

A simple frequency-scaling rule for animal communication

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Different animals use widely different frequencies for sound communication, and it is reasonable to assume that evolution has adapted these frequencies to give greatest conspecific communication distance for a given vocal effort. Acoustic analysis shows that the optimal communication frequency is inversely proportional to about the 0.4 power of the animal's body mass. Comparison with observational data indicates that this prediction is well supported in practice. For animals of a given class, for example mammals, the maximum communication distance varies about as the 0.6 power of the animal's mass. There is, however, a wide spread of observed results because of the different emphasis placed upon vocal effort in the evolution of different animal species. © 2004 Acoustical Society of America. [DOI: 10.1121/1.1694997]

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I. INTRODUCTION

Different animals employ widely different frequencies for their sound communication—communication that has the purpose of defining territory, seeking a mate, warning of danger, or simply social interaction. It is reasonable to suppose that evolution has led to the use of a frequency that gives greatest conspecific communication distance in at least the former cases, but what is the rule that governs this choice of frequency?

A detailed description of acoustic communication in a wide variety of animals has been given in two excellent books by Stebbins¹ and by Bradbury and Vehrenkamp,² and also in two classic collections of papers edited by Busnel³ and by Lewis,⁴ respectively. These books contain a wealth of information on many different animal species and give copious references to the original literature. Bradbury and Vehrenkamp also provide a clear, qualitative discussion of the physical processes underlying sound production, propagation, and hearing. A book by the present author,⁵ in contrast, concentrates on the physical principles involved, and attempts to provide a quantitative mathematical basis upon which an understanding of individual cases can be built. A condensed account has been published elsewhere.⁶

Noting that small animals generally use higher frequencies in their calls than larger animals, one might conjecture a rule stating that call frequency is inversely proportional to the linear size L of the animal ($f \propto 1/L$ or $f \propto M^{-1/3}$, where M is the mass of the animal). Such a rule was proposed by Bradbury and Vehrenkamp² and justified by the observation that the radiation efficiency of an opening such as the mouth increases with increasing frequency until it reaches saturation when the wavelength of the sound is comparable with the diameter of the mouth (actually about equal to $\pi/2$ times the diameter⁵). While on the whole this suggests rather higher frequencies than are actually used, the fit to the observational data is quite good, as will be shown later. It is the purpose of the present note to derive a refinement of this rule

on the basis of the physical principles underlying sound production, propagation, and hearing. The anatomic variety, lifestyle, and habitat of animals are, of course, immensely diverse so that a wide variation is to be expected, but perhaps the analysis will add to our understanding.

Most vertebrate land-dwelling animals produce sound by expelling air through a vibrating valve in the larynx, or syrinx in the case of birds. This valve leads to the upper respiratory tract, where air-column resonances, or “formants,” modify the spectral envelope of the richly harmonic sound generated by the oscillating valve, and sound is finally radiated through a mouth or beak, the diameter of which generally scales approximately as the linear size of the animal. Vocal information is generally encoded in the lowest two or three formant bands—regions of emphasis in the overtone spectrum—extending up to about 10 times the fundamental frequency. There is an exception to this statement in the case of many passerine birds and some frogs, which produce calls consisting essentially only of a fundamental with all its harmonics suppressed.

Insects, on the other hand, must produce sound by purely mechanical means, since they have no respiratory air supply under pressure. This is generally done by setting some thin membrane into vibration, for example by drawing a finely toothed leg or file across a wing panel, as in crickets, or by using a muscle to cause the progressive collapse of a stiff ribbed membrane covering a resonant body cavity, as in the case of cicadas. The result is generally a band of frequencies with little or no fine structure and a relative width of about 10 to 30 percent. The frequency scaling rule might be expected to be broadly similar for these cases, though perhaps displaced in reference frequency compared with vertebrates.

This discussion will not attempt to deal in detail with two other general cases. The first is scaling of the frequencies used by animals for echo location, for the optimization criteria are then very different from those for conspecific communication. The second is the case of aquatic animals, because the close match between the wave impedance of

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water and of body tissue introduces a new feature, and because propagation and attenuation in an ocean or lake environment, being nearly two-dimensional over long distances, has several features that are very different from an air environment.

