Chapter 4
Nasal-Emission and Nose leaves

Scott C. Pedersen and Rolf Müller

Abstract Despite all other craniodental adaptations, the head of most bats must function as an ultrasonic emitter and receiver. Not all echolocation calls are ultrasonic, but all either are emitted from an open mouth (oral-emission) or are forced through the confines of the nasal passages (nasal-emission), and some nasal-emitting bats alternate between modes as the situation demands. The conspicuous baffles that surround the nostrils of nasal-emitting bats are not ornamental structures; rather, these "noseleaves" serve several important acoustic functions and are considered to be the earmark of nasal-emitting bats. For many readers, the difference between oral- and nasal-emission is viewed as a simple character state, most likely tied to the vagaries of foraging ecology in some tangential manner. However, Pedersen and Timm (Evolutionary history of bats: fossils molecules and morphology. Cambridge University Press, Cambridge, pp 470–499, 2012) reviewed a considerable volume of literature discussing how the advent of nasal-emitting bats required a dramatic redesign of the microchiropteran rostrum and skull base during development. Nasal-emission is therefore a key innovation responsible for two of the most dramatic morphological radiations in the Chiroptera—phyllostomid and rhinolophid + hipposiderid bats. Herein, we summarize and update that review and then discuss recent advances in the numerical analysis of form and function in regard to the beamforming function of noseleaves (Müller, J Acoust Soc Am 128:1414–1425, 2010).

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4.1 Bat Heads

The vertebrate head is an evolutionary novelty—most of its genes, tissues, and segmental arrangement were cannibalized from old postcranial material. The differential sequence of events that occur during construction of the mammalian head is typically ignored in phylogenetic reconstructions. Instead, the skull is presented as an immutable structure into which the brain, ears, and eyes are squeezed during development. The converse is in fact true—the skull should be seen as a complicated cast of, and not a mold for, craniofacial evolution (Carroll 2005; Chai and Maxson 2006; Creuzet et al. 2005; Fondon and Garner 2007; Hallgrìmsson and Lieberman 2008; Hallgrìmsson et al. 2007, 2009; Marcucio et al. 2011; Radlanski and Renz 2006; Young and Badyaev 2007; Young et al. 2010).

Using cephalometric data collected from skulls of fetal and adult bats, Pedersen (2000) described the inertial and acoustic axes of the chiropteran skull. These data showed that skulls of bats that produce echolocation signals with their larynx (Microchiroptera; sensu Dobson 185) follow one of two mutually exclusive sets of construction rules based on the ultimate use of either the oral cavity or the nasal cavity/facial skeleton as a waveguide. In general, the rostra of oral-emitting bats are stereotypically located well above the inertial axis of the head in flight (dorsiflexed), whereas nasal-emitting bats fly with their rostra at or well below the inertial axis of the head (ventroflexed; Fig. 4.1) and their noseleaves aligned perpendicular to the direction of flight.

This dramatic dichotomy in skull design and head posture is laid down very early in development. The plesiomorphic condition for mammalian embryos is exemplified by mormoopids, emballonurids, and vespertilionids wherein the fetal rostrum and hard palate rotate dorsally about the braincase until they are aligned with or elevated well above the basicranium. In contrast, the palate of nasal-emitting forms is retained ventral to the basicranial axis. This dichotomy between oral- and nasal-emitting baupläne imposes dramatic changes in the subsequent development of the entire head and the sensory organs therein, i.e., rotation of the eyes and otic capsules so as to align them with the inertial axis of the head. These baupläne are well established before the skull begins to ossify and well before the forces of mastication begin to effect other aspects of skull morphogenesis.

This dichotomy is not a simple reversible character state as some would suggest (see below). Rather, it reflects a fundamental renovation of the head and skull—arguably the most important innovation in bats beyond the evolution flight and echolocation.

4.2 Nasal-Emitters

There are, however, two different types of nasal-emitting head: (1) highly derived forms in which the organization of the nasal cavities is effectively dominated by the emission of acoustic signals (rhinolophid and hipposiderid bats) and (2) less-derived

