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## Long-distance, low-frequency elephant communication

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**Abstract** The production, transmission, and reception of and the behavioral response to long-distance, low-frequency sound by elephants is reviewed. The structure of low-frequency calls generated by elephants is separated into the “source” and the “filter” roles played by the lungs, larynx and vocal track, the composition of the expired air and the ambient air temperature. Implications regarding the size, age, sex, sexual and physical status follow from the call structure and detection. Reception of the signal is discussed in terms of the characteristics of the elephant’s ear with particular attention to the determination of the threshold of hearing and the ability to locate the source of low-frequency sounds. Factors which influence the transmission of near infrasound are related to atmospheric structure. The critical role played by the thermal stratification and vertical gradient and magnitude of the wind in determining both the range and the detection of a signal are discussed for open and closed elephant habitats. Infrasound plays a pervasive role in reproduction, resource utilization, avoidance of predation and other social interactions. Current and future technology can be expected to contribute to the detection and interpretation of elephant communication. This will aid in the understanding of behavior and in efforts to sustain the species.

**Keywords** Behavioral response · Calling · Elephant communication · Hearing · Transmission

### Introduction

In 1986, Payne and others drew attention to the fact that elephants generate low-frequency sounds which cannot

be heard by humans (Payne et al. 1986). Subsequent work confirmed these findings showing that many aspects of elephant behavior, previously inadequately understood, could be explained in terms of their use of low-frequency calls (Langbauer et al. 1991; Moss 1983, 1988, 2001; Poole 1987, 1989a, b, 1994, 1996; Poole et al. 1988).

Sound, as heard by animals, is defined in terms of the lower (20 Hz) and upper (20,000 Hz) limits of human hearing. Sounds with frequencies below and above these limits are referred to as “infra” and “ultra” sound. Frequencies between 1 and 20 Hz are called “near-infrasound”. Low-frequency sounds including near-infrasound as used by elephants for long-range (greater than ca. 1 km) communication are the primary focus of this review.

Reviews of atmospheric acoustics (Brown and Hall 1978; Wiley and Richards 1978; Beyer 1999), bioacoustics (Kroodsma et al. 1982; Spiesberger and Fristrup 1990; Naguid and Wiley 2001) and the physiology of animal sound production and detection (Titze 1994; Fitch and Hauser 2002) form a useful and necessary starting point for assessing the current state of knowledge of animals’ use of infrasound. These reviews, however, provide only limited treatment of low-frequency animal sounds. Only Larom (1996) and Langbauer (2000) review the use of low-frequency sounds by elephants.

There is no single comprehensive treatment of low-frequency sound generation by elephants, propagation of these sounds through the atmosphere or detection and interpretation of these sounds by conspecifics.

### Production of low-frequency sounds

Evolution and the physiology of elephant low-frequency sound

Forests were the dominant habitat until late in the evolution of elephants (McFadden 1997). Of the forms

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of elephant communication which might have evolved in forests, those of smell and hearing as opposed to sight, have the greatest potential range and are most likely to be highly developed in a social species such as elephants. By the time forests receded and savannas emerged (beginning of the Miocene, 24 Mya), many of the morphological characteristics of the present day elephant were well established (Shoshani 1998). These morphological characteristics such as long vocal tract, suggest the evolution of the ability to produce low-frequency sounds. Frequencies between 15 and 20 Hz have wavelengths on the order of 17–23 m. Sounds with such long wavelengths suffer little or no attenuation by obstacles such as trees and other forest vegetation (Heimann 2003). Elephants may, therefore, have emerged onto the savannas with the ability to communicate at low-frequencies over large (kilometers) distances.

Sounds generated by vertebrates depend upon lung capacity and the mass, length and elasticity of the vocal folds in the larynx. These fundamental sounds are then modulated as they pass through and emerge from the passageways which constitute the vocal tract. The vocal tract acts as a filter and operates independently of the source (Fitch and Hauser 2002).

This independence between the “source” and the “filter” is considered to be the best current working hypothesis of how animals produce sound (Fitch and Hauser 2002). However, much of what is known about the relationship between the source and filter has been learned from the study of humans, non-human primates and other animals such as species of deer (Titze 1994; Willmer et al. 2000; Fitch 2000; Fitch and Reby 2001; Reby and McComb 2003; Wilson et al. 2001; Fitch and Hauser 2002). Little is known of the source-filter relationship in elephants (Reby and McComb 2003) yet it is useful to view the production of low-frequency elephant calls in these terms.

### The source

Air driven from the lungs sets the vocal folds in the larynx in motion. With their own elasticity and mass, these folds responding to the air flow over them, act as mechanical vibrators which can generate self-oscillation (Titze 1994; Fitch and Hauser 2002). When the folds close to the appropriate “phonatory” position they generate acoustic energy. The period and thus the frequency, of the opening and closing of the vocal folds produces the fundamental frequency (FO). This frequency is set passively by the muscle tensions, mass of the vocal cords, and lung pressure. There are small non-linear oscillations around this fundamental frequency. These non-linearities in the periodic vocal production provide structure to the morphology of the call and have been described in terms of deterministic chaos (Reby and McComb 2003). Because the length, mass and elasticity of the vocal folds are related to body size, the FO can be related to body size. However, these

parameters (length, mass, elasticity) can change, e.g., with age, and the relationship between FO and body size is not robust (McComb 1991; Rendall 1996; Fitch 1997; Riede and Fitch 1999; Reby and McComb 2003). The inverse relationship between the length and mass of an elephant’s vocal folds predicts that it is capable of producing lower frequency sounds than any other terrestrial animal. However, the prediction that larger animals produce lower frequencies than smaller animals of the same species has not been well verified by observations (McComb 1991; Reby and McComb 2003).

### The filter

The supra-laryngeal vocal tract of the elephant is the respiratory tract from the larynx to the tip of the trunk. For the elephant the pharyngeal pouch, nasal cavity, membrane near the tip of the trunk, the highly mobile tip of the trunk and the length and ability to change the length of the trunk are, in combination, unique *Elephantidae* features. Their individual and collective role in controlling the air column in the vocal tract has not been carefully studied.

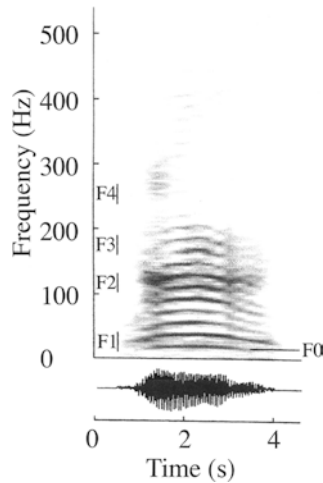
The air column in the vocal tract has elasticity and mass which will vibrate preferentially at certain frequencies termed normal modes or resonances. In the simplest terms this column of air acts as though it is in a tube closed at one end such that the length ( $L$ ), of the tube is one-quarter of the wavelength ( $\lambda$ ), i.e.,  $L = \lambda/4$ . The vocal tract will act as a filter depending upon the transit time of the sound waves up (and down) the column. The speed of sound ( $C$ ) in this tract expressed as

$$C = \sqrt{\gamma RT}$$

will govern the transit time and thus will depend upon the composition of gases in the tube, and the temperature of those gases (Pierce 1981). The quantity,  $\gamma$  is the ratio of specific heat at constant pressure and volume of the mixture of gases,  $R$  is the gas constant governed by the mean molecular weight of the mixture and  $T$  is the temperature of the mixture in degrees Kelvin.

The filter will act upon *all* of the frequencies being generated in the larynx (i.e., the FO and the non-linear oscillations about the FO). The filter will thus shape the final form of the vocal signal. Prominent in this ultimate form of the signal will be “formants”. These formants are selectively amplified parts of the vocal signal, clearly visible in the sonogram of the call of an elephant as nearly equally-spaced bands of acoustic energy (Fig. 1). Embedded in this signal envelope but independent of the formants, is the FO and the integer harmonics of the FO.

The vocal tract length governs formant spacing. Formant spacing is a better predictor to body size than the size of the vocal folds or larynx (Fitch 2000; Fitch and Hauser 2002; Reby and McComb 2003). In addition to changing the length of the vocal tract by extending its



**Fig. 1** Waveform of a female contact call showing the fundamental frequency (FO) and harmonics, and the position of the first four formants (F1–F4). Frequency bandwidth: 8.74 Hz; FFT size: 1,024 points; overlap: 50%. (After McComb et al. 2003)

trunk, the elephant may be able to elongate the vocal tract by contraction of the larynx or laryngeal descent (Fitch and Reby 2001; Reby and McComb 2003). The presence or absence of water in the pharyngeal pouch may also influence vocal tract length. The function of the narrow connective strip of tissue running across some 10–13 cm above the nostril openings and the ability to open or constrict the nostril openings is unknown.