II. SCALING ANALYSIS FOR VERTEBRATES

The lung pressure p driving the vocal air flow depends upon the pressure in the animal's lungs, which is in turn proportional to the thickness of the abdominal muscle walls and inversely proportional to the linear dimensions of the lung sac. These two variations cancel in animals of similar anatomy, so it can be concluded that vocalization pressure is approximately independent of animal size. The oscillating volume flow of air through the vocal valve is therefore

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

where A_v is the wide-open area of the valve and ρ is the density of air. If the oscillation frequency of the vocal valve is f , then since, in the cases we consider, the diameter of the valve and of the animal's mouth are both much less than the sound wavelength, the radiated sound power P can be shown^{5,7} to be

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

where c is the speed of sound in air. As the sound propagates, its intensity decreases, first because it is spread over a larger area, giving an inverse-square-law dependence, and second because of molecular atmospheric absorption.

Atmospheric absorption γ depends in a rather complex way upon frequency, temperature, pressure, and humidity, but overall it increases with frequency about as $\gamma = \alpha f^n$, with n close to 1.5 and α a constant with numerical value about $3.6 \times 10^{-8} \text{ m}^{-1} \text{ Hz}^{-1.5}$, in an atmosphere of normal humidity.^{8,9} This gives a sound attenuation γ due to atmospheric absorption of about 0.5 dB/100m at 1 kHz, and correspondingly less at lower frequencies. The sound intensity $I(r)$ at a distance r from the source is therefore

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

In more realistic evolutionary environments, such as forests of grasslands, a rather similar behavior can be expected, but with a higher value of the proportionality constant α .

The acoustic stimulus $S(r)$ provided to the auditory nerves of a listening animal of the same species at distance r is

$$S(r) = I(r) A_e, \quad (4)$$

where A_e is the area of the external ear. Ignoring for the present the problem of interfering noise background, the sound will be audible at the distance r provided $S(r)$ exceeds some threshold value T that should not vary significantly from one species to another, if it is assumed that their neural transduction mechanisms are equally efficient. (This is, of course, an assumption, but there is no compelling evidence

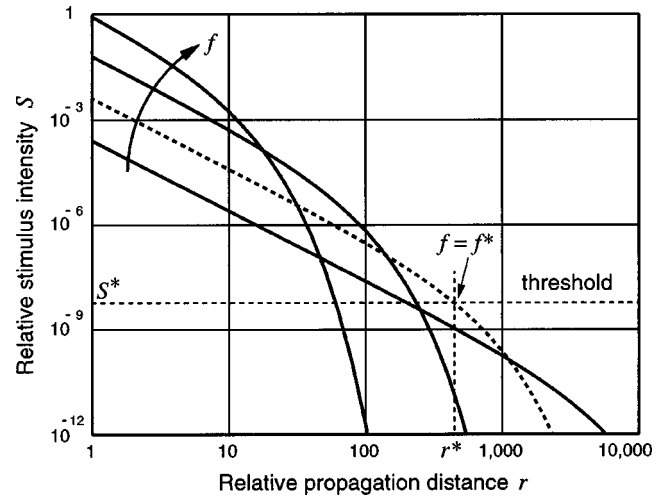


FIG. 1. Radiated sound intensity as a function of distance for a range of sound frequencies, assuming other parameters remain constant. The frequency increases in equal steps in the direction indicated. If the threshold level is as shown, then there is an optimal frequency f^* giving maximum range r^* , as shown by the broken curve.

to suggest any systematic variation of efficiency with size. It is, of course, possible that some species have hearing abilities differing markedly from what is expected, and this may explain in part the scatter of observational data.) In summary then, the audibility requirement is that

$$S(r) \equiv \frac{p f^2 A_v^2 A_e}{4c r^2} \exp(-\alpha f^n r) \geq T. \quad (5)$$

The problem is now to vary the frequency f so as to maximize the distance r at which the animal call remains audible to members of the same species. The behavior of $S(r)$ as a function of r for various values of f is shown in Fig. 1. For high frequencies the sound level close to the animal is high, but it falls off rapidly with distance because of molecular absorption in the air, while at low frequencies the near-field sound level is lower, but it falls off less rapidly with distance. At the optimal frequency f^* , the range r^* at which the sound level equals the hearing threshold T is a maximum, so that the derivative $dr/df = 0$, and this relation can be used in Eq. (5) to deduce that, at this optimum, $\alpha f^n r = 2/n$. Substituting this back in (5) gives

$$f^* = \left(\frac{16cT}{\alpha^2 n^2 A_v^2 A_e p} \right)^{1/(2n+2)}. \quad (6)$$

Assuming that both mouth and ear diameters are proportional to the average linear body dimension L gives the result that f^* is proportional to $L^{-3/(n+1)}$. Since the animal's mass M is proportional to L^3 , this is equivalent to stating that the optimal communication frequency f^* is proportional to $M^{-1/(n+1)}$. Inserting the approximate value $n = 1.5$ gives the result that f^* should be proportional to $M^{-0.4}$.

