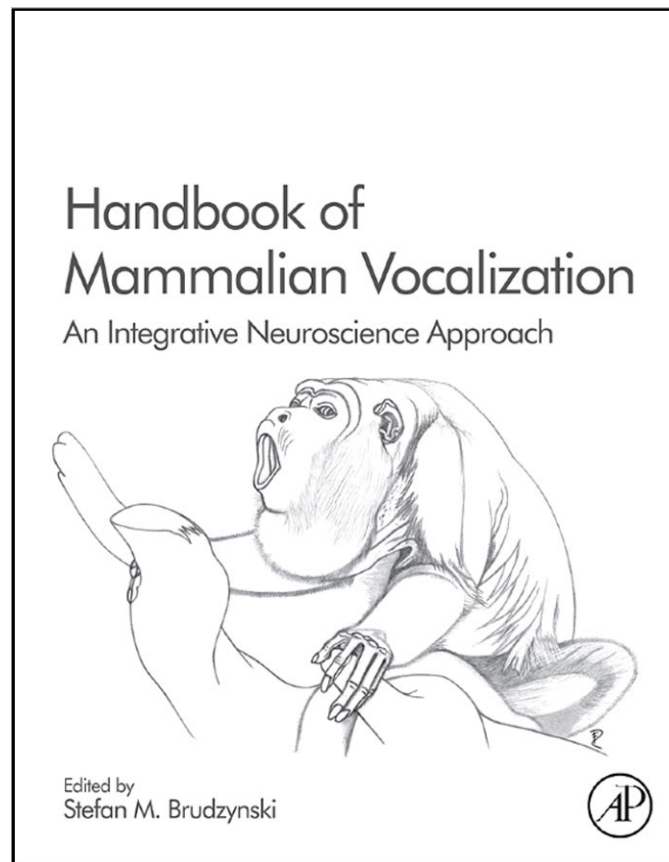


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SECTION 3

Diversity of Vocalizations

Mammalian vocalizations evolved in many directions with sound frequencies ranging from infrasounds to ultrasounds. The vocal system allows for a high variability of produced sounds and suitable adaptations, for example, for long-range (infrasound) or short-range (ultrasound) communication.

CHAPTER 3.1

A frequency scaling rule in mammalian vocalization

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Abstract: The main biological purpose of mammalian vocalization is communication with other members of the same species, and it is generally beneficial to maximize the distance over which this can be done, though in some instances short-range confidential communication is desired. Considering the anatomical and acoustical parameters involved, a scaling rule for maximized communication distance is predicted, with frequency proportional to body-mass to a power of about -0.4 , and this agrees well with observation over a very large size range. The communication distance varies about as body mass to the power 0.6 .

Keywords: frequency of vocalization; frequency scaling; animal size; communication distance; vocalization and body mass; hearing; underwater communication

I. Introduction

Animals produce sounds mainly for communication with other members of the same species for a variety of purposes, such as to define territory, attract a mate, warn of predators, or signal the existence of a food source. For most of these purposes it is an advantage to be heard over as long a distance as possible. In just a few situations, however, it is desirable to have communications that cannot be detected by predators. These two styles of communication are analogous to normal speech or loud shouting in human communication on the one hand, and to whispering on the other. In this section we shall be concerned mostly with the former type of vocalization. Mention should also be made of sounds produced by whistling, as in the traditional whistled languages of some African tribes and in the ultrasonic calls of rats, the frequencies in each case being around five times that of the usual vocalization frequency. These will not be included in the discussion of the present section, but are treated in the following chapters. Land-based

mammals will be the main concern, with a small section towards the end devoted to the very different rules for those that live in the sea.

A detailed treatment of acoustic communication in a wide variety of animals has been given by [Stebbins \(1983\)](#) and by [Bradbury and Vehrenkamp \(1998\)](#), and also in two collections of papers edited by [Busnel \(1963\)](#) and by [Lewis \(1983\)](#). The acoustics underlying the subject has been described in detail by [Fletcher and Thwaites \(1979\)](#) and by [Fletcher \(1992\)](#), while there are many papers on the acoustic behavior of individual animal species. The matter of frequency scaling has been discussed by [Fletcher \(2004\)](#), and it is on this paper that the present section is largely based.