Formants of a constant diameter tube stopped at one end are related to the length ( $L$ ) of that tube by  $F_i (2i-1) C/4L$ , where  $F_i$  is the frequency of the formant in Hertz and  $C$  is the speed of sound. It follows that the formant spacing or formant dispersion ( $\Delta F$ ) in Hz is  $\Delta FC/2L$  (Fitch and Reby 2001).

McComb et al. (2003) obtained an average formant spacing of 60.4 Hz from sound recordings of elephant low-frequency calls in the field. They assumed a speed of sound of  $350 \text{ m s}^{-1}$  to obtain a vocal tract length estimate of 2.8 m.

The speed of sound in the vocal tract of an elephant will depend upon the composition of gases making up the expired air and the temperature of that air. Expired air will be enriched with carbon dioxide (up to 5% by volume). Carbon dioxide has a much higher molecular weight ( $44 \text{ g mol}^{-1}$ ) than nitrogen and oxygen ( $28$  and  $32 \text{ g mol}^{-1}$ ) and will change both the ratio  $\gamma$  and the gas constant,  $R$ , thus influencing the speed of sound,  $C$ .

The temperature of the expired air will also influence the speed of sound and hence the frequency of the sounds produced. The body temperature of an adult elephant at rest is about 36°C (Folk 1966, p. 125; Kavalier 1981, p. 103). The temperature of the expired air, however, is linearly related to the ambient temperature (Willmer et al. 2000). Air temperatures in dry habitats typical of the African or Asian savannas undergo a pronounced and regular daily change (Garstang et al.

2004, in preparation). Daytime temperatures within trunk height of the surface in the dry season may exceed 45°C. Nighttime temperatures at the same height and time of year can drop to below 5°C constituting a daily range of more than 40°C. The temperature of the air in the vocal tract of an elephant is thus dependent in part on the ambient air temperature. By the above equation for vocal tract length and within the possible limits of gaseous composition and tract column temperatures of the expired air, estimates of vocal tract lengths can vary by as much as 13 cm at 30 Hz and nearly 20 cm at 20 Hz or about 5% of the mean vocal tract length. More significantly, however, is the suggestion that there is a physiological bias towards the generation of lower frequencies under cold nighttime conditions.

#### Characteristics of low-frequency sounds at the source

Sound emitted at the source is measured in terms of power density which is the rate of energy generated per unit time expressed in watts. The rate of flow of that energy through a unit area ( $\text{W m}^{-2}$ ) is the flux density. The flux density is the sum of all sound ray directions perpendicular to a unit area. The sound intensity is measured with reference to a zero threshold. Thus, a decibel is defined as the intensity of sound above a zero threshold taken as  $10^{-10} \mu\text{W cm}^{-2}$  and measured in decibels (dB). The sound pressure level (SPL) is defined by  $\text{SPL} = 10 \log_{10} (p^2/p_r^2)$ , where  $p^2$  = mean squared pressure at the source, and,  $p_r^2$  = mean squared pressure at the reference distance (radius,  $r$ ), often at 1 m from the source and the SPL is stated as SPL in decibels re. 1 m (Pierce 1981).

There have been few measurements of the intensity of low-frequency elephant calls. Poole et al. (1988) measured SPL re 1 m of up to 117 dB at frequencies between 14 and 35 Hz for an unstressed female African savanna elephant. It is possible that the loudest low-frequency calls of elephants could reach 120 dB re. 1 m. Low-frequency calls have been recorded and played back to elephants under observation through a loudspeaker which can approach the required power levels at the appropriate frequencies (Langbauer et al. 1991; Langbauer 2000; McComb et al. 2000). Playback experiments have focused on range determination (Langbauer et al. 1991) with more recent work directed at determining and interpreting responses to recorded calls (McComb et al. 2000). Such experiments may lead to an understanding of the relative importance of frequency (pitch), sound intensity (loudness), and waveform (quality or timbre) at the source (Wiley and Richards 1978; Langbauer 2000).

These characteristics govern the “content and context” of the call in communication terms (Ruyst and Schilling 2002). Communication can be defined as an association between a signaler’s and receiver’s behavior as a consequence of the signal (Wiley and Richards 1978). A signal contains a specific pattern of energy at the source referred to as broadcast information.

Broadcast information is a function of the diversity of signals that can be generated and their association with behavior. The received information can be significantly degraded to the point where the receiver cannot detect the signal or cannot discriminate between variations (which contain information) in the signal structure. Hearing a signal as opposed to being able to interpret a signal, however, still constitutes communication. Communication thus depends upon both the broadcast information at the source and the received information at the detector. The broadcast information always equals or exceeds the received information.

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## Transmission

Principles governing the transmission of low-frequency elephant calls

Both male and female elephants at the height of their reproductive years are capable of generating sounds below 20 Hz. Size constraints may limit the capacity to produce sounds below 10 Hz but cold nighttime conditions with temperature as low as 5°C could extend the capacity of a large elephant (5–6,000 kg and 4 m at the shoulder) to produce calls at frequencies as low as 10 Hz.

While it is convenient at times to visualize the transmission of infrasound in terms of ray theory, quantitative treatment of the propagation of low frequencies must be considered in terms of a spherical wave which propagates outwards in all directions from a source. In an atmosphere at rest and with no gradients in temperature (isothermal), sound from a point source far from the surface may be visualized as a series of concentric spherical surfaces expanding outwards from the source. The energy per unit area at the source must be distributed over the surface area of each successive sphere.

If the distance from the source,  $r$ , is doubled, then the area of the sphere over which the spherical wave must be distributed is increased fourfold and the  $SPL = 10 \log 4 \cong 6$  dB. Spherical spreading of the low-frequency sound wave means that the SPL drops 6 dB for every doubling of distance from the source. The level of the low-frequency signal emitted must exceed this attenuation (excess enhancement) and be above the receiver's threshold of hearing if the signal is to be detected.

Sound propagation in a stratified atmosphere (i.e., in the presence of vertical temperature gradients) is approximated by the Helmholtz form of the acoustic wave equation. A two-dimensional version of this equation can be considered in which the gradients of temperature are approximated by  $N$  homogeneous layers, with the first layer next to the ground and successive layers (hemispheres) governed by any significant change in the speed of sound due to vertical changes of temperature and wind. This means that changes in the meteorological variables are in the vertical only and the

effects of cross winds are neglected. A flat (no topography) and a moderately hard surface is assumed. With these assumptions a numerical solution in two-dimensional cylindrical coordinates can be obtained using the Fast Field Program (FFP) (Raspet et al. 1985; Lee et al. 1986; Franke and Swenson 1989; West et al. 1991; Garstang et al. 1995; Larom 1996).

Application of the FFP provides useful estimates of the propagation of elephant calls in many but not all habitats. Propagation will be influenced by topography, boundary conditions (surface and vegetation) and changes in atmospheric structure in different environments (savanna versus forest). The degree to which low-frequency signals are attenuated must be examined before interpreting the results of the simplified FFP calculations.

## Attenuation

Sounds produced near a plane boundary (the surface of the earth) with equal intensity in all directions (isotropic) in the hemisphere would only diverge spherically if the boundary were completely absorbing. Attenuation of a signal thus must include the height of the source above the surface, the nature of the surface as well as the properties of the atmosphere. At the surface sound can be absorbed as well as reflected. The reflected sound can interfere with the propagation of the signal.

The absorption of sound obeys an exponential law similar to Beers Law for light where the extinction coefficient is replaced by an absorption coefficient. For a mixture of gases such as air the absorption coefficient is proportional to the square of the frequency. High frequencies thus have large absorption coefficients while low frequencies have much lower absorption coefficients (Brown and Hall 1978; Wiley and Richards 1978).

