Commentary

The Role of Sound in the Reproduction of African Elephants

Michael Garstang*

Emeritus Research Professor, Department of Environmental Sciences, University of Virginia, USA and Senior Scientist, Simpson Weather Associates, Inc., USA

***Corresponding Author:** Michael Garstang, Department of Environmental Sciences, University of Virginia
Charlottesville, VA 22904, USA, Tel: (434)979-3571; Fax: (434)979-5599

First Published **December 24, 2018**

Abstract

Proboscidians, the ancestors of today's elephants, can be traced back for more than 35 million years.[1] They evolved in dense, closed-canopy rain forests. By the time that Elephantidae in the form of the mammoth and present day Asian (*Elephus maximum*), African savanna (*Loxodonta africana*) and forest (*Loxodonta cyclosis*), elephants emerged as distinct species their morphology was well established, the forests had receded and the elephants had moved onto the open plains.

Elephants sense of sight, smell, touch, taste, hearing and production of sound was developed in the forest. The dense vegetation of the rain forest limits the use of vision to less than a few meters. Sight is, thus, poorly developed in elephants. Smell is highly evolved and plays a role in reproduction. At the floor of the forest, however, the air motion is weak or absent, limiting the distance and reliability of detecting smell. Touch and taste operate only when animals are in close contact with each other. Sound is the most effective means of communication, particularly over distance that is exploited by elephants.

Yet the dense vegetation of the forest, including tree trunks, limits part of the elephant's sound repertoire. High frequency sound (> 1 kHz), audible to humans as well as elephants, is particularly affected. Low-frequency sound (< 100 Hz), however, does not "see" the vegetation including the trunks of trees and can travel considerable distances. This propagation of infrasound is enhanced by the presence of cool air between the floor and canopy (Figure 1). Calm or low winds at the floor of the forest reduce attenuation of sound and wind noise across the ears (Figure 2). Evolving in the rain forests, elephants developed the ability to generate and detect infrasound.

[1]This chapter draws heavily upon previously published work by the author.

Sound Generation

The elephant generates the sounds it makes from a "source" conditioned by a "filter". The "source" is driven by large capacity lungs which set the vocal folds in the larynx in motion. The vocal folds have an inverse relationship between length and mass which together with the length of vocal track (up to 4.6 m), produces the lowest frequency sound of any other terrestrial animal. The vocal track acts as the "filter".

Hearing

Equally evolved is the elephant's ability to hear and to locate low-frequency sounds. The hearing mechanism of the elephant is the largest of all terrestrial mammals. Each outer ear or pinna measures on the order of 2 m^2 (or 20 ft^2) and is highly mobile so that it can be extended outwards and raised (together with the head) indicative of listening [1,2] (Figure 3). The middle ear structures of the African elephant are large in comparison to humans providing structures that enhance their ability to detect frequencies down to and below 10 Hz.

The size of the elephant's head and ears may govern how well it can locate sounds, particularly using low-frequencies at large distances. Elephants can localize low-frequency sounds (<1 kHz) to within an azimuth angle of 1° at a range of at least 2 km (1.25 mi). Sounds are localized by using interaural time differences (ITD) where for the size of the elephant's head and pinnae, the path traveled by the sound is greater than the skull perimeter for low-frequencies.

Playback experiments, using recorded low-frequency estrous calls showed that male savanna elephants can locate such calls in the middle of the day, at a range of 2 km (1.25 mi). The loudness of such calls has been measured at 117 dB [3].

Elephants may also be able to determine the distance (range) between themselves and another calling elephant. They may infer distances from the progressive attenuation of the higher frequencies within received calls. Elephants may also react to the frequency of calling of a distant elephant. Females in heat do not emit a characteristic estrous call. They do, however, make loud low-frequency calls more often than when not in heat. This rate of calling may be recognized by the males as a signal that the female calling is in estrous.

Reproduction

Moss et al. have described the highly organized social state of the African elephant (4). Social organization is founded upon a family unit of one or more adult females and their offspring with a high frequency of affiliation to one another and a limited association with adult male elephants.

The female elephant has one of the longest reproductive lives of any terrestrial mammal. Her reproductive life extends over 30 years from 15-45 years and can extend for an additional 15 years. She carries her young for 22 months, nurses her calf for 22 months and may come into estrous again some 4 months later, for a total cycle of 4 years. She will remain in heat for about 4 days. If she does not conceive she will recycle in a much shorter period than the previous 4 years.

Her family unit will contain one or more of her daughters who may remain, together with other females, in the family group for the rest of their lives. Females without calves will serve as allomothers to new borne calves often paying closer attention to the calf's welfare than the mother herself. Male offspring are ejected from the family unit at puberty (about 15 yrs old). Other mature males will visit and briefly remain with the family. These males, however, may not coincide with any of the unit's female in estrous cycle. More typically the family unit will not contain a mature male.