A. Experimental data

It is difficult to obtain good data from which to plot the way in which fundamental vocalization frequency depends upon body mass for a wide range of animals. This is partly

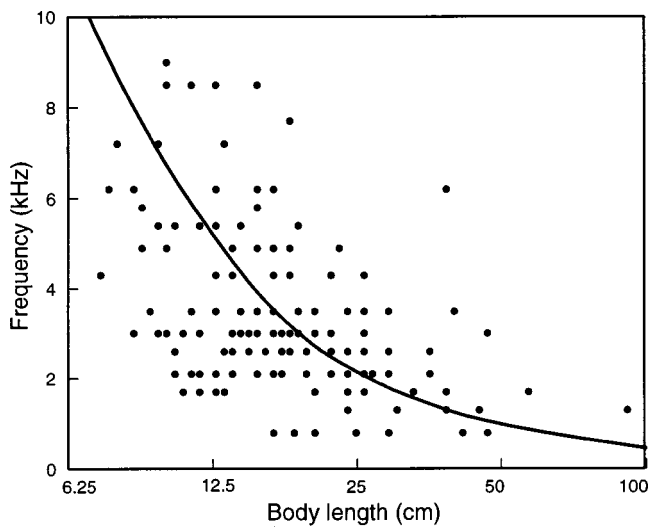


FIG. 2. Replot of the data of Ryan and Brenowitz (Ref. 10) on birdsong dominant frequency, with a superimposed curve of the form $f=AL^{-1.2}$ or $f=BM^{-0.4}$, as predicted by the theory given here.

due to the variability of the behavior of individual animals, and partly to variation between measurement techniques and decisions about exactly what is to be recorded. For the most part researchers have recorded the “dominant frequency,” which is probably a good basis for comparison.

Ryan and Brenowitz¹⁰ report a very wide set of measurements on three different classes of birds—nonpasserines, suboscines, and oscines—in three different types of habitats. The data points for dominant frequency—the maximum in the spectrum—are rather widely scattered and were in each case fitted with an arbitrary regression of the form $f=A-B\log L$, where L is body length and A and B are positive constants. (This regression actually predicts a negative song frequency for birds larger than those plotted!) Figure 2 shows the complete data set. The regression line has been omitted since it is not meaningful. The complete data for birds are, however, fitted very well by a curve of the predicted form $f=BM^{-0.4}$, or equivalently $f=AL^{-1.2}$, as shown in Fig. 2, A being the only variable parameter. A regression curve of the form $f=CM^{-0.33}$, as conjectured from simple linear scaling would, however, fit the data just as well.

There is great difficulty in finding comparably extensive data for other groups of vertebrates, partly because of the wide variation in the sort of calls produced by higher animals. The published measurements, understandably, do not give the approximate body mass, so that it has been necessary to estimate this, and are mixed between fundamental frequency and dominant frequency. Figure 3 shows the approximate range of the dominant frequency of a wide set of animal vocalizations, plotted against their approximate body mass, using whatever data have been found. Data sets used, in part, to construct this figure have been published in individual chapters of the volume edited by Busnel³ by Zhinkin, Dumortier, Bremond, and Tembrock, but other sources have also been used. Drawn in the figure is a line of the predicted slope -0.4 passing through the calculated optimal frequency for humans, and it is clear that this gives a reasonably good

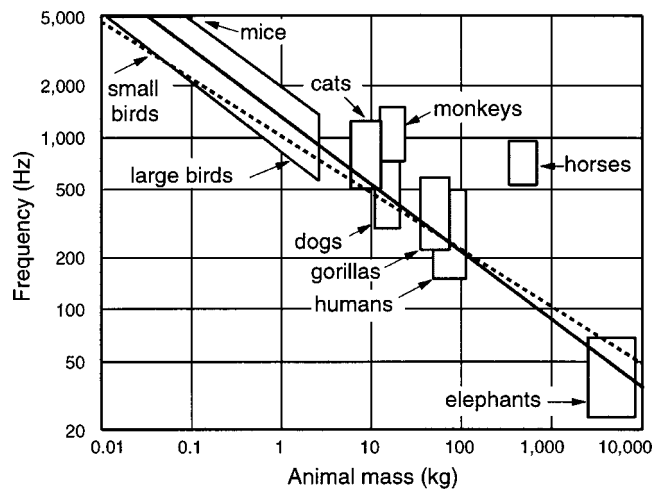


FIG. 3. Correlation between body mass and vocalization frequency for the animals shown. The full line shows the $M^{-0.4}$ power relationship predicted in the text and the dashed line the $M^{-0.33}$ relationship derived from simple linear size scaling.

general account of the evolutionary optimization behavior over a range of about 10^6 in body mass. A considerable range of deviation from the theoretical line is to be expected, largely because of variation in the social patterns for which communication is used. Also shown in the figure is a broken line representing the simple linear scaling $f=M^{-0.33}$. This is seen to fit just as well.