Absorption of sound in air is due to viscosity, heat conduction and molecular absorption. Viscous and heat losses termed classical atmospheric absorption, increase in direct proportion to temperature and frequency squared. Molecular absorption in the atmosphere depends upon humidity, temperature and frequency. For frequencies below approximately 8,000 Hz attenuation increases with decreasing humidity. Total atmospheric attenuation for an 8,000-Hz signal at 20°C and 100% relative humidity (2.4% water) and 40% relative humidity (1% water) is about 7 dB/100 m and 20 dB/100 m, respectively. In contrast, an 8-Hz signal under the same conditions shows no measurable attenuation (Brown and Hall 1978; Wiley and Richards 1978). Attenuation of a 30-Hz signal for completely dry air can reach 1 dB km<sup>-1</sup>. More realistically a 30-Hz signal in an atmosphere with relative humidities  $\geq 20\%$  absorption never exceeds 1 dB/10 km (Zuckerwar and Meredith 1984; Bass et al. 1990; Larom 1996 (p. 37)). Absorption at the molecular level for infrasound for most ambient conditions of temperature and humidity, can, for all practical purposes, be neglected.

The surface (ground) can absorb sound being propagated in the air. Such absorption is frequency dependent with lower frequencies absorbed less than higher frequencies. Most soils have sufficiently low impedance to attenuate signals with frequencies  $\leq 30$  Hz by less than 6 dB over 10 km (Price et al. 1988). Only soft sand and thick forest humus might exceed this value. At 15 Hz all but the softest surfaces including new snow are excellent acoustic reflectors (Nicholas et al. 1985).

The height of the sound source and the height of the receiver in the range of 1–10 m above the ground are not important for frequencies at and below 30 Hz (Larom 1996, p. 50). Source/receiver heights for all elephants fall well within this range.

Ground attenuation can also be caused by interference between direct and reflected waves at the receiver. Such attenuation is dependent upon the wavelength of the sound and the height of the source. Ground attenuation reaches a maximum when  $0.1 < \lambda/h < 0.7$ , where  $\lambda$  = wavelength and  $h$  = height of source (Wiley and Richards 1978, p. 78). For an assumed source height of 3 m ground attenuation decreases for frequencies  $\geq 1,000$  Hz (wavelength  $\lambda \leq 0.33$  m) and for frequencies  $\leq 100$  Hz (wavelength  $\lambda \geq 3$  m). Ground attenuation and reflection from obstacles such as vegetation will not play a significant role for elephants at these low-frequencies.

Reverberation, scattering, and refraction remain as possible processes which enhance or attenuate infrasound. Reverberations can be caused by repeated reflections from obstacles such as trees (Beranek 1988). Amplitude fluctuations due to atmospheric turbulence can also result in reverberation. Both amplitude fluctuations and reverberations are frequency-dependent, increasing for higher frequencies. Irregular amplitude fluctuations are most severe in open habitats with strong daytime heating and heat-driven turbulence. In closed canopy forests or at night in the open savannas, pronounced stratification due to surface cooling eliminates most if not all turbulent fluctuations and with it amplitude fluctuations and reverberations. It is possible that these fluctuations can degrade infrasound during the day in open habitats but they will not play a significant role within forests or at night on the open plains.

Scattering is the deflection of sound by obstacles such as leaves, limbs, trunks of trees as well as turbulence and turbulent eddies in the atmosphere. Scattering is wavelength-, and thus, frequency dependent. Because foliage has surfaces mostly with maximum linear dimensions of less than 12 cm, it will scatter most effectively at wavelengths below 12 cm (or frequencies above 3,000 Hz). Atmospheric turbulence and turbulent eddies will effectively scatter sound. Wiley and Richards (1978, p. 69) suggest that frequency-dependent attenuation does not differ among major classes of terrestrial habitats. The premise is that non-stationary heterogeneous turbulence increases as vegetation decreases producing scattering in open habitats equal to that in forests. This might be true in the absence of atmospheric stratification. In the

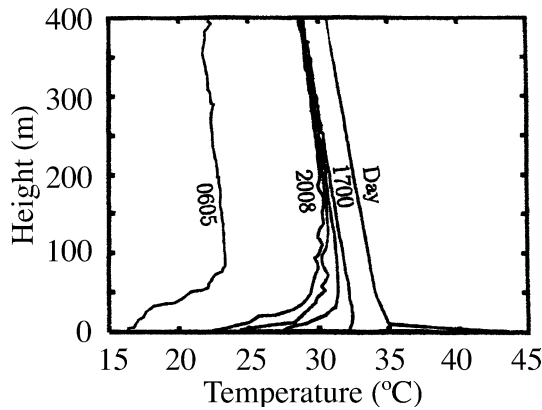
presence of a stably stratified atmosphere (most pronounced in open habitats at night) turbulence is essentially eliminated and with it scattering. There are thus important differences between scattering at the same frequencies in open versus closed habitats as a function of atmospheric stability.

Frequencies lying between 100 and 10,000 Hz (wavelengths of approximately 3 m–30 cm) interact with the atmospheric turbulence in the range of centimeters to less than 100 m. While turbulence in the atmosphere near the surface is mainly in the meter range, eddies emanating from a strongly heated surface are on the scale of the depth of the mixing or less. The daytime mixed layer over a strongly heated tropical-subtropical savanna can reach to 1,500 m. Eddies on the scale of 1,500 m are therefore possible. Under strong unstable daytime conditions over open savannas and grasslands, turbulent eddies with diameters on the order of infrasound wavelengths will attenuate a signal. The theoretical framework which provides an estimate of the magnitude of this attenuation is limited (Blumrich and Heimann 2002; Salomons et al. 2002; Heimann and Blumrich 2004). Random aerodynamic sound is produced by turbulence further confounding the role of turbulence in the propagation of sound (Brown and Hall 1978). However, as will be seen below, attenuation of low-frequency signals by atmospheric turbulence is negligible compared to the effects of refraction.

Scattering of infrasound by atmospheric turbulence selectively attenuates the higher frequencies. This frequency-dependent attenuation might be used by animals to obtain an estimate of range or even size discrimination of the sender (Langbauer 2000; Naguid and Wiley 2001). Any scattering would complicate the ability of the receiver to locate the sender (see section on reception).

#### Atmospheric controls

The speed of sound changes with altitude in a stratified atmosphere with temperatures and wind speeds changing with height (Wilson et al. 2003). Sound is refracted and sound waves are “bent” either upwards away from the surface (decreasing temperature and/or wind with height) or towards the surface (increasing temperature and/or wind with height). With vertical changes in the effective speed of sound, the sound waves (or pressure fronts) are bent upward and away from the surface of the earth when temperatures and winds decrease with height and downwards towards the surface when temperatures and winds increase with height. In this latter case, the layer of inverted temperatures (temperatures increasing with height, Fig. 2), creates a shallow almost horizontal layer in which the sound waves are refracted downwards from the top of this layer towards the surface and upwards towards the top of the layer from the surface. The refracting layer acts as a wave guide or duct. A further consequence of this wave guide to the propagation of low-frequency sounds is the absence of



**Fig. 2** Vertical temperature profiles for the indicated times for a typical dry season day in western Etosha National Park, Namibia. Because of the role played by solar heating and nocturnal terrestrial cooling, local standard time (LST) is used throughout the paper in favor of universal time (UT)

spherical spreading increasing the distance over which the sound can be detected.

Waves reflected from the two boundaries of the wave guide establish interference patterns within the layer. Constraints on the wave number (reciprocal of wavelength) in the wave guide limits the angles of incidence for any one frequency. Conceptually, the result approximates a single wave. Thus, audible and silent zones occur at the surface (Wilson et al. 2003). The region where sound is not detectable is referred to as a shadow zone. The distance,  $S$ , from the source to shadow zone is

$$S = 4\sqrt{zT_o}/\ell$$

(Wiley and Richards 1978, p. 76). Where  $T_o$  is the absolute temperature, taken as the highest temperature in the inversion layer,  $P$  is the lapse rate in EC/m, and  $z$  is the depth of the inversion layer. For a typical depth of 100 m and a positive lapse rate of 5°C/100 m the distance from the source to the shadow zone is just over 3 km. The distance,  $S$ , increases (decreases) with increasing (decreasing) depth of the inversion. Typical shadow range distances at night over open habitat in the dry season lie between 2 and 5 km.