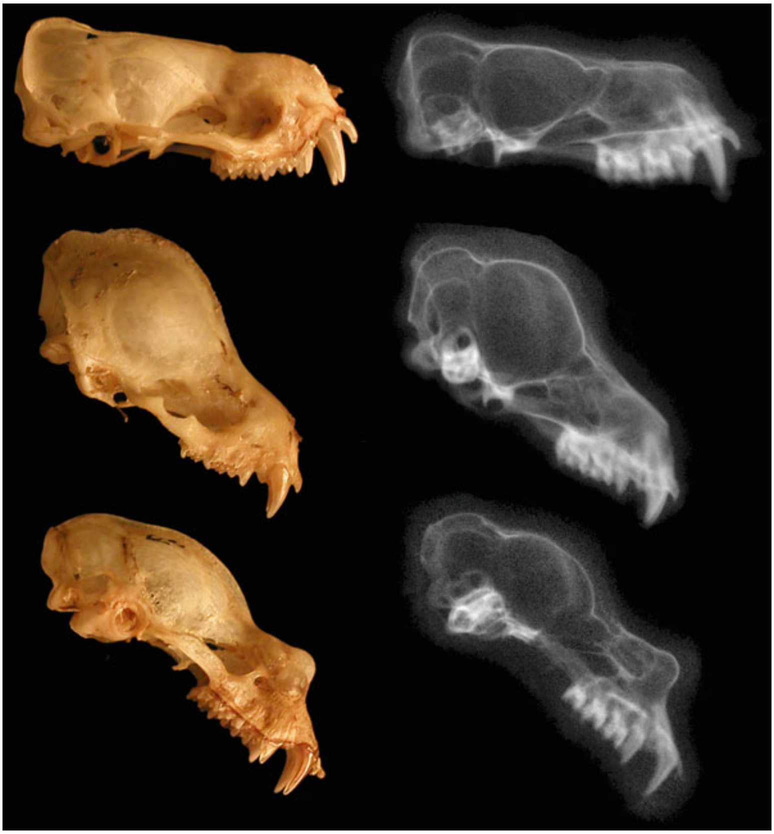

Fig. 4.1 Representative photographs and radiographs (*top* to *bottom*): oral-emitting molossid, *Eumops glaucinus* (male); nasal-emitting phyllostomid, *Lophostoma silvicolum* (male); and a nasal-emitting rhinolophid, *Rhinolophus yunanensis* (male). Each image is oriented such that the plane of the semicircular canals is elevated equally above the horizontal. This orientation is a crude approximation of how the heads are held in flight. Images are not to scale and are for comparison purposes only

forms in which nasal-emission is not the primary modality driving the layout of the head and face. In these bats, other functions may be equally or more important than nasal-emission, e.g., vision, olfaction, and perhaps the suspension of the tongue (phyllostomids). Given that the packaging of the embryonic head is a balancing act between many competing factors (differential growth of various soft tissue elements, morphogenetic plasticity of skeletal elements, dental ontogeny, tongue size, etc.), Pedersen (2000) suggested that there was only enough room in the rostrum of a nasal-emitting bat skull to develop 1–2 sensory modalities at any one time—having either large olfactory fossae or expansive resonating chambers, but not both. This is a readily testable hypothesis. Have phyllostomids retained olfaction at the cost of sound pressure amplitude of the call, whereas rhinolophids and hipposiderids have emphasized sound pressure amplitude of the call at the expense of olfaction?

This superficial dichotomy is misleading because many phyllostomids are not obligate nasal-emitters and the oral-emission of their calls may result in higher pressure amplitudes (Marcías et al. 2005; Mora and Marcías 2006).

4.3 Skull Mechanics

Regardless of their relative position on the neurocranium, opposing jaws, teeth, and muscles function together as components of a well-integrated system (Soukup et al. 2013; reviewed by Pedersen and Timm 2012). During mastication, the rostrum and zygomatic arches brace the palate against the braincase posteriorly, which then transfers these forces to the occiput, cervical spine, and thorax. In oral-emitting skulls that are strongly dorsiflexed (e.g., *Thyroptera*) or in the strongly ventroflexed crania of *Rhinolophus*, the distribution of bone mass suggests that these skulls are poorly designed to resist torsional/bending forces. Thus, soft tissues such as muscle, ligament, and tendons must compensate in part for the significant reduction of boney architecture, or alternatively, these extreme forms are limited to soft-bodied prey items. Despite sharing the nasal-emitting bauplan (and excluding the highly derived nectivorous forms), phyllostomid skulls are considerably more robust than those of most rhinolophids or hipposiderids (Davis et al. 2010; Monteiro and Nogueira 2011; Nogueira et al. 2009; Santana et al. 2012). It would therefore be of interest to see if durophages (Dumont 2004; Dumont et al. 2011; Freeman 2000; Freeman and Lemen 2010) exhibit more moderate skull angulations within their particular oral- or nasal-emitting construct.

4.4 Rostrum as Vocal Tract

Gross modification of the rostrum and midface is related to vocalization in many mammals (Frey et al. 2007). Of interest, the sound produced by the larynx is not necessarily what nasal-emitting bats emit from their nostrils. Differential filtering of the source spectrum is effected primarily by the dimensions of the vocal tract and discontinuities in the walls of the pharynx and trachea. In taxa with minimal modification to the rostrum, the projection of sound through the high impedance of the nasal passages may restrict those taxa to the use of low-intensity multiharmonic calls (nycterids, megadermatids, and many phyllostomids). Conversely, extensive modification of the nasal cavities and pharynx may well restrict the range of craniodental adaptations available to a taxon, e.g., rhinolophids.

Depending on prey type, foraging strategy, and habitat complexity, both oral- and nasal-emitting bats may shift between different types of calls or modulate where they put energy into each call (Fenton, Chap. 3). Within a taxon, this variation in call structure may be best viewed as a behavioral response to clutter and selection of prey type (Surlykke and Moss 2000). Call design has also been mapped onto various molecular and morphological phylogenies but with only limited success (Eick et al. 2005; Jones and Holderied 2007; Jones and Teeling 2006), but this is not surprising given the remarkable behavioral plasticity demonstrated by extant bats. However, what constraints are imposed on call design or call structure as sound is projected through the confines of the nasal passages?