With the female in heat for about 4 days in 4 years, successful propagation of the species depends upon selection. This requires the presence of two or more competitive mature males. A mechanism is needed to effectively bring the female together with a number of suitable males. While the sense of smell undoubtedly plays a role, long range, low-frequency sound may be the most effective means of attracting these males.

Sound and Reproduction

As elephants moved from shrinking rainforests to open dry tropical and subtropical savannas, they carried with them capabilities of communication which evolved within the forests. They had adapted to the use of low-frequency sounds (< 100 Hz) in the face of the attenuating effects of the forests on high frequency sound. They had also benefitted from the low wind speeds at the floor of the forests together with the inverted temperature profile in between the forest floor and the canopy. Both calm conditions (absence of turbulence) and the ducting of sound supported the distance over which their calls travelled, the area and the number of male elephants attracted.

Over the daytime open savannas hot air rises off the surface and by mid-morning is creating turbulence and mixing. Stronger higher level winds are mixed downwards to the surface. By midday, gusty winds are blowing and conditions for transmitting sounds have substantially deteriorated.

Yet, by an hour before sunset, the solar angle has decreased enough such that less solar heat is entering the surface than is leaving the surface. With the net loss of heat, the surface must cool and temperatures begin their rapid nighttime cooling.

The air near the ground is now cold, dense and stable. Winds are calm and turbulence is non-existent. A cold layer of air from the ground eventually extends up to about 100 m (320 ft) (Figure 4). This quiet, cold layer of air forms a duct or channel for the transmission of low-frequency sound remarkably like the conditions in the forest where the elephants acquired their communication skills.

With these contrasting day-to-night conditions, calls made by elephants during the middle of the day travel about 2 km and cover less than 10 km^2. The same calls, once nighttime conditions settle in, cover over 300 km2 (Figure 5).

The expectation would be that a female calling in the middle of the day in the open savanna would not find a single male let alone have a choice of more than one male. In contrast, as soon as nighttime conditions set in, she may find 10 males in the 300 km^2 she was able to reach with her call.

Substantiating Evidence

Figure 1 shows the vertical profile of the combined thermal effect of temperature and humidity in the rain forest. The rain forest creates a pervasive inversion of temperature between the top of the trees and the floor of the forest persisting over both day and night. Figure 4 shows that the rain forest conditions are replicated between dusk and early morning over the open tropical savannas. Figure 2 also shows that the forest floor has calm to very light winds while savanna has strong winds centered on midday (Figure 6). The lightest surface winds over the savannas are around sunset (1800 local solar time). Higher surface winds are observed over the savannas during the early morning and near dawn.

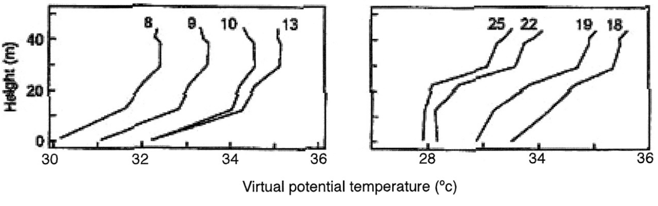

Figure 1: Mean profiles of virtual potential temperature (°C) includes the contribution of moisture to the temperature in the closed canopy of a rain forest for daytime (lefthand box) and nighttime (righthand box) labeled for the hours of the day in solar time where 25 h equals 0100 a.m. (After Garstang, 2010, p. 62.).

Figures 5 and 6 demonstrate that low-frequency calls are made and received by elephants propagating over the widest areas under the conditions of the most stable and low surface wind speeds described above.

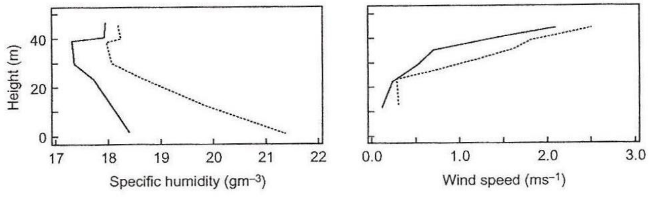

Figure 2: Mean profile of specific humidity for night (solid) and day (dotted) in left hand. Box and wind speed for night (solid) and day (dotted) in right hand box within a 45 m rainforest. (After Garstang, 2010, p. 62.).