### Model results

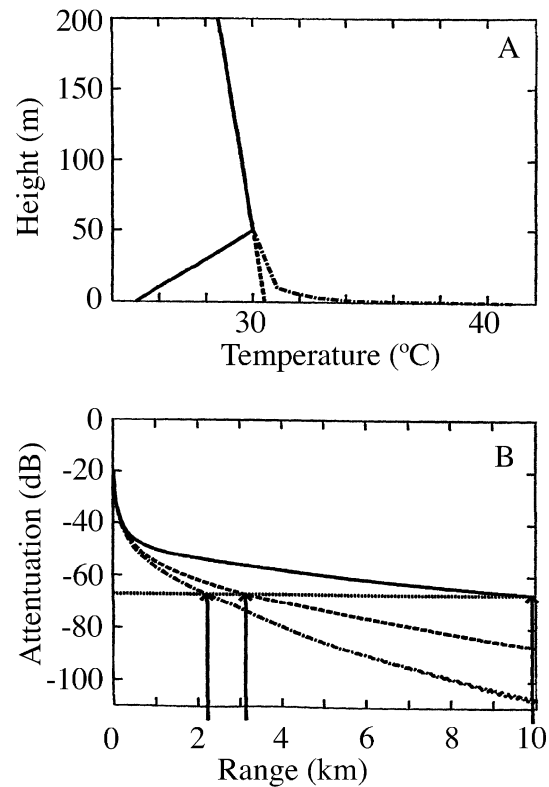
The rate of change of temperature with height or the strength of a nocturnal inversion, will influence the refraction of sound in the duct and the distance over which sound propagates. Similarly, propagation of sound in the layer will depend upon the depth of the layer of air or the thickness through which temperatures are increasing with height and the height of an elevated inversion above the ground (Heimann and Gross 1999).

Garstang et al. (1995) and Larom (1996) used the FFP to describe the effect of a surface inversion strength, thickness, and height upon infrasound propagation.

Details of the simplifying assumptions and calculation procedures used can be found in the two references cited.

Figure 3 (Larom et al. 1997) shows three temperature profiles: a typical nocturnal inversion (5°C/50 m, 50 m thick with the base of the inversion at the surface), an adiabatic lapse rate (0.5°C/50 m) representative of conditions in the early morning (0900–1000 hours LST) and late afternoon (~1600–1700 hours LST) and a super-adiabatic lapse rate (~10°C in the first 10 m above the surface) typical of conditions in the middle of the day (1000–1600 hours LST).

Range of the call in Fig. 3 is determined when a 117-dB signal at 15 Hz reaches the threshold of hearing of an elephant assumed to be 50 dB. The range changes from 2.2 to 9.9 km between daytime and nighttime conditions. Stratified stable nighttime conditions clearly favor propagation over the superadiabatic unstable or turbulent daytime conditions. Range expands threefold in the 2 h between late afternoon (1700 hours LST) and early evening (1900 hours LST). The area over which a call can be heard changes from about 15 km<sup>2</sup> in the middle of the day to 300 km<sup>2</sup> soon after sunset and sunrise. The simulations suggest that the most pronounced effect of

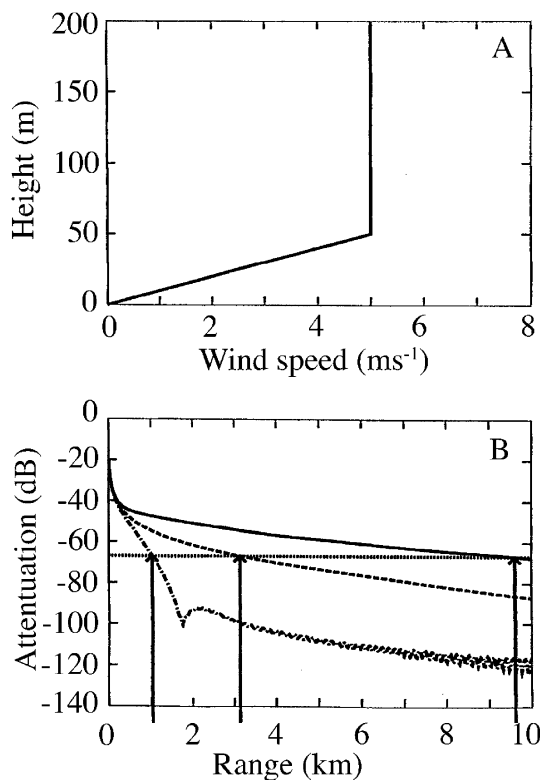


**Fig. 3** Idealized temperature profiles (a) and the 15-Hz attenuation profiles predicted from them (b). The temperature profiles show: midday super-adiabatic (occurring without loss or gain of heat) lapse (dash-dot line); late afternoon, adiabatic lapse (dashed line) and evening inversion (solid line). The hypothesized elephant low-frequency calling range based upon a -67 dB difference between call strength and hearing threshold is shown by a horizontal line in b. After Larom et al. (1997)

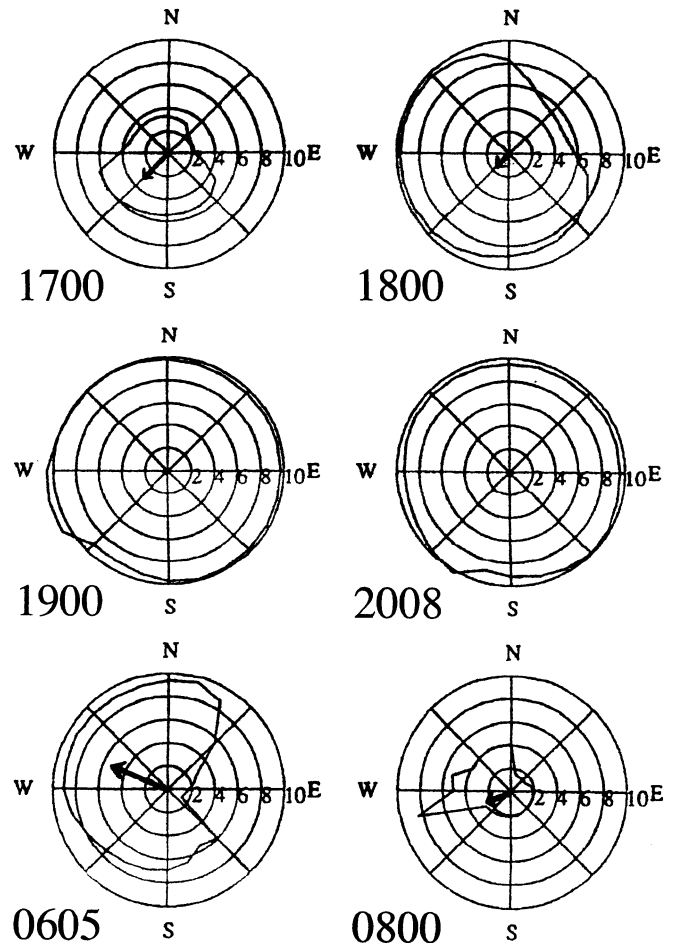
the temperature lapse rate on the area ensonified is confined to the first 100 m above the surface.

Low-level wind shear has a strong effect upon the range and direction over which low-frequency sound will be propagated at the surface. In an isothermal atmosphere (temperature constant with height), with wind direction constant with height but with wind speed changing as shown in Fig. 4 (Larom et al. 1997), a 15-Hz signal is transmitted over markedly different distances in the downwind, crosswind, and upwind directions. Downwind propagation is enhanced, upwind propagation is significantly degraded.

Figure 5 (Larom et al. 1997) shows an example (18–19 September 1992) of how the temperature and wind structure influence the area over which a 15-Hz elephant call can be heard by another elephant. An hour before sunset the area ensonified is 58 km<sup>2</sup>, 2 h after sunset the area has expanded to over 300 km<sup>2</sup>. Inadequate measurements during the middle of the day limited the calculation of range and area made by Larom et al. (1997). Estimates suggest, however, that under midday conditions range could be limited to less than 1 km and area to less than 3 km<sup>2</sup>. Midday to post-sunset areas may change by as much as two orders of magnitude.