4.4.1 Phyllostomids

The low-intensity calls of many phyllostomids led Griffin (1958) to refer to them as “whispering bats.” However, recent work has shown these bats are capable of being much louder than previously believed (Brinkløv et al. 2009, 2011). There is considerable variation amongst phyllostomid bats in terms of which harmonics and the number of harmonics that are differentially recruited into the call under different circumstances (Jennings et al. 2004). The fundamental frequency (f_1) is commonly used by these bats during search and commuting, but they often shift up into the second and/or third harmonics when moving into clutter or running up onto a roost; this pattern is observed in several subfamilies (*Macrophyllum*, Brinkløv et al. 2010; *Phyllonycteris*, Mora and Marcías 2006; *Phyllops*, Marcías et al. 2005).

In contrast to rhinolophids and hipposiderids, the rostra of phyllostomids have not been grossly modified to accommodate nasal-emission, and differential use of the upper harmonics in many of these taxa would seem to be a flexible behavioral adaptation. However, the diversity of noseleaf shapes (see below), in conjunction with the moderate inflation of the rostrum in *Lonchorhina*, and the limited modification of the paranasal sinuses in *Micronycteris* (Vanderelst et al. 2010a) suggest that the acoustics of phyllostomine skulls may be unique amongst phyllostomids. Otherwise, morphological diversity in the phyllostomid rostrum is well correlated with membership in a specific feeding guild and structural allometry (Dumont et al. 2012; Monteiro and Nogueira 2011; Nogueira et al. 2009; Wetterer et al. 2000).

4.4.2 Rhinolophids and Hipposiderids

The unique shape of these skulls is characterized by the gross dilation of the nasal cavities and paranasal sinuses. This modification reduces the impedance of the nasal passages, effectively transforming them into a major component of the vocal tract. In addition, the robust larynx of many rhinolophids (and presumably hipposiderids) is retained within the nasal shunt by a unique arrangement of muscles of the soft palate and the cartilages of the larynx. This arrangement implies that rhinolophids may be obligate nasal-emitters. In concert, these extensive modifications effect a derangement of adjacent musculoskeletal elements associated with the soft palate and pharynx, e.g., pterygoid width, abbreviated hard palate, large-bore choanae, and otic capsule separation. Arguably these are the most extensive structural modifications to the skull within the order.

Ossification of bat skulls follows the common mammalian pattern. The few exceptions to this plan are found in rhinolophids and are related to this unique distortion and packaging of the midface. Shifts in the ossification sequence also include skeletal elements involved in the suspension of the larynx from the basicranium in rhinolophids and hipposiderids. Perhaps future discussion concerning the evolution of echolocation would be well served by evaluating the embryology of the trachea, tracheal diverticula, and basicranial pits in the skull base (Cretekos et al. 2005; Debaeremaeker and Fenton 2003; ten Berge et al. 1998; Veselka et al. 2010). Many oral-emitting bats and nearly 70 % of phyllostomid taxa exhibit these pits; however, they are rare (6 %) in rhinolophids and hipposiderids. It would be interesting to see if there is a reciprocal arrangement between the presence of supra- and subglottal resonators across taxa.

4.4.3 Linear Model of the Rhinolophid Vocal Tract

Simple linear models of the supraglottal vocal tract suggested previously that the composition of the midface and differential development of the paranasal sinuses could be associated with fixed cavity resonances which subsequently affect the sound levels and frequency profiles permitted by the supraglottal vocal tract (Armstrong and Coles 2007; reviewed by Pedersen and Timm 2012). In general, the nasal passages have been viewed as a band-pass filter for the second harmonic, i.e., they suppress the fundamental and several of the remaining harmonics. We reopened this line of inquiry to readdress the physics of the enormous sound levels produced by some species. We used micro-CT to reconstruct the airway of *Rhinolophus ferrumequinum* to quantify vocal tract dimensions (Fig. 4.2). We also evaluated the resonant mechanics of this system, testing both linear and nonlinear numerical models of the sub- and supraglottal vocal tract. The relative position of several landmarks along the length of the vocal tract matches the predictions of the model and those expectations of previous studies regarding the dominant spectral component of the call (f_2 wavelength, 4.45 mm; 77 kHz).

Due to their simplicity, linear models of the vocal tract have been instructive in a variety of studies. Recordings of foraging bats have shown that their foraging ecology is better explained by the dimensions of the nasal cavities than by body size or environmental variables in both *Rhinolophus* (Odendaal and Jacobs 2011) and *Rhinonicteris* (Armstrong 2002; Armstrong and Coles 2007; Armstrong and Kerry 2011), even despite excessive respiratory water loss in arid environments (Nelson et al. 2007). Developmentally, neither the nasal cavities nor the pinnae of *Rhinolophus* seem to exhibit the linear dimensions necessary for sending or receiving the dominant spectral component of the adult call (f_2) until well after birth (Funakoshi et al. 2010; Liu et al. 2007). Similar data were used to model the differential filtering of other harmonics in the developing rostrum (Pedersen 2000).