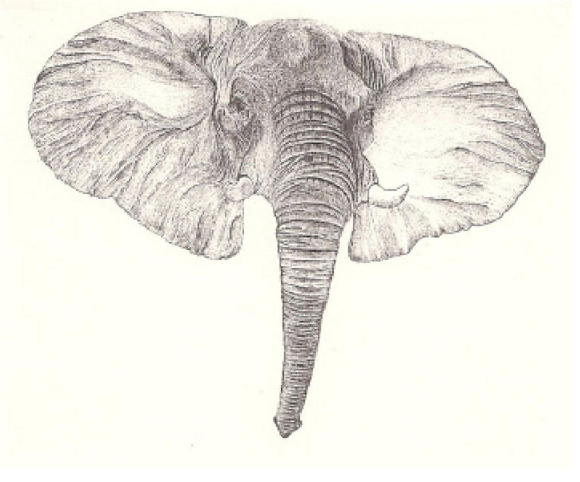

Figure 3: Adult elephant with raised head with fully spread ears. (Pen and ink by author, Garstang, 2015, p. 60.)

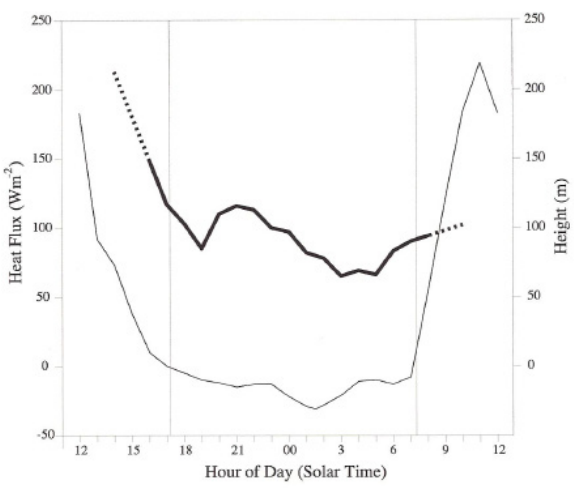

Figure 4: Sensible heat loss and gain from the surface of the open savanna shown by the light curve in watts per m2 (left hand ordinate). The light vertical lines show the location of the transition of the surface from nighttime cooling (negative heat flux) to daytime heating (positive heat flux). Note that this transition takes place before sunset (1800) and after sunrise (0600) with the surface at night always loosing heat. They heavy black line shows the height of the nocturnal inversion of temperature at a depth of about 100 m (right hand ordinate). (After Garstang, 2010.)

A final question is whether the savanna elephant calls at the time of day predicted. Figure 7 presents the number of loud, low-frequency calls received from 14 collared elephants in the Sengwa Reserve in Zimbabwe. The results show a pronounced maximum in calling in the hours following rapid surface cooling and the presence of an inversion and low wind speeds near to and just after sunset.

Figure 8 presents the number of low-frequency calls recorded on 8 sound recorders surrounding a water hole (Mushara) in the Etosha National Park.

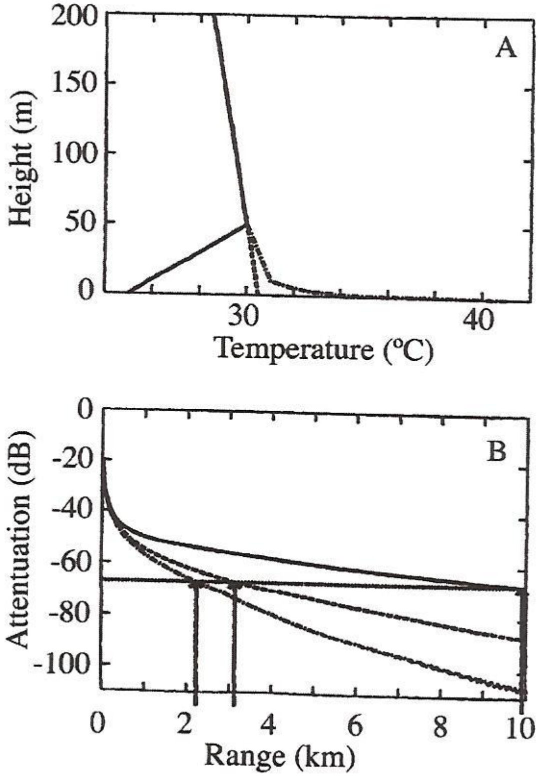

Figure 5: Temperature profiles (upper figure) at midday (dash-dot), transition from day-night and night-day (dashed) and for the nocturnal inversion (solid). The distance travelled by the low-frequency call for each of the profiles is shown by the arrows in the figure below. (After Garstang, 2010.)