B. Communication distances

Within a general class of species such as land mammals, or birds, the available lung pressure should be approximately independent of size, as discussed before. This then allows us to calculate the relative conspecific communication range r^* by setting $f=f^*=(2/nar)^{1/n}$, as was deduced from the differentiation of Eq. (5). The result is that r^* should be about proportional to $M^{0.6}$. No experimental data are immediately available to check this conclusion, but it does seem established that large mammals, such as elephants, can generally communicate over very much larger distances than small mammals, such as cats or mice, and large birds such as cockatoos over greater distances than small birds such as finches.

C. Actual frequencies

Although the scaling analysis outlined above is informative, the actual predicted scaling law for frequency is very close to the rule $f\propto M^{-1/3}$ that would be expected for a simple inverse scaling of frequency with body length. It is therefore important to go to the next stage and predict actual optimal communication frequencies. As a first step this can be done for the free-atmosphere case, though the effect of forest or grassland absorption should then be included. It must also be noted that, in most cases, vocal information is carried not just at the fundamental frequency but rather in the vocal formants, which have a frequency centroid at about 10 times the fundamental frequency in most animals. This sort of scaling is to be expected since the formants are produced

by longitudinal resonances of the vocal tract, the frequency of which varies inversely with this length and this with animal size.

Equation (6) requires some anatomical assumptions to lead to a predicted vocalization frequency, and an appropriate example is for a human when shouting loudly. In this case, it is a reasonable approximation to take $A_v \approx 10^{-5} \text{ m}^2$, $A_e \approx 10^{-3} \text{ m}^2$, and $p \approx 1000 \text{ Pa}$. The normal auditory threshold in the middle of the vocalization band around 1000 Hz is about $10^{-12} \text{ W m}^{-2}$, so that $T \approx 10^{-15} \text{ W}$. Equation (6) then predicts an optimal vocalization frequency of about 450 Hz, which is about three times the fundamental frequency of human male vocalization, and about equal to that of female vocalization, and so approximately in the range of maximum vocal output. This is also close to the frequency of the first vocal-tract resonance. Given that the variation of vocalization fundamental frequency with body mass is quite well predicted, as indicated in Figs. 2 and 3, this means that there is probably comparable agreement in absolute predicted vocalization frequencies across the whole range of species and body masses encompassed in that plot.

As noted before, however, this optimal frequency varies with the air absorption αf^n as shown in (6). Assuming that $n = 1.5$ in forest or grassland environments, and that the only change is an increase in the value of α , the prediction is that $f^* \propto \alpha^{-1/(n+1)} = \alpha^{-0.4}$, so that these environments would lead to a lowering of the optimal vocalization frequency. An increase in α by a factor 10 would lower the optimal frequency by a factor close to 0.4, giving 180 Hz for human vocalization. This is not such a good fit as the original free-air prediction. Such measurements as are available,⁹ however, suggest that the variation of absorption with frequency is very much more complex in these environments than a simple power-law relation, so that this modification of the free-air prediction is perhaps not justified.

D. Background noise

There is, of course, another possible assumption that could be made about the optimization process, and that is that the criterion should be to maximize the signal-to-noise ratio at the receiving position, rather than just the signal level. In the modern world, a large proportion of background noise in places of human habitation is due to human activities such as transport, but this is too recent to have had any evolutionary impact. Background noise due to other causes, predominantly air turbulence, ocean waves, and biological sounds, has a frequency distribution that varies greatly with local environment, but on a larger scale has about constant noise power in each octave band across the spectrum. Since the auditory systems of vertebrate animals have roughly a constant fractional bandwidth f_{\max}/f_{\min} of about 4 octaves (a factor 16) at the 10-dB point, this means that they tend to receive a constant noise input, regardless of their center frequency.

Assuming that the external ear is large enough that noise is, in fact, the limiting factor, the optimization of communication frequency therefore amounts to maximizing $I(r)$ rather than $I(r)A_e$ for each size of animal. Going through the optimization procedure as before leads to the scaling law

$f^* \propto M^{-2/(3n+3)}$, or $f^* \propto M^{-0.27}$. While not completely ruled out by the available data, this power law appears to fit rather less well. It is possible, however, that the animal neural system can disregard noise lying outside the immediate vicinity of the signal frequency, a situation known as selective masking, in which case a rather different conclusion can be reached,⁵ with the optimal frequency depending upon the available signal power.