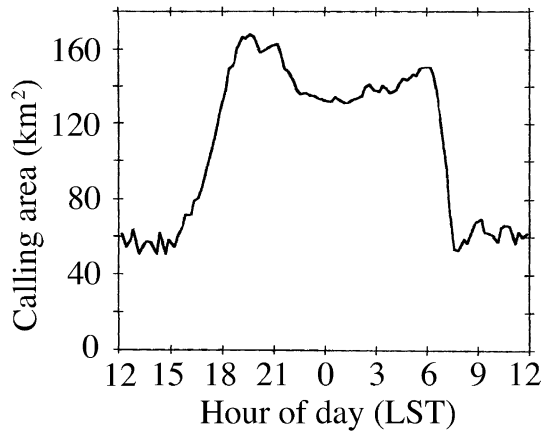


**Fig. 4** A simple model of low-level wind shear (a) and the 15 Hz attenuation (b) predicted by the Fast Field Program (FFP). The atmosphere is assumed to be isothermal ( $T/z=0$ ). Downwind attenuation is shown by the *solid line*, crosswind by the *dashed line* and upwind by the *dash-dot line*. The hypothesized elephant low-frequency calling range is determined as in Fig. 3. After Larom et al. (1997)



**Fig. 5** The  $-67$  dB attenuation contours of calling range calculated using the FFP (*irregular solid line*) and mean wind in the first 300 m above ground (*vector arrow*). Note that there are no *vector arrows* for 1900 and 2008 when the winds are very low or calm. *Circular rings* depict both range (in km) and wind speed (in  $\text{m s}^{-1}$ ). Data from tethered balloon soundings made in the Etosha National Park, Namibia, on 18–19 September 1992 were used in the FFP. Cardinal points of the compass are shown to indicate wind direction and directional dependence of calling range. Time of sounding is given at the lower left of each plot. After Larom et al. (1997)

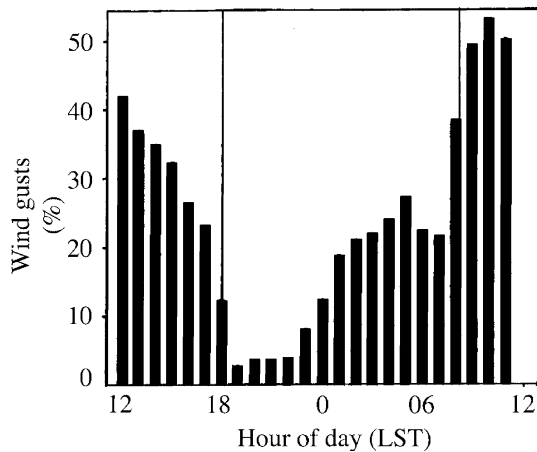
Figure 6, based on measurements that do not adequately reflect the extreme changes in range, shows that the nighttime area ensonified is between five and six times that of the midday area. The area reached by the  $-67$  dB line, however, displays a clear day-to-night signal with the primary maximum in the area ensonified occurring in the first hour after sunset. The secondary maximum occurs near sunrise. The area ensonified decreases towards midnight increasing again towards sunrise. The area ensonified during the day is uniformly much less than at night (Wilson et al. 2003). While nighttime conditions are most likely to favor the propagation of low-frequency sound over the daytime conditions, day-to-day variability in weather will reduce the day-to-night differences. In the near steady state weather conditions of the dry tropics and subtropics day-to-day variability in weather is at a minimum.



**Fig. 6** Model predicted (FFP) area ensonified by a loud (117 dB) low-frequency (15 Hz) elephant call assuming an attenuation of  $-67$  dB (threshold of hearing of 50 dB) over the course of a typical clear dry season day in Etosha National Park, Namibia. Local standard time (LST) is based on 30th E meridian. After Garstang et al. (1997)

Garstang et al. (2004, in preparation), were able to obtain continuous detailed observations of temperature and wind speed from the surface to 200 m by using an instrumented tower, a tethered balloon and a vertically pointing sounding system (SODAR).

The diurnal cycle of wind speeds (and direction) are a function of daytime mixing, nighttime stratification and topography. Figure 7 shows the net result of all of these factors on the surface wind speeds and gustiness. Wind speeds and wind gusts show a periodicity with minimum speeds and gustiness occurring soon after sunset. Wind and wind gusts effect both the transmission of sound (through turbulent scattering) as well as the detection of



**Fig. 7** Number of minutes with gusts over  $4 \text{ m s}^{-1}$  in each hour expressed as a percentage (%) for the 17 days of observations at the end of the dry season over the open bushveld of Eastern Etosha National Park, Namibia. The vertical solid lines define the initiation (near 1800 hours LST) and termination (near 0800 hours LST) of nighttime stratified conditions when a nocturnal inversion is established as in Fig. 2. (After Garstang et al. 2004, in preparation)

the signal at the receptor. Wind shear results in refraction and introduces directionality in the transmission of a signal. Wind noise at the receptor seriously attenuates both the quality of and ability to detect a signal.

### Habitat

Topography influences the transmission of sound directly (Heimann and Gross 1999) and indirectly by generating nocturnal wind jets which by mechanical mixing propagate wind and wind gusts downwards to the surface in the late night (Garstang et al. 2004, in preparation). Topography alters the pattern of shadow zones (Piercy et al. 1977; Canard-Carauna et al. 1990). Modest slopes of 1:60 produce enhancement and attenuation of low-frequency sound. Enhancement occurs at or in front of the ridge top while peak attenuation occurs at the base of the ridge on the far side from the source (Robertson et al. 1989). At 20 Hz enhancement and attenuation may add or subtract 10 dB to the strength of the source.

Studies of the effects of different habitats on the transmission of animal calls have been focused mainly on frequencies above infrasonic. There is extensive literature on vocalizations of non-human primates using low-frequency calling (but not infrasound) (see for example, Altmann (1967); Waser and Waser 1977). Forest dwelling primates are believed to select an optimum elevation from which to benefit from inversion conditions within or above the canopy (Wiley and Richards 1978). Few studies have focused upon infrasound generated and detected within a few meters of the floor of the forest.

Heimann (2003) used modeling studies to investigate the attenuation of a 100-Hz signal by multiple reflections and scattering by tree trunks. Tree trunks in an idealized 50 m wide stand of trees attenuated the 100-Hz signal by 5–6 dB. The indirect effect of the trunks reducing downward refraction by modifying the internal canopy wind field contributed less than 1 dB to the total effect.

Discrimination of significant variations in the signal as opposed to detecting the signal, constrains effective communication. In a forest, reverberations from vegetation surfaces degrades the signal more than amplitude fluctuations (Richards and Wiley 1980). Irregular amplitude fluctuations are due primarily to atmospheric turbulence from wind. Winds within a closed canopy forest are low and thus turbulence is low.

Reverberations in a forest take the form of discrete echoes from canopy foliage or in the change in acoustic impedance across the canopy. Reverberations are found to be least between 2,000 and 8,000 Hz but may also decrease significantly below 200 Hz (Richards and Wiley 1980).

The extreme changes in stratification observed over the open savanna (Fig. 2) are absent within a tropical or equatorial forest. Water content in the air within these forests is also high. To account for both temperature

and humidity effects on stratification, virtual temperature is used instead of temperature. Virtual temperature is the temperature which a parcel of moist air would have if at the same pressure and density all of the latent heat contained in the water vapor of the parcel were converted to sensible heat (AMS 2000, p. 820). Virtual temperature is, therefore, always greater than the actual temperature. The forest canopy in Fig. 8 is near 45 m. Daytime maximum temperatures at the forest floor may reach 30°C while nighttime minimums are no lower than 25°C. The range of day-to-night surface temperatures in a forest is almost an order of magnitude less than over the open tropical and subtropical savannas (5°C versus 40°C). Conditions below the canopy are stably stratified (i.e., less dense or warmer air overlying more dense air at the surface) over the 24 h. The inversion depth is greatest during the day when the upper canopy temperatures are highest. Under nighttime conditions an elevated (25 m) shallower inversion exists. Lapse rates range from 1°C/10 m during the middle of the day to about 0.5°C/10 m at night.

Wind speeds near the forest floor (below 10 m) and within the canopy are low with mean winds increasing from zero below 10 m to 2.5 m s<sup>-1</sup> at the top of the canopy (Fig. 8). There is essentially no difference in the wind speeds or wind profiles between day and night. Wind shear and turbulence is low (Garstang and Fitzjarrald 1999, pp. 119–121).

Atmospheric conditions within a closed canopy rainforest are significantly different from the counterpart conditions over the open tropical and subtropical savannas. Ducting of low-frequency sounds generated by an elephant within 10 m of the floor of the forest can occur at any time of day or night. The virtual temperature and wind profiles shown in Fig. 8 suggest that slightly better acoustic conditions might exist during the

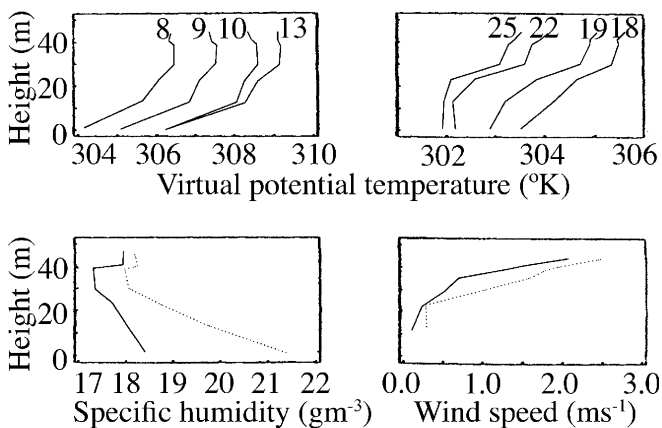
day as opposed to the night. The marked diurnal changes which influence the range over which low-frequency signals can be transmitted and heard over the savannas is absent in the rainforest. Both field measurements and model calculations are needed to determine low-frequency transmission characteristics of elephant calls in a closed canopy forest. Even less is known about acoustic conditions in intermediate habitats between open savannas and closed canopy rainforests.

