COMMENTARIES

'Silent' signals: selective forces acting on ultrasonic communication systems in terrestrial vertebrates

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Through technological innovations, humans have attained the unique ability to observe and study perceptual phenomena occurring outside the limits of our own sensory capabilities. In the study of acoustic communication, one such realm is the frequency channel above the upper limit of human hearing (ca. $\geq$20 kHz), which is defined in human terms as 'ultrasound'. The ultrasonic frequency boundary is biologically somewhat arbitrary; the ability to hear ultrasound is widespread among terrestrial vertebrates and is thought to be an ancestral trait of mammals (Masterton et al. 1968; Sales & Pye 1974). However, within the context of acoustic communication, distinguishing between audible (i.e. within the human audible range, ca. 20 Hz to 20 kHz) and ultrasonic communication provides a foundation upon which to explore intriguing questions regarding the adaptive utility of animal communication systems. The ever-expanding selection and quality of ultrasonically sensitive microphones and recorders have provided the opportunity to address such questions with increasing sophistication.

For effective acoustic communication to occur, an emitted signal must reach a receiver with enough clarity to allow an appropriate behavioural and/or physiological decision to be made. After Endler (1993), we can therefore consider clear reception to be the minimum requirement of a successful communication system. With this in mind, it becomes apparent that factors inherent in the

transmission properties of ultrasonic frequencies place some restrictions on the environments and social conditions in which they are useful as information-bearing elements (sensu Suga 1972). Higher-frequency sounds attenuate more rapidly with distance (Morton 1975; Lawrence & Simmons 1982; Surlykke 1988; Römer & Lewald 1992) and are more directional than low frequencies (Kinsler & Frey 1962). In addition, the short wavelengths of high-frequency sounds make them susceptible to reflection and scattering by relatively small objects, such as twigs, leaves and blades of grass (Marler 1955; Sales & Pye 1974). Thus, in the interest of signal clarity, we may expect animals engaging in long-distance communication, or communicating in environments with small-scale scattering properties, to focus their vocal efforts in the audible frequency range; in this way, they can ensure that their calls have a higher probability of maintaining fidelity during transmission from emitter to receiver. However, additional environmental and behavioural complexities can place further, and in some cases competing, selective constraints on signal frequency. In addition, certain ecological scenarios may encourage the exploitation of ultrasound's distinctive transmission properties. We will discuss some biological and ecological scenarios in which evolution may favour the development of an ultrasonic communication system, and we provide examples of terrestrial vertebrates that have apparently been subject to such selection pressures. We focus on terrestrial vertebrates because the study of ultrasonic communication in this group is a rapidly expanding field. By defining biophysical, behavioural and environmental conditions under which ultrasonic communication is likely to evolve in terrestrial vertebrates, we are well situated to identify additional organisms that may use similar strategies. The

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discovery of ultrasonic communicators among terrestrial vertebrates that run the evolutionary spectrum from amphibians to mammals provides an opportunity to gain more complete understanding of the behavioural foundations of high-frequency communication. In addition, comparative studies of ultrasonically communicating taxa may give insight into the fundamental physiological mechanisms that underlie the ability to both produce and perceive extraordinarily high-frequency sounds.

Exaptation of Noncommunicatory Ultrasounds

In evolutionary theory, the idea of exaptation was first introduced by Gould & Vrba (1982). These authors suggest that an adaptation is 'any feature that promotes fitness and was built by selection for its current role'. Other characters, however, 'evolved for other usages (or no function at all), and later [were] ''coopted'' for their current role' (Gould & Vrba 1982, page 6). To these latter characters, they assign the term exaptation. In this context, if an ultrasonic utterance is emitted for a function other than intraspecific communication, or as an incidental by-product of a physiological process or biomechanical strain, it cannot be said to be adapted for communication. However, if the ultrasounds have a consistent influence on conspecific behaviour, then the vocalization may be considered exapted for communication. In these cases, the evolution of the ultrasonic communication system may have been guided by conspecifics' advantageous use of inadvertently provided sensory information.