The geometry of the vocal tract influences the coupling of laryngeal sound and its propagation towards the nostrils; however, utilitarian linear transfer functions

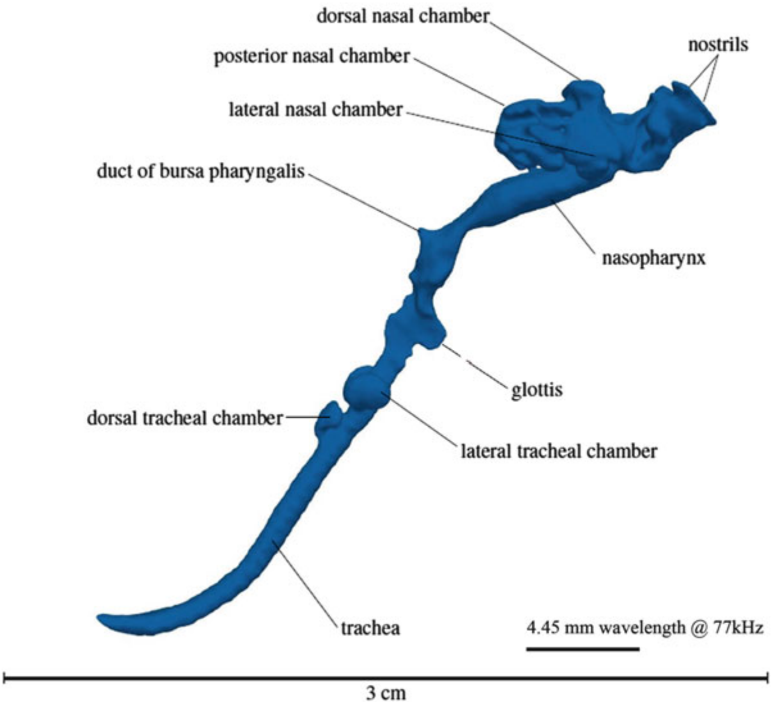

Fig. 4.2 Micro-CT reconstruction of the vocal tract of *Rhinolophus ferrumequinum* (from Pedersen et al. 2009)

alone are insufficient to explain the reactance of the pharynx or the efficiency of the larynx—both of which would clearly benefit from further study.

4.5 Noseleaf Structure

Noseleaf size, shape, and complexity exhibit considerable variation among taxa. Two structural elements can be found in most noseleaves: an anterior leaf that resembles a horn-shaped baffle and a posterior leaf that is often ornamented with a wide variety of cavities, furrows, or ribs. In rhinolophids, a third structure resembling a gnomon-like spike (sella) is found just above and between the nostrils, but it is unclear if and how this element is represented in the closely related hipposiderids. The majority of phyllostomid bats exhibit a noseleaf with a distinct horseshoe and a posterior element referred to as the spear—a diminutive sella appears in a small number of phyllostomines (Wetterer et al. 2000). Phyllostomid spears often exhibit shallow depressions that are oriented vertically along the sides of a central rib (Wetterer et al. 2000). The dramatic spears of megadermatids also exhibit deep vertical furrows (e.g., *Lavia*) and beg further analysis (Göbbel 2002a).

The relative proportions and ornamentation of these various parts of the noseleaf are useful as character states in phylogenetic reconstructions (Csorba et al. 2003; Wetterer et al. 2000).

The homology of noseleaves is still under debate (Göbbel 2000, 2002a; Springer et al. 2001a; Yokoyama and Uchida 2000). However, noseleaf primordia appear before the eyes and external ears are visible in many bat embryos, indicating that such ornamentation is related to deep taxonomic differences in developmental timing and the construction of the head in general (Göbbel 2000, 2002a, b; Chen et al. 2005; Cretekos et al. 2005, 2007; Giannini et al. 2006; Nolte et al. 2008; Wyant and Adams 2007; Yokoyama and Uchida 2000).

Additional work is clearly warranted if we are to understand noseleaf function in (a) taxa where we observe dramatic reductions in the size and complexity of the leaf (*Centurio*, vampires, brachyphyllines, many glossophagines) or (b) oral-emitting taxa that exhibit fleshy masses around the nostrils (plecotines, *Antrozous*, *Craseonycteris*, or *Rhinopoma*). The articulated facial cleft of nycterids is unique, but its components seem homologous to the noseleaves of hipposiderids. Pedersen (1995) was incorrect in thinking that the volume of space within the cleft might function as a "resonating chamber outside the bony nasal cavity." Rather, this cleft and its associated palps function much like a noseleaf—the upper portion of the concavity is a focus-reflecting baffle for the near field but also narrows the far-field beam for the third and possibly the fourth harmonics (Zhuang et al. 2012).

4.6 General Function and Dimensions of a Noseleaf

Sound produced by the vocal folds travels through the nasal passages and is subsequently radiated from the nostrils into a three-dimensional free field around the bat's head. The noseleaf is therefore situated at a critical position in the bats' biosonar system, where it could act as an acoustic horn which will gradually match the high acoustic impedance of the nostrils to the low acoustic impedance of the free field. Beyond a short transition zone (the acoustic near field), the distribution of acoustic energy in the radial dimension is determined by the geometrical spreading losses and the absorption associated with propagation in air. Here again, the noseleaf is in a critical position to determine the distribution of energy as a function of direction and frequency. Hartley and Suthers (1987) argued that without a noseleaf, the directionality of nasally emitted ultrasound is considerably degraded, i.e., the evolution of nasal-emission may have predicated the subsequent evolution of noseleaves.