## Reception

Hearing as an act of perceiving sound can be defined in a number of ways: as a behavioral response to sounds, to obtain and interpret information in an animal's (auditory) environment, and to identify and localize sound sources (Fay and Popper 1994, pp. 3–7). How animals hear is distinct from how their communication system receives, decodes, and interprets signals. Both signals and noise must be processed to extract information from the sounds received. Of interest in this review is how elephants hear and interpret low-frequency sounds, what if any particular physiological characteristics equip elephants to detect and react to infrasound, what is their threshold of hearing, how do they process frequencies with wavelengths in excess of 10 m to determine the location of the source in terms of both azimuth and range and can they detect signals below fundamental frequencies produced by abiotic sources? Because hearing can only be demonstrated and described through an analysis of the effect of the received sound on behavior, discussion of the reception of sounds must be linked with the discussion of behavior in the section which follows below (Webster et al. 1992).

As stated earlier, the broadcast information at the source is always greater than the information reaching the receiver. The higher the quality of the signal (signal-to-noise ratio) the more the information contained in the signal will be preserved and potentially assimilated. This quality depends upon attenuation between the source and the receiver. As we have seen in the case of low-frequency sound, atmospheric conditions play a crucial role in determining the degree of this attenuation. While the maximum range over which a signal can be transmitted and received is of fundamental importance, range and quality of the signal at the receiver are ultimately linked. The quality of the signal received at comparable distances from the caller will be greatest under acoustic conditions which produce the longest ranges.

While higher winds are directly related to turbulent dissipation and attenuation of a signal, higher winds increase ambient noise everywhere but in particular they increase flow noise over the elephant and its ears (Garstang et al. 2004, in preparation). Under windy conditions information contained in a signal reaching the elephant will thus be further degraded purely by wind noise over the elephant.



**Fig. 8** Mean profiles of virtual potential temperature,  $\theta_v$  (EK) specific humidity  $q$  ( $\text{g m}^{-3}$ ) (night is solid, day is dotted), and wind speed  $U$  ( $\text{m s}^{-1}$ ) (night is solid, day is dotted) within a 45-m rainforest. The  $\theta_v$  profiles are identified by the hour of day over which they were averaged (12 = 1200; 25 = 0100, local time). After Garstang and Fitzjarrald (1999)

## Physiology of elephant hearing

The ability of animals to detect low-frequencies is connected with the size of the body, head and distance between the ears (Heffner and Heffner 1982; Rosowski 1994). In general, the largest terrestrial mammals are most sensitive to sound frequencies below 10,000 Hz. Size-related segregation of hearing capabilities in mammals is not, however, clear cut and is poorly understood. The African elephant has large, mobile pinnae with an area on the order of  $10^4 \text{ cm}^2$  or in linear dimensions, about 1.0 m by 0.5 m for each external ear. Moss (1988, pp. 113, 124, 128) describes a number of changes in posture in which the pinnae are raised, extended and flapped.

The elephant's eardrum (tympanic membrane, von Békésy 1960, p. 11) has an area of  $10^3 \text{ mm}^2$  (Heffner et al. 1982). Animals with large tympanic membrane and foot plate area are thought to be better equipped for hearing low-frequency sounds. A study of 56 terrestrial animals including *Loxodonta africana*, suggests that the tympanic membrane area grows as a fourth root of body weight (Rosowski 1994, p. 199). The eardrum vibrates in response to a sound pressure wave and the vibrations are transferred by the three small bones known as ossicles. The size, shape and attachments of the ossicles vary greatly among mammals. In general, the larger the mammal, such as the elephant, the larger the ossicles. The size of the ossicles is inversely related to frequency. The ossicles serve to both amplify the sound and transmit it to the oval window of the cochlea or inner ear. The precise relationship between the structural features of the external and middle ears and their auditory functions are not well understood in any mammal, let alone in the elephant. Sensitivity to low-frequencies is, however, thought to be associated both with large tympanic membrane areas and large, compliant middle ear spaces. In *Loxodonta*, the linear dimensions of the malleus in the middle ear are about twice those of the incus. The long arm of the malleus (the manubrium) in *Loxodonta* is nearly vertical, placing it perpendicular to the horizontal plane (Rosowski 1994, p. 173).

The cochlea has the characteristic spiral shape and is filled with fluid. The cochlea in *Loxodonta* has two spiral turns and a total length of the basilar membrane of 60 mm (von Békésy 1960, pp. 506–509). Von Békésy (1960) measured the resonance of the cochlea dissected from an elephant finding it responsive down to 30 Hz. Von Békésy (1960) also concluded that of the animals studied, the elephant cochlea exhibited the sharpest resonance indicating that elephants may be well equipped to distinguish between frequencies (Long 1994, pp. 26–27).

## Threshold of hearing

Heffner and Heffner (1980, 1982) measured the threshold of hearing for a 7-year-old female Asian elephant (*Elephas maximus*). The study shows a threshold at 17 Hz of 60 dB SPL and at 16 Hz of 65 dB SPL.

Langbauer et al. (1991), in successful playback experiments of African savanna elephants, used a SPL of 112 dB with a sensitivity threshold of 46 dB SPL.

## Sound localization

The localization of the source of a sound is for all animals a crucial function of hearing. High frequency sounds detected by an acute hearing system rapidly directs the eyes to the source of the sound. The relationship between hearing and sight is less clear in the case of long-range, low-frequency sounds or calls (Fay and Popper 1994, pp. 9–12).

Localization of sound depends upon the difference in wave form phases between the two ears. Such phase changes correspond to interaural time delays. A phase difference of  $\Delta\phi$  for a given frequency,  $f$ , corresponds to an interaural time difference of  $\Delta t$  where  $\Delta t = \Delta\phi / 2\pi f$  (Hartman 1999). Lower frequencies can thus produce longer interaural time differences. Heffner et al. (1982) demonstrated that elephants are not able to locate sound sources with frequencies  $\geq 4,000$  Hz.

The path traveled by a wave front between the eardrums is larger than the skull perimeter for low-frequencies but equal to the skull perimeter for high frequencies (Kuhn 1977, 1987). For humans, the effective acoustic circumference for low-frequencies is 150% that for high frequencies (Brown 1994, pp. 64–69). The size and position of an elephant's ears and the presence of the trunk and forehead structure would suggest that this expansion in perimeter distance for low-frequency signals might be considerably greater for elephants (Kuhn 1977). In tests carried out by Heffner and Heffner (1982, 1984), elephants could localize low-frequency sounds to within an azimuth angle of  $1^\circ$ .

## Determination of range

How animals determine range using infrasound is poorly understood. Elephant behavior with respect to low-frequency calls by familiar and unfamiliar elephants clearly indicate an acoustic perception of range (Moss 1988; Poole 1996; Payne 1998). McComb et al. (2003) used low-frequency playback calls which provide evidence of a sense of distance between the listener and the sender of 1–2.5 km. From personal observations in the field (Etosha National Park in 1999), the time from initial reaction of elephants at a water hole to the arrival (10 min) of a new group of elephants and the pace of the incoming group (8.0–9.6 kmph), suggest that the range at which their presence is first detected is between 1.5 and 2.5 km. Distances in excess of 1 km eliminate sight (and perhaps smell) from the potential cues being used in determining these ranges.

Only candidate theories exist which might explain how and how well elephants determine the distance of the sound source from their location: there is clearly a

loss of higher frequencies with distance which changes the frequency spectrum. It is likely that for ranges above 1–2 km only low-frequencies remain. The amplitude of the signal at each ear varies with head size, azimuth, signal frequency and transmission distance. It is possible that elephants can detect differences in amplitude which can be related to range.

Payne et al. (2003), have shown that there is a relationship between elephant numbers, calling rates, social complexity and vocalization. Changes in the acoustic components of these behavior patterns may be used to recognize distance. The detection of the rate of calling may, for example, change substantially with distance between the listeners to the callers.