The initial discussion in what follows will be based on the simple assumption of sound propagation in the open air, which gives a surprisingly good prediction of the variation of vocalization frequency with animal mass. To be more realistic, however, it must be recognized that animals live in environments that contain vegetation of many kinds, including grassy surfaces or dense woodlands. The latter part of the section therefore examines the effects these have on the conclusions reached earlier.

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II. Sound production and transmission

While communication through vibrations produced by stamping feet or similar impacts is used by some animals such as elephants, the major communication medium is by vocal sounds produced by pressurized air released through a vibrating valve – the vocal folds – in the larynx. In any vibrating system, the frequency scales inversely with the linear size, provided all dimensions are scaled similarly and density and elastic moduli remain unchanged. If we take L to be a measure of the length or linear size of the animal and assume all parts of its anatomy to scale similarly, then the obvious scaling rule is that the dominant vocalization frequency f is proportional to $1/L$ or equivalently to $M^{-1/3}$ where M is the mass of the animal. This rule was proposed by Bradbury and Vehrenkamp (1998) and, as will be discussed below, requires only minor modification to take proper account of other acoustic matters.

The acoustic power of the radiated sound depends on the lung pressure, the oscillating area of the vocal fold aperture, and the frequency of the vocal fold vibrations. If A_v is the amplitude of oscillation of the vocal fold area and p is the lung pressure, then the oscillating airflow amplitude U is given by:

$$U = \left(\frac{2p}{\rho} \right)^{1/2} A_v, \quad (1)$$

where ρ is the density of air. Since both the mouth opening and the head of the animal are small compared with the dominant wavelength of the animal's call, the radiated power P at the call frequency f can easily be shown to be (Morse, 1984; Fletcher, 1992):

$$P = \frac{\pi \rho f^2 U^2}{2c} \quad (2)$$

where c is the speed of sound in air.

As the sound propagates away from the animal, its intensity decreases because it is spread over a larger area, giving a decrease as r^{-2} where r is the distance from the source. In addition, there is a decrease in intensity because of energy absorption by the air, caused by its viscosity and thermal conductivity. This absorption depends in a complex way upon temperature, pressure, humidity and frequency, but overall it increases with frequency about as αf^n with n close to 1.5 and α about $3.6 \times 10^{-8} \text{ m}^{-1} \text{ Hz}^{-1.5}$ under typical

atmospheric conditions (Bass et al., 1995; Sutherland and Daigle, 1997). This gives a sound attenuation due to atmospheric absorption of about 0.5 dB per 100 m at 1 kHz, with smaller absorption at lower frequencies.

Combining the spreading effect with the absorption, the sound intensity $I(r)$ at a distance r from a source of frequency f and acoustic power P is therefore:

$$I(r) \approx \frac{P}{4\pi r^2} \exp(-\alpha f^n r). \quad (3)$$

This relationship for the assumed values of α and n is valid only under normal conditions in an open environment. Even in such an open environment, however, propagation can be changed by inversion layers of low temperature air near the ground, which tend to capture the sound waves and confine them to the thickness of the layer, thus increasing propagation distance. Wind will generally have little effect, except for the noise it produces, since wind speed is small compared with the speed of sound in air. In an environment such as a forest, of course, the value of the attenuation coefficient α may be increased significantly, as is discussed later.

III. Sound reception

The acoustic signal provided to the cochlea of a listening animal of the same species at a distance r is:

$$S(r) = I(r)A_E \quad (4)$$

where A_E is the cross-sectional area of the outer ear or pinna. The pinna amplifies the pressure signal (Fletcher and Thwaites, 1988) and feeds it through the tympanic membrane and a bony link to the cochlea, where hair cells ultimately translate it into action potentials. The acoustics and physiology of this transduction process are both complex to model, but experimental results (Fay, 1988, 1997) show that most animals have about the same auditory threshold S^* within about ± 10 dB, although the frequency of this optimal response and the upper and lower frequency limits of hearing may differ greatly between species, becoming higher for smaller animals. This accords with a scaling model in which the neural output is proportional to the angular deflection of the auditory hair-cells.

