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REVIEW

THE INFLUENCE OF SURFACE ATMOSPHERIC CONDITIONS ON THE RANGE AND AREA REACHED BY ANIMAL VOCALIZATIONS

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Summary

Low-level vertical changes in temperature and wind exert powerful and predictable influences on the area ensonified by animal vocalizations. Computer modelling of low-frequency sound propagation in measured atmospheric conditions predicts that the calls of the savanna elephant at these frequencies can have ranges exceeding 10 km and that the calls will be highly directional in the presence of wind shear. Calling area is maximized under temperature inversions with low wind speeds. Calling area changes substantially over 24 h periods; on any given day, the calling area undergoes an expansion and contraction which may be as large as one order of magnitude. This cycle is modulated by topography, regional weather patterns, seasonality and possibly by climate variation. Similar influences affect the somewhat higher-frequency calls of lions and may be a selective pressure towards their crepuscular and nocturnal calling behaviour. Coyotes and wolves, which also live in areas with strong and prevalent nocturnal temperature inversions, show similar calling patterns, maximizing their chances of being heard over the longest possible distances. The pronounced dawn and evening vocalization peaks in other animals including birds, frogs and insects may reflect the same influences in combination with other factors which selectively limit high-frequency sound propagation. Atmospheric conditions therefore need to be taken into account in many field studies of animal behaviour. A simplified method for estimating sound propagation during field studies is presented.

Key words: active space, animal communication, bioacoustics, calling area, calling range, infrasound, elephants.

Introduction

Many animal species use long-range calls to establish their use of space and their relationships with members of their own and other species. Several attempts have been made to quantify the factors which affect the calling range of animals, primarily primates and birds (Marten and Marler, 1977; Waser and Waser, 1977; Wiley and Richards, 1978; Richards and Wiley, 1980; Brenowitz, 1982; Brown, 1989). Ground reflection, topography, vegetative attenuation, reverberance, masking, wind noise, turbulent scattering, relaxation attenuation by O_2, N_2 and H_2O, and refraction due to vertical wind and temperature gradients interact with source and receiver height, call strength, hearing threshold and frequency signature to define calling range.

For the most part, these studies concern creatures in forest habitats. In forest habitats, and at the call frequencies used by most forest primates and birds, all the acoustic effects described above must be considered. It is difficult to determine the effects of each influence separately. Efforts to characterize physical controls on long-distance calls are hampered by the sheer complexity of the problem. The present paper avoids this difficulty by focusing primarily on animals that make very low-frequency vocalizations in the simpler acoustic environment of a flat savanna.

Most of the energy in the calls of the African savanna elephant (*Loxodonta africana africana* Blumenbach; Allen, 1939) is concentrated at 14–35 Hz (Payne *et al.* 1986; Poole *et al.* 1988; W. R. Langbauer, R. Charif, R. Martin, K. Payne and L. Wilson, in preparation). These frequencies are near or below the lower threshold of human hearing. Low-frequency sound is less attenuated than higher-frequency sound (Pierce, 1981)

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and is therefore superior for long-distance calling. Long-range calls enable male elephants to find females for reproduction and may be a factor in the coordination of movements of widely spaced foraging herds (Poole *et al.* 1988; W. R. Langbauer, R. Charif, R. Martin, K. Payne and L. Wilson, in preparation). Playback experiments in Etosha National Park, Namibia, show that free-ranging African elephants perceive the low-frequency calls of conspecifics over distances of at least 4 km (Langbauer *et al.* 1991). Garstang *et al.* (1995) suggest that, under optimum conditions, this range can expand to distances greater than 10 km.

The African savanna elephant is arguably the easiest choice for the prediction of active space and calling area as a function of physical effects. On a savanna, at low sound frequencies, the problem of determining physical effects is greatly simplified by comparison with a tropical forest at higher sound frequencies. During low-to-moderate wind conditions, when reception in the 14–35 Hz bandwidth is good, the only factors influencing sound propagation for a source and receiver in the first 10 m above flat, hard ground are call strength, hearing threshold, frequency signature and atmospheric wind and temperature to 300 m elevation or less (Garstang *et al.* 1995; Larom *et al.* 1996).