Evidence presented earlier in this review suggests that low-frequency vocalizations are subject to significant changes in range as a function of the acoustic state of the atmosphere. Under poor acoustic conditions (very hot surface and strong winds), powerful (117 dB) low-frequency (15 Hz) calls by elephants assuming a threshold of hearing of 50 dB are predicted to only be heard by conspecifics 1 km away. Under ideal atmospheric acoustic conditions for the same frequency, loudness and threshold of hearing the call may be heard more than 10 km away. Elephants under such changing atmospheric conditions might adjust the timing and frequency of their low-frequency calls (see section below). It is possible that because the quality of the call received is a function of the range, that elephants have, over evolutionary time, developed the ability to relate the acoustic state of the atmosphere to range.

Elephants can hear and apparently interpret and react to infrasound produced by abiotic sources (Poole 1987). It is likely that elephants can detect frequencies down to and below 10 Hz, well below the infrasonic frequencies that they are thought to be capable of generating. Elephants hear many low-frequency sounds other than those generated by conspecifics. Numerous anecdotal examples exist of elephants responding to distant (10's of kilometers) culling operations which were employing helicopters. Helicopter blades produce infrasound (K. Payne and R. Garstang, personal communication). Elephants in the Etosha National Park leave the park in a northeasterly direction towards the advancing rains some 2–3 weeks before the rains arrive in Etosha (M. Lindeque, personal communication). Convective motions within vigorous cumulonimbus clouds typical of tropical rain storms produce strong infrasonic signals (Nicholls and Pielke 1994; Bedard and Georges 2000). Sources of infrasound generated by humans in and near conservation areas should be clearly documented and possibly constrained (Larom 2002; Partan and Marler 2002).

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## Behavior

The complex social relationship between elephants has been extensively documented (Douglas-Hamilton and Douglas-Hamilton 1975; Moss 1988; Poole 1996; Payne

1998). Moss (1988, p. 126) presents in diagrammatic form a picture of elephant social structure beginning with the matriarch and the immature offspring at the center of the family unit, expanding outwards to embrace family groups, clans, central subpopulations and populations. McComb et al. (2000), showed that elephants in the family units recognize the vocalizations of about 100 other females in the population.

The family unit consists of a dozen or so related females and their offspring (Payne 1998, p. 45). While related females may remain in the family unit, males are forced out of the unit at puberty to form bachelor herds and ultimately lone mature bulls (often with a younger companion called an askari). The social bonds among family unit members are very strong with communication playing a central cohesive role.

Leong et al. (2004) studied the vocalizations of eight captive adult African savanna elephants (six female, two male). They defined eight categories of calls in a total of 983 calls recorded. Only 5% of the recorded calls did not contain infrasonic components. Of the eight categories of calls, three categories were infrasonic (12–18 Hz). Despite the close proximity of these eight captive elephants, infrasonic calls, as in the wild, dominated the frequencies used in vocalizations (Langbauer 2000). McComb et al. (2003) found that the distance (0.5–2.5 km) over which information on social identity can be recognized is of potentially greater importance than the ability to communicate over greater ranges. These observations leave little doubt that low-frequency communication influences elephant behavior. The role played by low-frequency calls in reproduction, resource utilization, avoidance of predation and effects on these behavioral patterns of the acoustic state of the atmosphere is examined below.

## Reproduction

Reproductive behavior of the African elephant (*L. africana*) can fluctuate widely in response to environmental conditions, predation, population densities and other factors. Onset of puberty for females can vary between 12 and 22 years of age and the average interval of calves for a given female can be as much as 8 years but not less than 4 years (Moss 1988, pp. 239–240; Moss 2001). The estrous period in which females are receptive to males and can conceive ranges between 2–6 days (Moss 1983; Poole 1994, pp. 185–193). Males also experience an elevated reproductive state of musth which is a function of age and health (Poole 1987, 1989a, b; Schulte and Rasmussen 1999). A male can come into musth at any time of the year and remain in this heightened state for as much as 3 months (Moss 1988, p. 115). Musth males are more successful in finding mates and estrous females choose older musth males for both mating and guarding (Poole 1989b).

With females and males in a reproductive state separated in space and limited in time, long-range, low-frequency communication becomes an essential part of

the survival of the species. Elephant population densities can vary over a wide range (from 1 to 6 per km<sup>2</sup>) (Moss 1988, p. 240). While these numbers must be treated with caution, they are useful in demonstrating the role of long-range, low-frequency communication in reproduction. As shown earlier, the distance over which a loud, low-frequency elephant call can be heard by another elephant ranges from about 1 km to possibly more than 10 km depending upon the acoustic state of the atmosphere. At a range of 1 km the likelihood of an estrous call being heard by a musth male is small even at the highest population density. At a range of 10 km the area ensonified by an estrous call expands by two orders of magnitude to potentially include elephant numbers greater than 300. The likelihood of an estrous call being heard by one or more musth males is now large.

Leong et al. (2004), examined the use of low-frequency vocalizations in different phases of the estrous cycle. No distinct calls were noted in the ovulatory follicular phase. The rate of low-frequency calls, however, was highest in the first period of follicular growth which may serve as a cue to males early in the estrous cycle, attracting males prior to ovulation, resulting in both male–male competition and female choice. Payne et al. (2003) note that females in estrous make long sequences of powerful low-frequency calls. Similarly, for conditions in the wild, as opposed to the captive elephants observed by Leong et al. (2004), Payne et al. (2003) find that there is a relationship between elephant numbers, social complexity, vocalization and calling rates. Thus, there are a number of long-range cues, varying in potential information content, which are available to musth males from females in or about to come into estrous.

#### Resource utilization

An adult elephant consumes between 150 and 170 kg of vegetation per day (Gröning and Saller 1999, p. 67). After 4–5 months without rain at the end of the dry season in many elephant habitats in the subtropics, the available vegetation and nutrients are at a very low level. Even an average family group containing eight adults and sub-adults will consume over 1.2 tons of vegetation per day along their foraging path. Under extremely hot conditions with daytime surface temperatures between 45 and 50°C, conservation of energy is critical to survival. Martin (1978), Payne (1998), and Langbauer (2000) have noted that family groups maintain a separation of 3–5 km for days to weeks. This strategy, certainly aided by using low-frequency communication, serves to conserve energy and ensure that each group feeds along a different corridor of vegetation.

#### Predation and conflict avoidance

With the exception of humans, the only predators that threaten a healthy African elephant are lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) and then only

young elephants and calves. Both predators frequent water holes, particularly at the height of the dry season. A small family unit with only a few adult females with young calves is at considerable risk at a water hole. To counter this, elephants appear to use a low-frequency “assembly” call prior to going to water (Poole et al. 1988). Small family units combine into a large assemblage of elephants which can collectively stand off lions or hyenas.

McComb et al. (2003), investigated the social information contained in elephant calls in five frequency groupings ranging from 0–15 Hz to 390–405 Hz. When recorded sounds from elephants unfamiliar to the target group were played back at a distance of 0.5–1.0 km the target group took evasive action by leaving in the opposite direction.

#### Social behavior

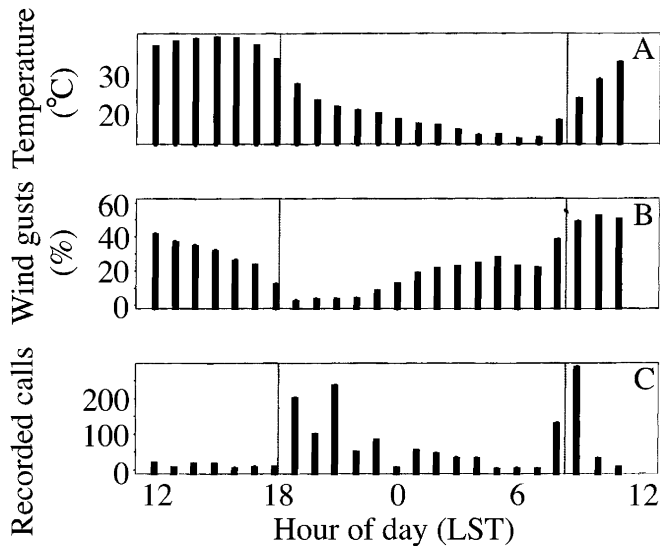
Thirty-one distinct calls have been described for the African elephant (Langbauer 2000). Most of the recognized calls are infrasonic and a number of them are both long- and short-distance calls.