The beamforming capacity of the noseleaf is currently receiving considerable attention (Fig. 4.3; Müller 2010). Certainly, narrow beams are advantageous for the spatial separation of echoes of interest from those of surrounding clutter—wide beams can be used to search for targets in open space and retain an overall awareness of obstacles in the environment (Müller and Kuc 2000). Models indicate that large noseleaves could potentially be more directional than small leaves. However, there are physical limitations on the overall dimensions of a large noseleaf in terms of structural

Fig. 4.3 Digital models of representative noseleaf shapes (after Müller 2010)

integrity and the risk of deformation in flight, let alone the additional energetic cost associated with pushing a large noseleaf through the air (Bullen and McKenzie 2008; Gardiner et al. 2008). Interestingly, Brinkløv et al. (2011) showed that big noseleaves are not necessarily associated with a narrower beam but rather provide the bat with some degree of flexibility in terms of beam steering as the situation demands.

Nevertheless, a nasal-emitting bat of a given body mass could theoretically improve the directionality of its call by (1) building a bigger noseleaf, or (2) generating higher frequencies in the larynx, or (3) differential use of the upper harmonics, or (4) tuning the nasal passages to enforce specific harmonics with an efficient resonator. Whether deployed singly or in combination, each of these options is physically limited by the allometry of the body and respiratory tract, the atmospheric attenuation of sound, and certainly taxonomy.

4.7 Beamforming

Previous analyses of the functional morphology of noseleaves were limited to measurements of size and shape, but it was difficult to say *a priori* how each measurement might relate to our understanding of the acoustic functions of noseleaves (see Müller 2010). More recently, computational numerical methods have been used to investigate the relationships between baffle geometry, acoustic mechanisms, and resulting beam patterns in nasal-emitting bats. Key advantages of such approaches are the efficient, high-resolution estimation of beam patterns and the malleability of the underlying shape representations. Readers are directed to a great volume of literature concerning the pinnae of nasal-emitting bats (De Mey et al. 2008; Firzlaf and Schuller 2003; Ma and Müller 2011; Reijniers et al. 2010; Vanderelst et al. 2012; Wang and Müller 2009; Zhao et al. 2003). In this context, we will limit our discussion to noseleaves.

In *Rhinolophus rouxi* (Zhuang and Müller 2007), there would seem to be a "division of labor" between the various parts of the noseleaf, in which the primary function of the anterior leaf and sella appears to be an overall focusing of the beam, whereas the sella and lancet introduce a frequency-specific widening. The phyllostomid noseleaf does not seem to be as sophisticated (Vanderelst et al. 2010a, b). The frequency specificity of these various structures would allow the bat to use separate frequency channels for performing tasks that are better served by either wider or narrower beams—narrow beams for targeting and wide beams for landmark identification and contour following. Each component of the noseleaf will be dealt with in turn below.

4.7.1 Anterior Leaf and Nostrils

The horn-shaped baffle that encircles the ventral aspect of the nostrils exhibits considerable variation amongst nasal-emitters. At the extremes, it takes on distinctly conical shapes (e.g., *Rhinolophus*, *Rhinonicteris*, and several phyllostomines). In other cases, it appears as a less distinct dish-shaped baffle (e.g., some stenodermatines and hipposiderids) or is significantly reduced in some forms such that a baffle is not grossly distinguishable (e.g., brachyphyllines, *Desmodus*, *Centurio*).

The tissues of the anterior leaf surround and support the nostrils. However, the nostrils and anterior leaf are not necessarily coplanar, and the connection between each nasal cavity and the plane of the nostril is not a simple tube. Instead, this passage is a very complicated waveguide, the construction and embryology of which differentiate phyllostomid from rhinolophid noseleaves (Göbbel 2000) and those in turn from the unique floor of the facial cleft in nycterids (pers. obs.; Zhuang et al. 2012).

In contrast to the single point source of oral-emitting bats (mouth), the spacing between the two point sources (nostrils) could influence the forward constructive interference and directionality of the nasally emitted sound (Schnitzler and Grinnell 1977). Narial cartilages and their associated musculature are embedded within the body of the anterior leaf and are in a position where they could effect the spacing of the nostrils and thereby affect the beamforming capacity of the noseleaf (Göbbel 2000 and references). In addition, nasal-emitting bats may have the option of steering or otherwise modifying the beam pattern via the differential positioning of the nostrils within the noseleaf (Göbbel 2002a, b; Vanderelst et al. 2010a) or by imposing differential impedance at either nostril via the valvular nature of the nostril itself.