Among terrestrial vertebrates, the most conspicuous ultrasonic vocalizers are the bats. Microchiropteran bats (and the *Rousettus* genus of the megachiroptera; Mohres & Kulzer 1956) are nocturnally active and have limited vision, relying on a sonar system comprising ultrasonic pulses (i.e. echolocation) to locate, identify and track moving prey, avoid obstacles, and orient in 3D space (Griffin 1958; Simmons et al. 1975; Grinnell 1995; Neuweiler 2000; Schüller & Moss 2004). The frequencies contained in echolocation pulses must have sufficiently short wavelengths to reflect from small targets as usable echoes. To overcome the rapid attenuation of such high-frequency signals, echolocation calls are often emitted at extraordinary intensities (e.g. ≥100 dB SPL). In addition, the auditory systems of many bat species are maximally sensitive to a frequency band corresponding to the dominant frequency of their echolocation pulses, facilitating the perception of faint echoes (e.g. Dalland 1965; Brown 1973; Pollak et al. 1978; Koay et al. 1997). Although echolocation can be seen as a form of self-communication in which bats use their own vocalizations to attain information about their environment, the primary functions of echolocation vocalizations are clearly prey capture and navigation rather than intraspecific communication. However, the ubiquitous use of intense echolocation signals by active individuals, coupled with elevated auditory sensitivity to the frequencies contained in these signals, makes it a system that is ideally situated for eavesdropping and exaptation for communication. Indeed, playback

experiments and call-feature analyses demonstrate that echolocation signals can be individually distinct (Jones et al. 1994; Masters et al. 1995; Fenton et al. 2004) and serve important intraspecific communication functions for a number of species (Mohres 1967; Habersetzer 1981; Barclay 1982; Leonard & Fenton 1984; Balcombe & Fenton 1988; Obrist 1995; Pearl & Fenton 1996; Kazial & Masters 2004). Echolocation calls have been implicated in synchronizing activity away from roosts (Fenton et al. 2004), aiding in localization of communal roosts (Barclay 1982), attracting attention to food sources (Griffin 1958; Barclay 1982; Balcombe & Fenton 1988) and communicating between mother and young (Matsumura 1981; Brown et al. 1983). Furthermore, increasing exploration of the intricate, acoustically mediated social system of bats has revealed that many social calls, while generally longer and more variable than sonar pulses, share spectral and/or structural features with echolocation signals (e.g. Kanwal et al. 1994; Behr & von Helversen 2004; Kanwal 2006; Ma et al. 2006); these data suggest that the two classes of vocalizations share a common evolutionary substrate. Indeed, ontogenetic studies imply that some species' echolocation signals derive from particular communication calls (Gould 1971, 1977; Matsumura 1981; de Fanis & Jones 1995), although for other species there is no clear precursor to the echolocation pulse (Brown & Grinnell 1980; Moss 1988). Future research in this area is likely to reveal additional ways in which echolocation calls have been exapted for use in intraspecific communication, as well as broadening our understanding of the evolutionary role of echolocation cries, and intentionally interindividual social signals, in shaping bats' ultrasonic vocal repertoire.

Rodents provide another interesting example of an ultrasonic communication system comprising a subset of signals that may have been exapted for their communicatory role. The majority of small rodent species use ultrasound to mediate a wide variety of social interactions (Sales & Pye 1974). The importance of ultrasonic communication by adult rodents has been suggested for an array of interrelated facets of sociality, including courtship and mating behaviour, aggression, territoriality and alarm behaviour. In addition, pups from all species studied in the families Muridae and Cricetidae emit ultrasonic vocalizations when they are separated from the nest, which reliably induces approach and retrieval behaviour by their mothers (Sewell 1970; Brooks & Banks 1973; Ehret & Haack 1981, 1982, 1984; Haack et al. 1983). It is generally accepted that most adult rodent ultrasounds are related to expiratory air movements deliberately produced as communication signals and may even be indicative of affective state in some species (Knutson et al. 1998, 2002; Burgdorf & Panksepp 2001). The proximate mechanisms inducing pup ultrasounds, however, are less clear. The traditional interpretation of infant rodent vocalizations is that they are distress calls produced by the pups to elicit attention from their mothers. Blumberg et al. (2000) argue, however, that pup ultrasounds are produced as an inadvertent acoustic by-product of a physiological process called an abdominal compression reaction (ACR). In an ACR, the abdominal muscles are contracted

during expiration to help propel venous blood back to the heart; this process may help maintain cardiac output during physiologically stressful situations, such as extreme cooling (Youmans et al. 1974). During an ACR by a rodent pup, the larynx is used as a brake during expiration, contributing to increased intra-abdominal pressure that results in the inadvertent production of ultrasounds (Blumberg et al. 2000). Ultrasounds resulting from ACRs that consistently occur during isolation from the nest, such as in response to cooling, could easily be interpreted as deliberate communication signals rather than incidental side-effects of behaviours and/or physiological state linked to external conditions. It is worth noting that this explanation for pup ultrasounds remains controversial and awaits conclusive correlative data linking ultrasound production with ACRs (Knutson et al. 2002; Shair & Jasper 2003; Shair 2007; Ehret 2005). Regardless of whether rodent pups' ultrasonic vocalizations represent wilful signalling or are by-products of biomechanical strain, it is clear that the signals consistently induce a behaviour from the mother that is beneficial to the signaller, and so serve a communication function. The implication of the argument of Blumberg et al. is that ultrasonic signals resulting from physiological or biophysical properties associated with the signaller's behavioural and/or physiological state can be exapted to serve a communicatory function and thus become fixed within a communication system.