Of course, many animals live in groups in noisy environments such as rainforest, and the optimization problem for them may be rather different. It hardly seems possible to decide much on this point except by looking at the optimization while taking into account the particulars of the animal and its situation, and assuming these have not varied greatly over the evolutionary time involved. This doubtless accounts for some of the variation observed between different species.

III. INSECTS

A similar analysis could be carried out for insects that produce sound by stridulation—the setting of wing panels into vibration through the action of a file on their leg. In this case, because the panel has two free sides, the source is an acoustic dipole, rather than a monopole, and this inserts an extra factor f/r into $I(r)$, but, in addition, the source amplitude now varies as d^3 , rather d^2 , where d is the diameter of the vibrating panel, because the effective distance between the two poles of the dipole is also proportional to d . Following through the argument as before, we conclude that the optimal frequency varies as $M^{-0.36}$ and the conspecific communication range as $M^{0.53}$ within a class of sound-producing insects with broadly similar anatomy. These scaling laws are broadly similar to those applying to mammals, but the constant of proportionality will, however, be different. Because insects are so much smaller than vertebrates, their communication frequencies are generally much higher, typically 3 to 5 kHz, in accord with the general trend of these scaling laws.

While most mammals devote a small and nearly constant fraction of their available energy to sound production, the situation is often very different in insects. Some Australian cicadas, for example, produce a sound power of around 1 mW at about 3 kHz, which is about equal to that produced in human singing. In another variety of Australian cicada of about the same length, *Cystosoma Saundersii* (Westwood), the male anatomy is so specialized for sound production¹¹ that the abdomen, which makes up nearly 90 percent of the volume of the animal, is a simple hollow sac that reinforces the vibration of the tymbals at the low-song frequency of 800 Hz. Some ground-dwelling crickets even dig burrows in the shape of exponential horns, so that an animal of mass less than 1 gram has an effective acoustic mouth diameter of several centimeters for sound radiation.¹²

IV. AQUATIC ANIMALS

In the case of aquatic mammals, similar evolutionary pressures should also have applied. Sea water has a similar variation of sound absorption with frequency to that of air,¹³ but the sound absorption in sea water is much less than that in air, leading to vastly increased communication distances.

Over such distances, which are much greater than the ocean depth, sound propagation is essentially two-dimensional, which adds further to the propagation distance. In addition to this, aquatic mammals do not simply discharge an oscillating airflow into the surrounding water, but rather generally discharge it from one body cavity to another. The linear dimensions of these cavities, however, are generally proportional to animal length, so the scaling is preserved. Carrying through the optimization in the same way leads to the conclusion that $f^* \propto M^{-3/(n+2)}$ or approximately $f^* \propto M^{-0.6}$, and thus a much greater predicted variation with size than for land mammals. Optimization has, however, taken a different direction with those mammals that use sound primarily for sonar detection rather than for conspecific communication.

In the case of sound-producing crustaceans, the scaling law should be very much like that for insects, perhaps modified for two-dimensional propagation since these animals often live in shallow water. This gives $f^* \propto M^{-0.44}$ for shallow water and $f^* \propto M^{-0.6}$ for deep water. Since, however, the clicking sounds produced by these animals seem to be by-products of their activity rather than optimized for long-distance communication, their frequencies may indeed be simply related to body size as $M^{-0.33}$. Variation of body shape between species makes it unlikely that any general rule applies.

V. CONCLUSION

While it is possible that vocal communication frequencies in animals are not optimized at all, but are simply the result of overall blind size scaling of the vocal apparatus which would give a power law $f^* \propto M^{-0.33}$, it seems more likely that the sort of evolutionary optimization discussed here has actually occurred, giving an approximate power law $f^* \propto M^{-0.4}$. Because these two predicted rules do not vary greatly in exponent, it is probably not possible to make a decision on this point, but it is interesting that the sort of optimization that would be predicted, based upon simple physical arguments, is so close to that found in nature.

Despite all the variations in purpose and method of conspecific communication, it is, we believe, instructive to examine general trends in the way that has been done here. Similar analyses could be made of the generation and detection of vibrations by insects that use this technique for communication and prey detection, and of the sound emissions by animals such as bats and dolphins, the purpose of which is echolocation rather than conspecific communication.

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