The requirement for audibility of a call from another animal at distance r can be deduced from Equations 1–4 to be that:

$$S(r) \equiv \frac{pf^2 A_V^2 A_E}{4cr^2} \exp(-\alpha f^n r) \geq SZ^*. \quad (5)$$

Fig. 1 shows how this relation operates at various frequencies (f). Remembering that the maximum lung pressure p is fixed and that A_V and A_E are determined by the overall size of the animal, the concern is with the way in which the acoustic stimulus intensity S varies with distance as a function of frequency. At small distances where atmospheric attenuation is not important, the animal can produce a louder signal if the frequency is raised, as detailed in Equation 2. A high frequency signal, however, is more steeply attenuated with propagation distance than a low frequency signal, as detailed in Equation 3. There is therefore a particular frequency f^* at which the signal strength exceeds the threshold value S^* for a maximum distance, and it is to be presumed that this is the call frequency that will have evolved for the animal species concerned.

To determine the optimal frequency for maximum communication distance we simply require that $dr/df = 0$ in Equation 5, which gives:

$$\alpha f^n r = \frac{2}{n}, \quad (6)$$

and when this is substituted back into Equation 5 this gives the optimal frequency as:

$$f^* = \left(\frac{16cT}{\alpha^2 n^2 A_V^2 A_E p} \right)^{1/(2n+2)}. \quad (7)$$

III.A. Relation to animal size

It is now simple to apply the resulting Equation 7 to deduce how the optimal vocalization frequency should vary with animal size. If L is a measure of the linear size of the animal and all anatomical parts scale similarly, then both the vocal valve area A_V and the external ear area A_E will vary as L^2 , so that Equation 7 predicts that:

$$f^* \propto L^{-3/(n+1)} \propto M^{-1/(n+1)}, \quad (8)$$

where M is the mass of the animal. Inserting the value $n = 1.5$ as a good approximation to the frequency dependence of sound attenuation in the atmosphere gives the result that the optimal call frequency f^* should be proportional to the animal length L to the power -1.2 or mass M to the power -0.4 .

It is interesting to see how well this scaling rule agrees with observations of the calls of mammals of different sizes. Fig. 2 assembles data collected from a wide

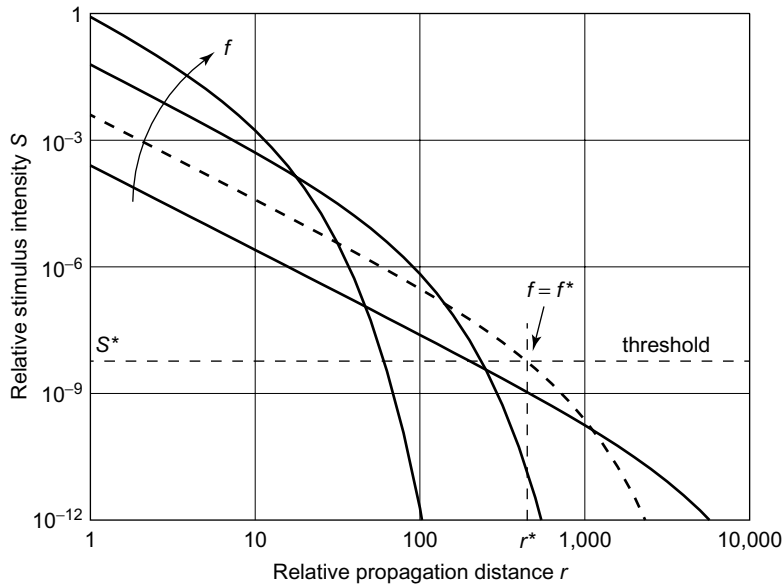


Fig. 1. Radiated sound intensity as a function of distance for a range of sound frequencies f , assuming other parameters to be constant. As shown by the broken curve, reception distance r for a threshold sensitivity S^* is maximized to the value r^* at frequency f^* (Fletcher, 2004).