Predator Avoidance

Auditory signalling offers a number of advantages as a sensory mode of communication. Vocal communication can rapidly transfer a substantial amount of information encoded across multiple channels (e.g. frequency, amplitude) and is not limited by light availability or the need for immediate proximity between signaller and receiver (Endler 1993). One of the primary disadvantages of vocal communication, however, is its vulnerability to eavesdropping (Peake 2005). Eavesdroppers may include conspecific competitors, as well as prey or predator species, and can exert strong selection pressure on the design of acoustic signals (Dabelsteen 2005). In the case of rodents, vulnerability to predation may be implicated in the development and elaboration of ultrasonic signal repertoires.

The perceptual abilities of predators can influence signal design on both the evolutionary and the proximate time scales (Owings et al. 2002; Snowdon & de la Torre 2002). It is unlikely, however, that rodent ultrasonic communication evolved because of its inaudibility to rodents' wide array of potential predators. Whereas some of these predators, such as humans, falcons, owls and eagles, are incapable of hearing ultrasonic frequencies, many others, including the domestic dog (*Canis familiaris*), domestic cat (*Felis catus*) and coyote (*Canis latrans*), can detect sounds up to at least 48 kHz (Schwartzkopff 1955; Peterson et al. 1969; Sales & Pye 1974; Klump et al. 1986). Nevertheless, the very properties of ultrasonic frequencies that limit their utility for long-distance signalling, namely atmospheric attenuation, directionality and susceptibility to scattering, can be beneficial for avoiding eavesdropping, even by predators that are

ultrasonically sensitive. Many rodent species are highly social and confine the majority of their activity to a limited area, such as a burrow or a nest. In this context, the ultrasonic vocalizations emitted by adult rodents to facilitate interindividual social encounters would benefit from the transmission limitations of ultrasonic frequencies. By emitting ultrasonic signals, individuals can effectively restrict the transmission of acoustic information to only those receivers in close proximity.

In addition to short-range social interactions by rodents, there is evidence that the acoustic properties of ultrasounds can be exploited in a context-specific manner during rodent alarm calling (Wilson & Hare 2004, 2006). Richardson's ground squirrels (*Spermophilus richardsonii*) produce two types of alarm vocalizations, audible (fundamental frequency ca. 8 kHz) and ultrasonic (fundamental frequency ca. 50 kHz; Koeppl et al. 1978; Wilson & Hare 2004). Wilson & Hare (2004) found that the probability of the squirrels producing ultrasonic rather than audible alarm calls increased with increasing distance from the call-inducing stimulus, thus taking advantage of the rapid attenuation of the ultrasonic frequencies to warn nearby conspecifics without alerting the predator. It has also been demonstrated that laboratory rats living in artificial burrows with conspecifics will emit ultrasonic calls in the presence of a threatening stimulus, and playback of these putative alarm calls promote freezing and avoidance behaviours (Blanchard et al. 1991; Brudzynski & Ociepa 1992; Brudzynski & Chiu 1995). Whether the frequency of rat alarm calls also differs with distance to the predator, or in another context-specific manner, is unknown. Additional field experiments like those of Wilson & Hare (2004) that examine the production and function of ultrasonic vocalizations emitted by wild rodents under natural conditions are necessary to understand fully their adaptive significance. Interestingly, Wilson & Hare (2006) make the point that humans are alarm-call-eliciting stimuli for ground squirrels; this observation is presumably true for many, if not all, alarm-calling rodent species. Thus, the increased likelihood that ultrasonic alarm calls will be produced when we are distant from the signaller, coupled with our inability to hear these calls, presents formidable challenges to observing these vocalizations and determining the behavioural contexts under which they are emitted in the field (Wilson & Hare 2006). The increased compactness and portability of ultrasound detection devices and microphone arrays (e.g. Hiryu et al. 2005) should increase the feasibility of such studies with a wide variety of species.