Long-distance, low-frequency communication occurs when signalers and receivers interact as well as when the receiver remains passive (McGregor 1993; McGregor and Dabelsteen 1996; McComb et al. 2000). Information contained in long-range signals is clearly available to intended receivers as well as to eavesdroppers (McComb et al. 2000). McComb et al. (2000) used playback of contact calls to evaluate the extent to which female subjects are capable of recognizing others in the population. They found that contact calls by females were used to locate members of the family unit and bond group members, suggesting that the recognition of an individual was possible.

Payne (1998, p. 224), delineates areas in which elephants in the Sengwa reserve in Zimbabwe spent at least 50% of their time. While there is considerable variation in the size of these areas, the majority corresponds to an area which has an equivalent radius of 3–4 km. Since low-frequency calls can at times of optimum acoustic condition travel and be heard at ranges greater than 4 km, these areas would be compatible with the audio envelope about a family unit. The acoustic world of this highly social animal is a pervasive one extending from intimate contact to distances up to a few hundred kilometres. Even the immediate acoustic environment created by conspecifics can occupy over 300 km<sup>2</sup> (Larom 2002; Partan and Marler 2002; Rundus and Hart 2002).

#### Calling patterns

Figure 9 shows the daily cycle of surface temperature, wind gust frequency and the number of low-frequency elephant calls that were recorded in each hour at a fixed water hole location (Garstang et al. 2004, in preparation). Also shown in Fig. 9 are the times of transition



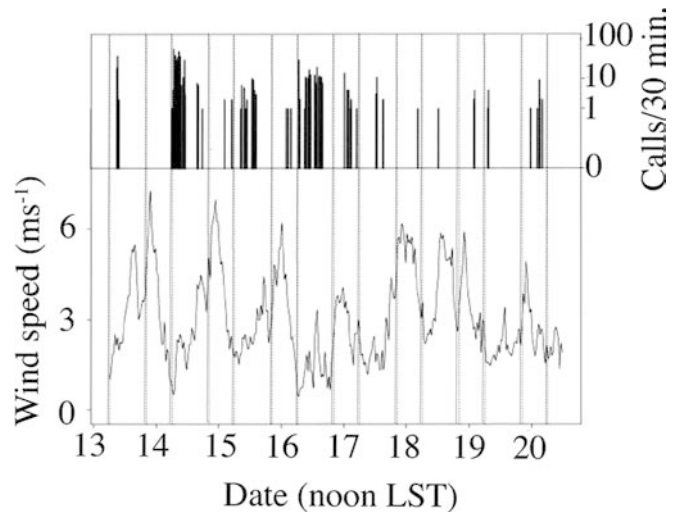
**Fig. 9** The 24-h distribution of temperature (*top panel*), gust frequency (%) for gusts over  $4 \text{ m s}^{-1}$  as for Fig. 7 (*middle panel*), and the number of recorded elephant calls for each hour of the day (*lower panel*). The meteorological data is taken from 13–30 September. The elephant calling data is from 12–26 September 1999 in the eastern Etosha National Park, Namibia. The vertical lines are as in Fig. 7. (After Garstang et al. 2004, in preparation)

between nighttime stable and daytime unstable conditions.

The early morning (after sunrise at 0600 hours LST) persistence of stable nighttime conditions shown in Fig. 9 would extend beyond sunrise, the secondary maximum in the model calculations shown in Fig. 6. This results in a general agreement between the bimodal distribution of recorded calls of Fig. 9 and the model predicted distribution of the area ensonified by an elephant call in Fig. 6.

While this general agreement between recorded calls and atmospheric acoustic conditions might suggest that elephants have adapted their long-range, low-frequency calling rates to atmospheric conditions, more definitive work needs to be carried out before such a relationship can be confirmed or rejected (Garstang et al. 2004, in preparation). Wind attenuates both the signal and the ability to detect the signal at the receptor. Figure 10 shows the occurrence of elephant calls recorded on individual days together with the surface wind speed on those days. Essentially all calls occur under the lowest wind conditions. The lowest wind speeds in turn occur around sunset and sunrise.

Habitat including differences in topography and vegetation plays an important role in governing atmospheric acoustic conditions (Heimann and Gross 1999; Heimann 2003). In a closed canopy forest better propagation conditions exist during the day than at night, reversing what is found in an open habitat. More elephant low-frequency calls might be expected in the day in a forest than at night. Patterns of calling are thus dependent both upon the structure of the near-surface atmosphere and upon habitat.



**Fig. 10** Eight consecutive days showing in the *top panel* the number of recorded calls in each half hour (log scale) and in the *bottom panel* the corresponding 30 min average wind. The vertical lines define the initiation (near 1800 hours LST) and termination (near 0800 hours LST) of stratified nighttime conditions. After Garstang et al. (2004, in preparation)

Langbauer, Payne and Charif (personal communication), using records of loud, low-frequency calls from 14 collared elephants in the mixed terrain and habitat of the Sengwa reserve in Zimbabwe, show a maximum in calling rate at sunset, a minimum near sunrise and an increase in calls during the day to the maximum at sunset.

## Concluding remarks

Progress in understanding the production, transmission, and reception of low-frequency sound together with the associated behavior in both *Loxodonta africana* and *Elephas maximus* has progressed a long way since the early documentation of the use of infrasound by elephants. The pervasive use of low-frequency sounds by elephants is now well established together with increasing evidence of the distances traveled and complex social functions of vocalizations at low frequencies.

Accompanying the understanding of the nature and role of long-distance, low-frequency communication in elephant society are advances in the technological capability to detect, record, and interpret these sounds.

Analytical tools now promise the ability to precisely locate the caller, potentially identify the caller by individual calling characteristics (audio signature and pattern recognition), associate calling patterns with elephant numbers, herd composition, and other complex social functions including those associated with reproduction. These tasks can be accomplished by employing in situ and remote sensors capable of recording information in habitats previously inaccessible or extremely difficult to work in.

Technological advances will continue to improve the understanding of the content and factors limiting the content of long-range, low-frequency calls. For example, robust characteristics of the structure of the call will potentially permit deductions to be made about the size, sex, sexual status and health of the caller.

Despite these advances we still do not know how far one elephant can hear another elephant's low-frequency call. While it is known that long-range calls are in the near-infrasound frequency range, the degree to which the information content is degraded by attenuation over distance is unknown especially in different habitats and under different atmospheric conditions. Knowledge of the maximum range over which loud, low-frequency calls can be heard and interpreted may well be closely linked to the area required for the survival of typical social units.

Conditions which favor maximum range also favor the retention of the maximum amount of information contained in the call. If content and range are conditioned by the atmospheric acoustic state then studies of the role played by communication must simultaneously be concerned with the physical state of the fluid in which these sounds are being generated, transmitted and received.

Research in the future and, in particular, in the field, must take increasing note of the highly interdisciplinary nature of the problems in long-range, low-frequency communication. While our consciousness of the Umwelt of these animals is increasing, this understanding is dependent upon delineating the boundaries of their acoustic world.

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## Errata Sheet for

Review paper on long-distance, low-frequency elephant communication  
(M. Garstang, J. Comp. Physiol. (2004), Vol. 190, 791-805)

I have found a few typographical errors in the review paper on elephant low-frequency communication cited above which, were, unfortunately, not caught in reviewing the proofs. The errors are as follows:

p. 792 – column 2, subheading “The filter”, 2<sup>nd</sup> para — wavelength (8) should be wavelength ( $\lambda$ ) where  $\lambda$  is the Greek symbol for length followed by  $L = 1/48$  which should be  $L = 1/4(\lambda)$ , i.e., one quarter of the wavelength.

p. 793 – column 1, 2<sup>nd</sup> para, lines 2 and 3 –  $F_i(2i-1) C/4L$  should be  $F_i = (2i-1)C/4L$

p. 793 – column 1, 2<sup>nd</sup> to last line, 2<sup>nd</sup> para –  $\Delta FC/2L$  should be  $\Delta F = C/2L$

p. 793 – column 1, middle of last para – 36EC should be 36°C – where E has been erroneously substituted for the degree sign

p. 796 – 1<sup>st</sup> column, 1<sup>st</sup> para — P should be lower case  $\ell$  and EC/m should be °C/m

p. 797 – Fig. 4 caption —  $T/z=0$  should be  $\delta T/\delta z=0$

p. 799 – 1<sup>st</sup> column, line 10 – 30EC should be 30°C

p. 799 – Fig. 8 caption —  $0_v(EK)$  should be  $\theta_v(^{\circ}K)$  and  $0_v$  should be  $\theta_v$

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