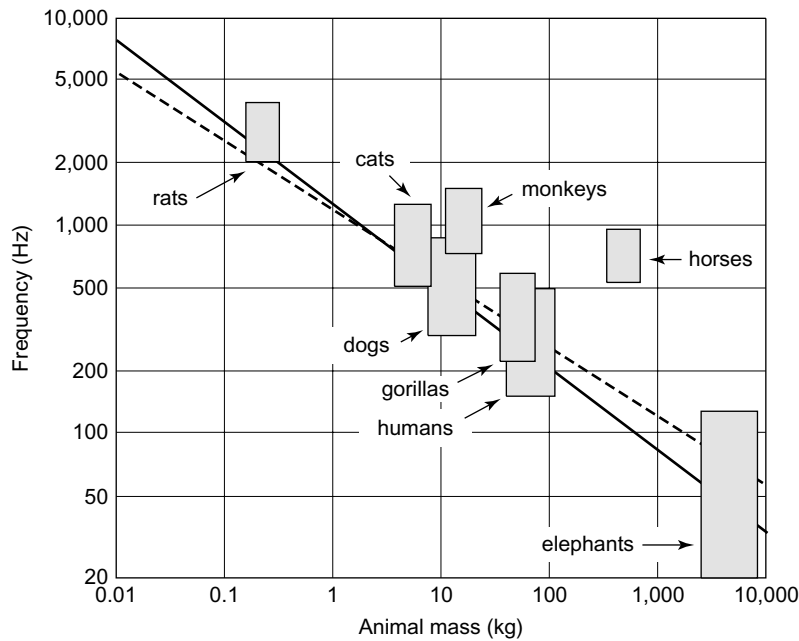


Fig. 2. Typical fundamental vocalization frequencies for a large range of mammals. The ultrasonic calls of rats and bats and the trumpeting of elephants are not included. The full regression line is for the relation $f \propto M^{-0.4}$ and the broken line is for $M^{-0.33}$ (modified from Fletcher, 2004).

range of sources and covers a mass range of six orders of magnitude, or a factor 10^6 . The overall agreement is very good, although there are significant deviations in the case of animals such as horses and monkeys. Rats and mice, and of course bats, also vocalize in the ultrasonic range above 20kHz (see Chapter 3.3), and elephants have “trumpetings” at higher frequencies than shown, but it is likely that these all involve vocal mechanisms different from those of ordinary calls.

It is now also interesting to see how the maximum communication distance r^* varies with animal size. This follows from Equations 6 and 8 which together give the relation:

$$r^* \propto M^{n/(n+1)} \propto M^{0.6}, \quad (9)$$

where the final result comes from inserting the value $n = 1.5$ for the measured behavior of the atmospheric attenuation, as discussed before.

III.B. The effects of habitat

As mentioned in the introduction, the discussion above really only applies to sound transmission in the open

air, such as might be possible from a cliff top or high rock. In reality, however, most communication takes place nearer to the ground and often through an environment such as a forest. Surely this will have a considerable impact on vocal behavior.

First consider the case of an open landscape with a nearly flat floor of sand or grass. As well as the sound wave propagating directly through the air, there will be another one that has been reflected from the ground and a third that is essentially “captured” by the ground impedance. The reflected wave will be weaker than the direct wave because of absorption during the reflection, and it will also be delayed a little in time because its path is longer. At the listening point these two waves may thus either reinforce or partially cancel each other, depending on phase difference and thus on the height of singer and listener above the ground. The contribution of the “ground wave” must also be added in, making a quite complex calculation even for an ideally flat surface (Embleton et al., 1976; Rasmussen, 1981; Embleton, 1996). For flat ground and a typical animal height of about 0.5m there is a reinforcement of up to 6dB at frequencies below about 200Hz, then attenuation increasing to a local maximum of about 15dB at 1000Hz at a distance of about 20m. At higher

frequencies or larger distances the attenuation increases and the maxima are less pronounced.