Increased Signal-to-Noise Ratio

Recalling the minimum requirement for clear reception for the evolution of a communication system, we see that any factor that decreases the signal-to-noise ratio of a call at its point of reception will negatively impact the active space of the signal (Endler 1993; Narins & Zelick 1988; Klump 1996). One such factor is environmental or 'background' acoustic noise, which is ubiquitous in the habitats of vocally communicating organisms. Noise sources include biotic sounds, such as those produced by

arthropods (Bradbury & Vehrencamp 1998), songbirds (Catchpole & Slater 1995) and anurans (Gerhardt & Huber 2002), and abiotic noise from wind, rain or running water. The degree to which ambient noise interferes with acoustic communication is contingent on the amount of frequency overlap between the communicatory signal and the noise (Dooling 1982; Klump 1996; Hulse 2002). Thus, consistent environmental sound in a particular frequency range may function as a selection pressure guiding the evolution of acoustic signals with nonoverlapping spectral components. Accordingly, among terrestrial vertebrates, the presence of continuous background noise has been implicated in the evolution of the frequency spectra of some bird, primate and anuran vocalizations (Morton 1975; Brenowitz 1982; Narins 1982; Wiley & Richards 1982; Ryan & Brenowitz 1985; Waser & Brown 1986; Slabbekoorn & Peet 2003; Narins et al. 2004).

Environmental noise sources differ markedly in their bandwidth. Some, such as rushing water, waterfalls and anthropogenic traffic noise, can span the entire human audible frequency range. Faced with such noise emitters, acoustic communicators may significantly increase the active space of their signals by shifting the spectral energy of their calls to ultrasonic frequencies; the concomitant gain in signal-to-noise ratio at the point of the receiver may outweigh the disadvantages to long-distance communication inherent in the transmission limitations of high-frequency sounds. Recently, it was found that the males of two frog species, *Odorrana tormota* (previously *Amolops tormotus*) and *Huia cavitympanum*, that live adjacent to torrents producing broadband, low-frequency-dominated noise, emit advertisement calls with substantial ultrasonic spectral energy and, in the case of *H. cavitympanum*, exclusively ultrasonic energy (Narins et al. 2004; Arch et al. 2008). Confirmation that *H. cavitympanum* communicates ultrasonically awaits further research, but behavioural and neurophysiological experiments demonstrate that the ultrasonic components of *O. tormota's* calls serve a communicatory function (Feng et al. 2006). The vocal output and hearing sensitivity of *O. tormota's* significantly exceed previously posited upper limits for anurans (Capranica 1965; Loftus-Hills & Johnstone 1970; Fay 1988; Glaw & Vences 1994), and Narins et al. (2004) suggest that this substantial upwards extension of communication frequency is an adaptation to avoid acoustic masking by the nearby torrents. This research suggests that long-term adaptation to habitat-specific noise may be a powerful selective force, encouraging upward shifts of vocalization frequencies among species, or even subspecies or populations (Slabbekoorn & Peet 2003), exposed to persistently high levels of low-frequency background noise. It is important to note that the same selective force may theoretically work in the opposite direction, selecting for a downward shift of vocal frequency, in habitats dominated by high-frequency or ultrasonic noise, such as the sound produced by many arthropod species.

Summary and Conclusion

For many terrestrial vertebrates, acoustic communication is essential for establishing and maintaining territories,

attracting mates, evading predators and locating prey. Successful acoustic communication requires that signals maintain sufficient integrity during transmission to convey the emitted information reliably from signaller to receiver. Thus, the inherent transmission limitations of ultrasonic frequencies resulting from their high rate of atmospheric attenuation, directionality and vulnerability to scattering place restrictions on the ecological conditions in which they represent useful communication signals. We have discussed some of the ecological and physiological factors that may select for the use of high-frequency communication channels. These scenarios suggest that additional ultrasonic communicators may be discovered among species that produce noncommunicatory ultrasounds correlated with specific behaviours that may be exapted for communication. In addition, social animals living in close quarters, and alarm-calling species, may take advantage of the limited transmission of ultrasounds to 'beam' communicatory signals selectively to nearby receivers without alerting competitors or predators. Finally, organisms subject to persistent acoustic interference from broadband, low-frequency environmental noise might gain a significant increase in the signal-to-noise ratio of their calls by shifting signal frequency up into a comparatively noise-free ultrasonic frequency channel. The communicatory advantage of this shift may be sufficient to offset the transmission disadvantages of high-frequency sounds. It is our hope that recognizing some of the conditions under which ultrasonic communication may be evolutionarily advantageous will enhance our ability to identify additional ultrasonically communicating species among terrestrial vertebrates. Pursuing the study of ultrasonic communication in the field offers an opportunity to understand more fully the adaptive utility of differential frequency use in communication within complex environments. In addition, comparative studies of ultrasonic communicators offer behaviourists and physiologists an intriguing opportunity to explore the fundamental mechanisms underlying the use of extraordinarily high frequencies in acoustic communication.

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