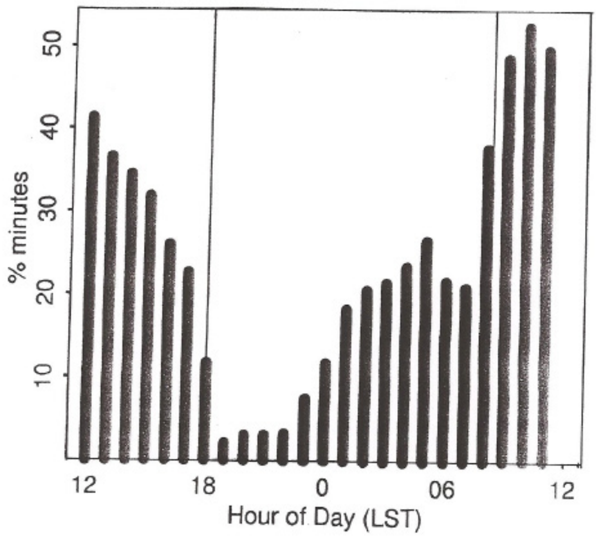

Figure 6: Frequency distribution of surface wind gusts over 4 m s-1. The vertical lines are as for Figure 4. (After Garstang et al., 2005.)

Figures 7 and 8 both support the thesis that elephants call most frequently near sunset and sunrise. Figure 8 is more supportive of calls at night or during the time when the surface is cooler than the atmosphere, ducting, is present and conditions more favorable for long-range communication.

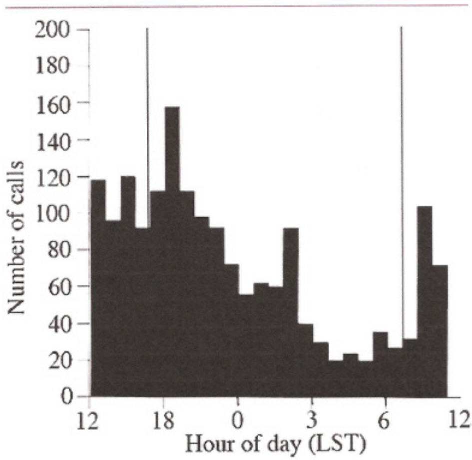

Figure 7: Frequency distribution of loud, low-frequency calls recorded from 14 collared adult elephants in the Sengwa Reserve in Zimbabwe. The vertical lines are as for Figure 4. (After Garstang et al., 2005.)

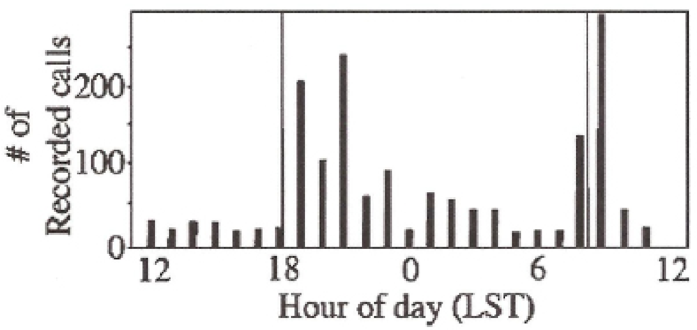

Figure 8: The 24-hr distribution of the number of elephant low-frequency calls (< 100 Hz) recorded over 8 consecutive days at the Mushara water hole in the Etosha National Park, Namibia. The vertical lines are as for Figure 4. (After Garstang et al., 2005.)

Conclusions

Elephant reproduction, in the broadest sense, depends upon long-range communication to attract the fittest males assuring survival of the species. Prolonged gestation, nursing and education of the young, together with the limited time and frequency of a female in estrous, and the absence of mature males within the herd, requires an effective means of communication to sustain wild elephant populations. Low-frequency sound generation, transmission and detection by elephants fulfills this vital role.

References

1. Moss C. Elephant Memories: Thirteen Years in the Life of an Elephant Family. New York: Ballentine Books. 1988; 335.
2. Poole JH, KB Payne, WR Langbauer Jr, CJ Moss. The social context of some very low-frequency calls of African elephants. Behav. Sociobiol. 1988; 22: 385-392.
3. Langbauer WR, K Payne, R Sharif, L Rapport, F Osborne. African elephants respond to distant playback of low-frequency conspecific calls. J. Exp. Biol. 1991; 157: 35-46.
4. Moss CJ, H Croze, P Lee, editors. The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Animal. Chicago: University of Chicago Press. 2011; 205-208.

Additional sources by Garstang are drawn upon to support this chapter:

- Garstang M. Elephant infrasounds: long-range communication. Chapter 3.2. In: SM Brudzynski, editor. Handbook of Mammalian Vocalization. Amsterdam: Elsevier. 2010; 57-67.
- Garstang M. Elephant Sense and Sensibility: Behavior and Cognition. Amsterdam Elsevier Academic Press. 2010; 133.

- Garstang M, DR Fitzjarrald, K Fristrup, C Brain. The daily cycle of low-frequency elephant calls and near surface atmospheric conditions. Earth Interac. 2005; 9: 21.