held, when lifted up in their plastic pipe shelters or when placed on a drum membrane in behavioural experiments (Volodin et al., 2012). These vibrations, at a frequency of 160 Hz, resemble the mobile phone "vibrate" mode and are apparently produced in response to a change in the substrate under their feet. These vibrations are always produced by non-vocalizing, silent animals (Volodin et al., 2012). At the same time, adult piebald shrews produce loud screech vocalizations with a deep, repetitive, sinusoid-like frequency modulation (pulse rate), coinciding in rate with the vibrations of the body (Volodin et al., 2012). In pups, the pulse rate of screeches is much lower than in adults (Volodin et al., 2015b). Body vibrations of 160 Hz are documented in piebald shrews from 34 days post-partum (Volodin et al., 2012), but have not been investigated in pups, so it is not known whether the screech pulse-rate increase, from pups to adults, is reflected in the ontogeny of body vibration too.

Piebald shrews represent a convenient model for studying vocal ontogeny, because the same call types and call variables can be measured across ages (Volodin et al., 2015b), and because of their rapid growth (Zaytseva et al., 2013). In mammals, body size and body mass increase progressively during ontogeny (Gaillard et al., 1997), whereas pathways of vocal ontogeny differ across species,

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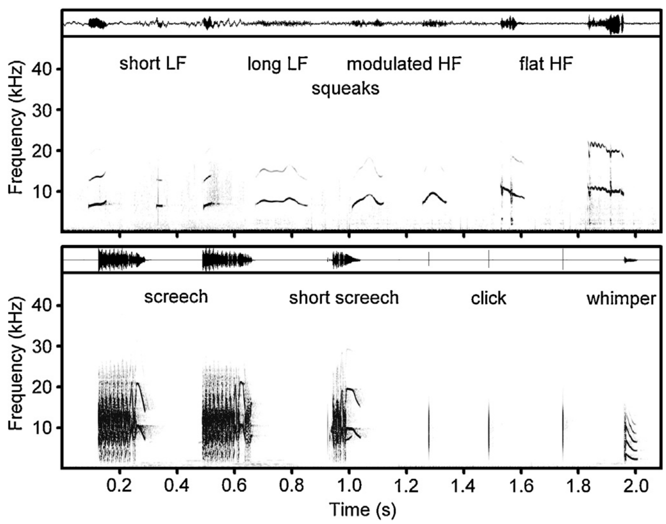

Fig. 1. Spectrogram illustrating eight call types of piebald shrew pups at 5 days of age. The spectrograms were created with a Hamming window, 48 kHz sampling rate, FFT 1024 points, frame 50% and overlap 87.5%. The audio files with these calls are provided in Supplementary material 2.

call types and call variables (Ey et al., 2007; Matrosova et al., 2007). The fundamental frequency (f0) is typically higher in juvenile mammals than in adults (Morton, 1977). This is because acoustic differences between juveniles and adults primarily result from the differences in sizes of sound-producing structures (Fitch and Hauser, 2002). In humans and many other mammals, the f0 is inversely related to mass and length of the oscillating portions of the vocal folds (Titze, 1994), and both mass and length increase together with the growth of the larynx (Kahane, 1978, 1982). In most mammalian species, the growth of these sound-producing structures is related to the growth of the body, which results in a steady descent of f0 with age (for instance, Briefer and McElligott, 2011; Efremova et al., 2011; Campbell et al., 2014). In humans, this pattern is complicated in males by an abrupt fall of f0 due to accelerated growth of the larynx at puberty (Fitch and Giedd, 1999; Lee et al., 1999). Nevertheless, in a few species of ground squirrels, the f0s of alarm calls are indistinguishable between pups and adults, in spite of much larger bodies and larynges in adults than in pups (Matrosova et al., 2007; Swan and Hare, 2008; Volodina et al., 2010). The f0 also increases with body growth in bat pups, in both echolocation calls and social calls (Jones et al., 1991; Hiryu and Riquimaroux, 2011; Jin et al., 2011, 2012).