If the ground surface is not ideally flat, as will generally be the case in nature, then things become even more complicated and it is impossible to give any reliable figures for the attenuation to be expected. Broadly viewed, however, the attenuation is greater at frequencies above about 500 Hz than at lower frequencies, and is greater though less oscillatory for a source close to the ground – a small animal – than for an elevated source or large animal. For a typical grassland surface, the attenuation is much greater than that for atmospheric absorption.

The other environment of interest is woodland, which may be either evergreen or deciduous. Here, in addition to absorption, there are scattering phenomena to be considered and perhaps even resonances with leaves or branches. Measurements (Embleton, 1963) for propagation distances over about 50 m show a nearly constant absorption for the forests studied of about 0.2 dB m^{-1} between about 200 Hz and 2 kHz and a steady increase for higher frequencies. This is again much greater than the free atmospheric absorption in this frequency range, but shows a similar general increase with increasing frequency.

An interesting example of the effect of habitat on vocalization occurs in the case of wild cats of the genus *Felis*. A study of several species of this genus by Peters et al. (2009) shows a surprising direct rather than inverse correlation between body mass and dominant frequency in the range 1.3–10 kg and 700–1000 Hz. While these ranges are both small, the explanation appears to lie in the fact that the smaller cats inhabit an open environment where absorption near 1 kHz is high, while the larger cats live in woodland and can benefit by using as high a formant frequency as possible, given their vocal anatomy.

Since the animals which we are interested in here are land-dwelling mammals, which live either in forests or else relatively close to the ground in grasslands, the high attenuation in both these environments calls into question some of the analysis above relating to propagation attenuation. Fortunately, this does not have any great influence on the final conclusions if we simply assume that, over a large range of animal sizes, anatomical scaling results in a vocalization frequency that is proportional to animal length or to its mass to the power $-1/3$ as suggested by Bradbury and Vehrenkamp (1998). The broken line in Fig. 2 shows the expected correlation on this assumption.

IV. Noise, bandwidth and close communication

Vocal communication between animals does not, of course, take place in an ideally quiet environment, instead there is competing noise produced by wind and by other animals. As a general rule, such noise tends towards a $1/f$ frequency distribution, which is equivalent to saying that it has the same average intensity per octave across the spectrum, so that the sound energy per hertz is much greater at low frequencies than at high. Animal vocal calls, however, and the related hearing sensitivity of animals, generally have a bandwidth that is about proportional to the central frequency involved, which means that the noise intensity obscuring the signal in the perception band is about constant, independent of the call frequency. What this implies, therefore, is that the analysis given above is still valid, except that the threshold sensitivity S^* should be interpreted to mean the detectable signal, which is again approximately constant because the detection bandwidth shrinks as the frequency is lowered and the noise level per hertz increases.

There is another interesting feature of the frequency-scaling rule for both call frequency and bandwidth, and this is that the rate of information transfer by the vocal signal decreases about as $M^{-0.4}$ in the same way as does the call frequency. While this might appear to be a disadvantage for large animals, it accords with the fact that the rate of relative motion of animals is about inversely proportional to their linear size – a mouse, for example, can jump around and run ten times its body length much more rapidly than an elephant can.

The analysis above is based on the assumed use of vocalization for conspecific communication over the largest possible distance, the signals being territorial, warning, or collaborative. In some cases, however, vocalization serves a different purpose and the aim is to communicate over relatively short distances and to avoid attracting predators. An example is the cry of baby animals to their mothers. These short-distance vocalizations use frequencies much higher than those for adult long-range communication, and the advantage of this is clear from Fig. 1. High-frequency signals are produced more efficiently, but are much more rapidly attenuated at large distances, achieving just the desired result.

V. Underwater communication

Some mammalian species such as whales and dolphins live under water but still use sound as a means of

communication, so it is interesting to see what modifications are necessary to the discussion above. The two main differences are that the surrounding medium is water, with a density 1,000 times that of air and an acoustic absorption coefficient α that is 100 times smaller than in air. Also, while the water medium is three-dimensional at close range, it becomes effectively two-dimensional once the range considered is large compared with the water depth.