4.7.2 Posterior Leaf: Lancet and Spear

The lancets of rhinolophids and many hipposiderids exhibit unique half-open cavities (furrows and cells) that are oriented transversely across the upper portion of the leaf. Numerical experiments suggest that these furrows act as half-open resonance

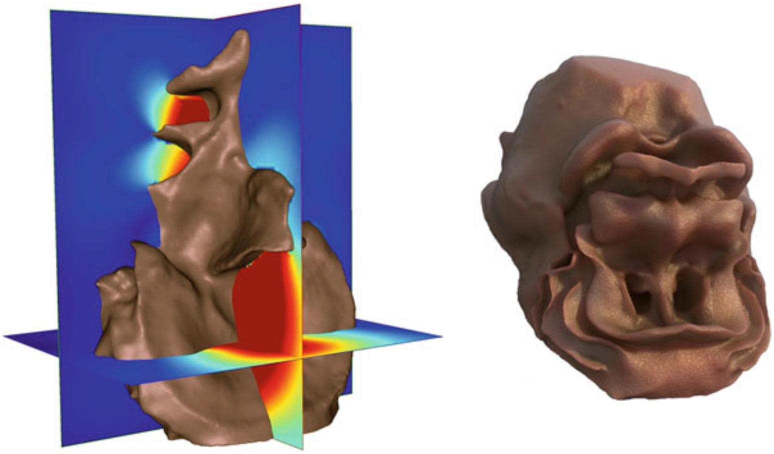

Fig. 4.4 *Left*: digital model of the noseleaf of *Rhinolophus rouxi* that indicates the sound pressure amplitude for 60 kHz in the near field. Note the spatial maxima associated with the lancet furrows (from Zhuang and Müller 2006). *Right*: digital model of the noseleaf of *Hipposideros armiger* (Via Dane Webster)

cavities (Zhuang and Müller 2006, 2007; Fig. 4.4). Sound waves emitted from the nostrils pass across the open face of these furrows and trigger cavity resonances therein. Such resonance effects are typically confined to a very narrow range of frequencies. As such, these furrows are well suited to alter the behavior of a device such as a noseleaf within an already narrow frequency band of operation (CF call). In *R. rouxi*, this effect was most notable in those lower frequencies found in the FM tail of their CF call wherein these furrows effectively widen the biosonar beam in a transient fashion. Horseshoe bats may use these resonances to produce both wide and narrow beam patterns within the confines of a single biosonar pulse. It may be advantageous for a high duty cycle CF bat to illuminate the environment simultaneously through both narrow beams (targeting) and wide beams to retain an overall awareness of obstacles in the environment (Müller and Kuc 2000). Wide beams, even if produced intermittently, are thought to assist in ground tracking while the bat is otherwise focused on targets of interest directly ahead (Ghose et al. 2007; Kuc 2011; Zhuang and Müller 2006, 2007).

In contrast, Vanderelst et al. (2012) found that these same furrows (*R. rouxi*) focus the FM portion of the beam rather than expand it in the vertical dimension (Zhuang and Müller 2007). Vanderelst et al. (2012) also argued that these furrows affect the acoustic near field in the same way that building a taller lancet might—that is, getting a narrower beam from a smaller, albeit highly modified, aperture. These contrasting results could be due to small differences in the specimens used in the construction of their virtual models (e.g., size and sex of the source head) or perhaps be the result of distortion during preservation of the original specimen (Müller 2010) or perhaps in regard to their assumptions about nostril position or leaf orientation in flight. It could also be that the bats can use their noseleaf musculature to reconfigure the leaf shape such that the cells could have a different effect. Clearly, a taller lancet would be a more pragmatic solution (from an embryological perspective) as the elaborate cavities and furrows seem extravagant by any measure (see above; Bullen and McKenzie 2008).

In *Hipposideros*, the posterior leaf does not assume the upright triangular form that characterizes the relatively delicate rhinolophid lancet. Instead, it is considerably fleshier and exhibits a more rounded, arcuate outline (coronet) when viewed anteriorly. Its anterior surface is often concave and may be divided into shallow cells separated by vertical septa. The posterior leaves of other hipposiderids are more delicate and quite ornate (*Rhinonicteris*, *Triaenops*). There are no obvious sellae in these bats. The nostrils lie at the bottom of a central facial hollow surrounded by the horseshoe.

The relative simplicity of the spear in phyllostomid bats has been shown to limit beam spreading in the vertical direction, e.g., *Carollia perspicillata* (Brinkløv et al. 2011; Hartley and Suthers 1987), *Micronycteris microtis*, and *Phyllostomus discolor* (Vanderelst et al. 2010a, b). Beam widths in these three bats are comparable, but not surprisingly, the beam would seem better focused in the gleaning insectivore *Micronycteris* (Vanderelst et al. 2010a). Several aspects of noseleaf structure, size, and shape have been tied to foraging behavior and diet in phyllostomid bats (Wetterer et al. 2000), but the function of the phyllostomid noseleaf may lie equally in the manner in which returning echoes pass around the head to the pinnae, i.e., the head-related transfer function (De Mey et al. 2008; Reijniers et al. 2010; Vanderelst et al. 2010a, b; Feng et al. 2012).

4.7.3 Sella

Morphological variation in rhinolophid sellae is remarkable, but they are apparently absent in hipposiderids and arguably insignificant in those few phyllostomids that posses them.