An ontogenetic study of body traits and body mass in 18 litters of piebald shrews demonstrated that they grow very rapidly (Zaytseva et al., 2013), similarly to other shrews (Dryden, 1968; Vlasák, 1972; Michalak, 1987). In piebald shrews, weaning is at about 20 days of age (Vakhrusheva and Ilchenko, 1995) and first copulations were recorded at 27 days in females and at 40 days in males (Ilchenko et al., 2011). At separation from the mother at 22 days, shrews are comparable in body length to reproductively mature adults (62 mm and 70 mm, respectively, Zaytseva et al., 2013).

In captivity, piebald shrews produce eight call types, all within the human audible frequency range (<20 kHz): short and long low-frequency squeaks with nearly flat contour, high-frequency squeaks with modulated contour, high-frequency squeaks with fractured contour, short screeches and screeches, clicks and whimpers (Fig. 1). Seven of the eight call types are shared by pups and adults, suggesting that this vocal repertoire is established at birth (Volodin et al., 2015b). The previous cross-sectional study revealed that the f0 of all four types of squeaks were indistinguishable between pups and adults, whereas the f0 of screeches was higher in adults than in pups (Volodin et al., 2015b). However, the rate of deep sinusoidal frequency modulation (hereafter "pulse rate") of screeches was found to be substantially and significantly lower in pups than in adult piebald shrews. While an ontogenetic study of body features and a cross-sectional study of call types and call variables already exist, an ontogenetic study of the acoustics is lacking for this species.

Body vibrations are produced by silent piebald shrews, independent of any vocalizations (Volodin et al., 2012). Perhaps they generate these vibrations for communication purposes, for example as a warning aimed either at conspecifics or potential predators. Alternatively, they might use 'seismic echolocation' for spatial orientation purposes, analogous to what has been proposed for subterranean *Spalax* mole-rats (Kimchi et al., 2005). During the night, piebald shrews patrol their semidesert habitats and dig up invertebrates from depths of 2–3 cm in sand (Dubrovskij et al., 2011), so it is possible that they detect reflected vibrations from substrate heterogeneities, such as those related to the presence of their prey. Hypotheses relating to intraspecific communication and seismic echolocation demand that the shrews have a means of detecting seismic vibrations. In principle, seismic vibrations could be detected following radiation into the air, resulting in airborne sound which is detected by the ear in the normal way. Alternatively, vibrations could be detected directly if the body or head is in contact with the vibrating substrate, by somatosensory receptors or by a form of bone-conducted hearing (see Mason and Narins, 2010 for a review). Bone-conducted hearing may be the sensory modality employed by golden moles, in which the hypertrophied mallei may be used as inertial sensors (Mason, 2003a,b; Willi et al., 2006a); some unusual features of the ear of the mole-rat *Spalax ehrenbergi* have also been interpreted as adaptations to promote bone conduction (Rado et al., 1989), although this view has been challenged (Mason et al., 2010). Although piebald shrews are not subterranean mammals, their ability to produce seismic vibrations might similarly be reflected in their ear morphology: this possibility has not been investigated previously.

The general focus of this study was to consider the relationship between vocal and body ontogeny, and to explore whether functional associations exist between vocalizations, vibration generation and ear morphology. The particular aims were (1) to define the relationships between changes in acoustic variables, body mass and head length during the ontogeny of piebald shrews, and (2) to examine the ear morphology to see if there are any obvious adaptations promoting vibratory sensitivity.

2. Materials and methods

2.1. Study site and subjects

Calls as well as measurements of body mass and head length were collected from members of a captive colony of piebald shrews at Moscow Zoo, Moscow, Russia, from 1 June to 22 August 2011. Our live subjects were 40 piebald shrews (24 males and 16 females from 11 litters) examined from birth to separation from the mother at 22 days of age. All study animals (3rd–6th generations in captivity) were descendents of 27 animals collected in 2008 in the Astrakhan Region, Russia (47°12′33″N; 48°18′45″E).

The animals were kept under a natural light regime at room temperature (24–26 °C), in family groups consisting of a mother and littermates. The animals were housed in plastic cages of 53 × 76 × 42 cm, with a bedding of sand and dry moss, various shelters and running wheels. They received custom-made small insectivore chow with insect and calcium supplements, and water *ad libitum*. Before parturition, females were checked twice a day for the appearance of a litter, and birth dates as well as the number of pups were recorded. Litter size varied from 3 to 6 pups