Aquatic mammals also produce sound by passing air through a vibrating valve, as in the larynx, and this air may either be vented through the nose or else stored temporarily in an air sac. Sound radiation mostly takes place through transmission of acoustic vibrations through the body tissues into the surrounding water, since these tissues have nearly the same acoustic properties as water. Analysis of the acoustic behavior follows much the same path as for animals in the air, except that r^{-2} must be replaced by r^{-1} . The result is a figure that is qualitatively like Fig. 1 except that the general slope of the curves is reduced by a factor of 2, and the values of r are increased by about a factor of 100. The conclusion is that aquatic animals should use much higher frequencies for communication than those living in air, and this is borne out by observation, quite large whales having communication frequencies in the 1–2 kHz range. The communication range of such large aquatic mammals is extremely long because of the low attenuation and $1/r$ spreading of the signal.

VI. Conclusion

This section has provided a wide-ranging theoretical background against which the acoustic communication behavior of mammals can be judged. Given this background, interest centers on deviations from the predicted norm for particular species, the reason for these deviations, and the effects that this has on their individual and social behavior.

References

- Bass, H.E., Sutherland, L.C., Zuckerwar, A.J., Blackstock, D.T., Hester, D.M., 1995. Atmospheric absorption of sound: recent developments. *J. Acoust. Soc. Am.* 97, 680–683.
- Bradbury, J.W., Vehrenkamp, S.L., 1998. *Principles of Animal Communication*. Sinauer, Sunderland, MA.
- Busnel, R.G. (Ed.), 1963. *Acoustic Behavior of Animals*. Elsevier, New York.
- Embleton, T.F.W., 1963. Sound propagation in homogeneous deciduous and evergreen woods. *J. Acoust. Soc. Am.* 35, 1119–1125.
- Embleton, T.F.W., 1996. Tutorial on sound propagation outdoors. *J. Acoust. Soc. Am.* 100, 31–48.
- Embleton, T.F.W., Piercy, J.E., Olson, N., 1976. Outdoor sound propagation over ground of finite impedance. *J. Acoust. Soc. Am.* 59, 267–277.
- Fay, R.R., 1988. *Hearing in Vertebrates: A Psychophysics Data-book*. Hill-Fay Associates, Winnetka, IL.
- Fay, R.R., 1997. Hearing and sound perception among vertebrate animals. In: Crocker, M.J. (Ed.), *Encyclopedia of Acoustics*. John Wiley and Sons, New York, pp. 1789–1797.
- Fletcher, N.H., 1992. *Acoustic Systems in Biology*. Oxford University Press, New York.
- Fletcher, N.H., 2004. A simple frequency-scaling rule for animal communication. *J. Acoust. Soc. Am.* 115, 2334–2338.
- Fletcher, N.H., Thwaites, S., 1979. Physical models for the analysis of acoustic systems in biology. *Quart. Rev. Biophys.* 12, 26–66.
- Fletcher, N.H., Thwaites, S., 1988. Obliquely truncated simple horns: idealized models for vertebrate pinnae. *Acustica* 65, 194–204.
- Lewis, B. (Ed.), 1983. *Bioacoustics: A Comparative Approach*. Academic Press, London, UK.
- Morse, P.M., 1984. *Vibration and Sound*. Acoustical Society of America, New York, NY, chap. 7.
- Peters, G., Baum, L., Peters, M.K., Tonkin-Leyhausen, B., 2009. Spectral characteristics of intense mew calls in cat species of the genus *Felis* (Mammalia: Carnivora: Felidae). *J. Ethol.* (in press).
- Rasmussen, K.B., 1981. Sound propagation over grass covered ground. *J. Sound Vibr.* 78, 247–255.
- Stebbins, W.C., 1983. *The Acoustic Sense of Animals*. Harvard University Press, Cambridge, MA.
- Sutherland, L.C., Daigle, G.A., 1997. Atmospheric sound propagation. In: Crocker, M.J. (Ed.), *Encyclopedia of Acoustics*. Wiley, New York, pp. 341–365.