Since the different components of the noseleaf operate in close proximity to each other to shape the acoustic near field, interactions between their acoustic effects are likely. An example of this was found in the interaction between the cavities of the lancet and the sella in the rufous horseshoe bat (Zhuang and Müller 2007). Due to its position, the ultrasonic waves emitted through the nostrils must diffract around the sella before they can trigger a resonance inside the lancet cavities. The ability of a wave to diffract around an obstacle depends on the ratio between wavelength and obstacle size. Low frequencies with longer wavelengths are better suited for propagation into the space behind an obstacle than higher frequencies associated with shorter wavelengths. This dependence of diffraction and shadowing on wavelength influences the interaction between the lancet cavities and the sella in terms of the beam pattern. Not only is the resonance of the furrows much stronger for the lowest frequencies in the FM portion of the call, but the higher CF frequency band is attenuated by the sella. Hence, the interaction between the two effects sharpens the differences between high and low frequencies (Müller 2010; Zhuang and Müller 2007).

4.8 Movement of the Noseleaf and Head Orientation

Echolocating bats can readily insonify a target by simply aiming the head at the target. However, nasal-emitting bats have the option of steering the beam independent of head movement, via gross movements of the noseleaf or the differential positioning of the nostrils within the noseleaf. Early work done on noseleaf function assumed a static baffle geometry; however, noseleaves are dynamic structures. Voluntary control over the associated facial musculature allows a bat to orient the leaf and to coordinate its movement with pulse emission (Feng et al. 2012; Göbbel 2000; Vanderelst et al. 2010a, b).

4.8.1 Rhinolophids

In rhinolophids, noseleaf displacements are not vibrations at the ultrasonic carrier frequency, i.e., they are not involved with sound radiation per se (contra Kuc 2010). Instead, during the emission of a pulse by *Rhinolophus ferrumequinum*, the outer rim of the horseshoe twitches forward and inward to decrease the aperture of the noseleaf and increase the curvature of its surfaces. This distortion is significant and may amount up to ¼ of a wavelength in the CF portion of the call. These nonrandom motions are not present in all recorded pulses and can apparently be switched on or off. Displacement amplitudes are significant in comparison with the overall size of the horseshoe and the sound wavelengths, but the measured velocities of the noseleaf are too small to induce Doppler shifts of any significance (Feng et al. 2012).

4.8.2 Phyllostomids

Phyllostomid noseleaves vibrate in concert with call emission as well (Hartley and Suthers 1987). At the time of this writing, the authors are not aware of studies being performed on phyllostomids in parallel to those done by Feng et al. (2012). However, numerical models have shown that different positions of the phyllostomid noseleaf may effect significant changes in the outgoing signal (Vanderelst et al. 2010a, b). As such, future attempts at understanding the function of noseleaves will have to incorporate a dynamic component and some novel approaches.

4.8.3 Head Aim

Given the importance of head orientation in terms of effective target illumination and subsequent acquisition of the echo, we can assume that the mutual alignment of the noseleaf, pinnae, inner ear, and general posture of the head should each convey some level of efficiency to the system. Arguably, there should exist some "null" head posture within each emission type (oral or nasal) about which the bat could actively scan. But is there any consistency amongst studies in regard to the quantifying what is meant by head posture, noseleaf orientation, and beam direction?

Using a variety of experimental approaches, several studies have related "head aim" with the subsequent illumination of a target in several species of bat, including *Myotis* (Surlykke et al. 2009b; Surlykke and Kalko 2008), *Eptesicus* (Surlykke et al. 2009a; Ghose and Moss 2006; Ghose et al. 2007), *Carollia* (Brinkløv et al. 2011; Hartley and Suthers 1987), *Macrophyllum* (Weinbeer and Kalko 2007), *Micronycteris* (Vanderelst et al. 2010a), *Phyllostomus* (Firzlaf and Schuller 2003), *Rhinolophus* (Schnitzler and Grinnell 1977), and *Rousettus* (Yovel et al. 2010). Despite their intrinsic value, the results of these various efforts can be difficult to reconcile as each is limited by unique methodological constraints.

In broad strokes, the accurate estimation of the diameter/orientation of the nares can be adversely affected by preservation artifacts in the original specimen or by inaccurate assumptions about the physiology of the head/noseleaf in a live animal. Data from intact (or mostly intact) live animals may in turn be biased by limitations imposed on bat behavior by restraint or sedation. In an attempt to register the axis of an emitted call, several studies have utilized the position of external landmarks as a proxy for the orientation of the vocal tract or head. However, such landmarks are unreliable due to the dynamic nature of the skin and tissue preservation. There is no obvious reconciliation. However, future studies that relate the soft tissues of the vocal tract, noseleaf, and pinnae with specific osteological landmarks of the skull would permit a most welcome integration of several fields of study.

4.8.4 Head Aim and Body Posture

Still photographs and high-speed video recordings of bats in flight substantiate the general dichotomy between oral- and nasal-emitting bats in terms of head posture. Many echolocating bats exhibit gross movements of the head about the body during slow flight, presumably scanning their environment. In directed flight or pursuit, bats keep the "head" aimed directly at a target and the body subsequently follows. Video and photographic data reiterate the great range of body posture exhibited by bats in different flight profiles: commuting, trolling, attack, moving through heavy clutter, on approach, or departure from roost/obstacle/target. Assuredly, body posture is related to flight dynamics (velocity, body size, forearm length, wing shape) and taxonomy. As before, technological difficulties limit our understanding of each of these behaviors, but where possible, a more integrated approach is desirable in the future.

4.9 Evolution of Nasal-Emission and the Yinpterochiroptera

Despite the wealth of morphological and behavioral data at hand, and acknowledging the derivation of powerful numerical and phylogenetic models by which we can process this data, much of what we think we know about the evolution of bats, let alone nasal-emission in bats, relies on a good number of assumptions regarding the *emergence* of form. Fortunately, this last decade has witnessed giant steps forward in the field of developmental genetics. As such, the driving force behind the evolution of morphological novelty in bats will likely not be found in some gene sequence, rather it will be from an understanding of developmental timing and the sequential activity of regulatory genes (Carroll 2005; Cretekos et al. 2005, 2007; Davidson 2006; Göbbel 2000, 2002a; Hallgrìmsson et al. 2007; Hockman et al. 2008; Morsli et al. 1999; Müller and Newman 2005; Radlanski and Renz 2006; Sears et al. 2006; Willa and Rubinoff 2004; Wang et al. 2010).

Nevertheless, recent reconstructions of bat phylogeny continue to rely on an ever-increasing volume of gene sequence data drawn from throughout the genome. This, despite the often considerable discordance between these molecular trees and those generated using morphological/fossil data (Giannini and Simmons 2007; Simmons and Geisler 1998; Springer et al. 2001b). Gene-based phylogenetics has suggested that nasal-emission evolved independently four different times (Rhinolo phidae + Hipposideridae, Megadermatidae, Nycteridae, and Phyllostomidae) and that the non-echolocating pteropodids and the highly sophisticated nasal-emitting rhinolophids and hipposiderids are closely related to each other within the somewhat contentious Yinpterochiroptera. Even if released from the morphological strictures of ultrasonic echolocation (Giannini and Simmons 2012), there is little or nothing about pteropodids (jaw suspension, hyoid suspension, dentition, brains, cranial development, cranial vasculature, neuroacoustic systems, flight musculature, thoracic compliance, or reproductive biology) that would support such a relationship (references in Pedersen and Timm 2012).

The evolution of functional genes that are directly/indirectly associated with vision and hearing in bats is of great interest. Unfortunately, our current understanding of the evolution of color vision in bats (Müller et al. 2007, 2009; Wang et al. 2004; Zhao et al. 2009) and arguably hearing (Li et al. 2007, 2008; Liu et al. 2011) is limited to a relatively small number of taxa which may explain why these data are often inconsistent with the species trees in regard to the status of Yinpterochiroptera.

It may also be that in our search for evolutionary patterns, we often confound correlation with causation/emergence which in turn may exacerbate the discordance between molecular and morphological trees.

4.10 Why Nasal-Emitting Bats?

From an evolutionary perspective, nasal-emission has been a successful innovation—over one-third of the extant microchiropteran species are nasal-emitters; approximately 190 are phyllostomids, 170 are hipposiderids and rhinolophids, and another 20+ from the apparently less successful megadermatids and nycterids. We have made progress in understanding various parts of the nasal-emitting system, yet, as to the question of why there are nasal-emitting bats in the first place, we have little but conjecture to offer.

Could the advent of nasal-emission have been driven by something so simple as the extent to which some early bats used their mouths? After all, an echolocating predator would have difficulty flying and orienting simultaneously with a large prey item in its mouth. Even if nasal-emission was used intermittently, noseleaves would have evolved in quick succession so as to restore directionality to the nasally emitted calls. Oral-emitting bats can increase the directionality of their calls by opening their mouths wider (larger aperture, narrower beam width; Surlykke et al. 2009a). As such, one might predict that directional selection would quickly drive the dimensions of a nascent noseleaf to match the minimum dimensions of the aperture that it was replacing (mouth). This prediction is readily testable, e.g., is the diversity in noseleaf morphology among the animalivorous phyllostomines a derived (Wetterer et al. 2000) or a basal character within the family (Baker et al. 2003)?

Noseleaves seem to be a corequisite of effective nasal-emission, but beyond that, the mechanism of beamforming and the differential application of call dynamics (FM, high duty cycle CF, qCF) seem to be a matter of behavior and foraging ecology (Fenton, Chap. 3). Only in the resonator-equipped rhinolophid and hipposiderid bats do we see significant morphological changes in the rostrum that would impose a relatively fixed effect on the emitted call (i.e., a band-pass filter for the second and third harmonics). Such resonators are intimately tied to the production of loud high duty cycle CF calls. Could it be that by adopting/co-opting such resonators, these bats reduced one aspect of behavioral complexity which then set the stage for experimentation with noseleaf form and function? It remains to be seen as to what extent the organization of the rostrum in fossil bats tell us about the evolution of nasal-emission and noseleaves (Hand 1998; Hand and Archer 2005).

In the future, we face great challenges if we hope to integrate studies of behavior, physics, and embryogeny. It may be even more difficult to determine the extent to which these things augment, compensate, or conflict with each other on the evolutionary stage. However, in the last decade, dramatic increases in computing power have led to rapid advances in X-ray microtomography, access to which has become almost commonplace. The generation of increasingly powerful numerical models has helped us better evaluate the physical limitations and continuity of form—we are beginning to quantify function where once only ornamentation had been perceived.

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