Larom *et al.* (1996) make use of the comparative simplicity of this problem to predict low-frequency propagation over the southern African savannas. As part of the Southern African Fire–Atmospheric Research Initiative (SAFARI) (Andreae *et al.* 1994), profiles of temperature and wind velocity with a height resolution of 1 m were taken by tethered balloon during a 45 day study at Okaukuejo, Namibia, in the Etosha National Park. Sixty-five profiles taken on 12 days at intervals throughout the 24 h period were used as input data for the Fast Field Program (FFP). FFP is an advanced numerical model of atmospheric sound propagation that has greater validity than simpler and more common ray-tracing methods at low frequencies (Garstang *et al.* 1995). Optimal conditions for propagation of low-frequency sound were predicted to occur 1–2 h after sunset, when low wind speeds and a strong ground-level temperature inversion are the norm. As the night progresses, wind shear increases owing to the formation of a low-level nocturnal wind maximum (jet); calling range consequently decreases and becomes more directional. Larom *et al.* (1996) predict that nocturnal calling ranges and calling areas remain greater than daytime ranges and areas.

The present paper employs the results of Larom *et al.* (1996) to show how, at any time, the calling range and area for African elephants is dependent on (a) the low-level temperature profile (thermal effects) and (b) the low-level wind profile (kinematic effects). Simplified calling area prediction methods, suitable for field use, are determined from these effects. The discussion is expanded to include the lion, another savanna species using low-frequency, long-range calls, and the North American coyote and wolf, which also communicate over long distances in areas subject to predictable nocturnal temperature inversions.

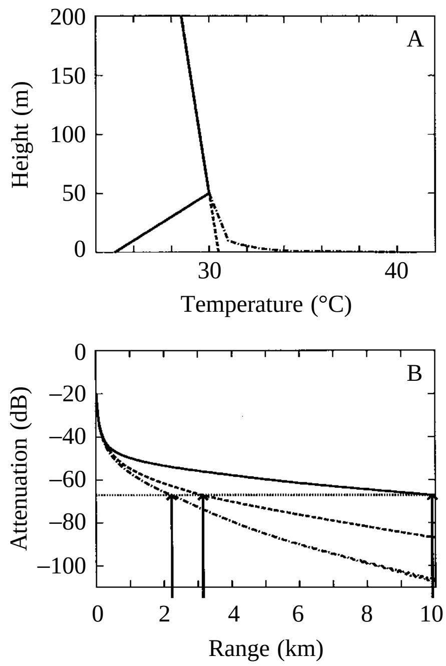


Fig. 1. Idealized temperature profiles (A) and the 15 Hz attenuation profiles predicted from them (B). The temperature profiles show: midday super-adiabatic (occurring without loss or gain of heat) lapse (dash–dot line); late afternoon, adiabatic lapse (dashed line) and evening inversion (solid line). The hypothesized elephant low-frequency calling range based upon a −67 dB difference between call strength and hearing threshold (horizontal line in B; see text) is indicated for each profile by a vertical arrow.

Atmospheric thermal effects on calling area size

This section considers the effects of atmospheric temperature gradients on sound propagation. The effects of wind speed gradients are discussed in the following section. The strength of the loudest low-frequency calls emitted by unstressed elephants as documented by Poole *et al.* (1988) is approximately 117 dB sound pressure level (SPL) (this and all subsequent references to dB are re 20 μPa rms at 1 m; rms=root mean square). The elephant hearing threshold in the low-frequency range is hypothesized to be 50 dB (Larom *et al.* 1996). The difference between the loudest call and the hearing threshold is thus 67 dB. We define an elephant's calling range as the distance its loudest calls will travel before being diminished by 67 dB.

Fig. 1 shows the calling range for a 15 Hz tone at 117 dB SPL with a 50 dB hearing threshold under three standard vertical temperature profiles occurring at Etosha, neglecting the effects of wind. The calling range changes from 2.2 to 9.9 km between daytime and nocturnal conditions; it can expand threefold in as little as 2 h between late afternoon and early evening. This expansion is due to the 'sound duct' formed by a temperature inversion. Temperature inversions form when the ground cools rapidly in the evening as the sun sinks. The inversion is a layer of air in which temperature increases with increasing height above the ground, as opposed to the more common condition for the lower atmosphere in which temperature decreases with

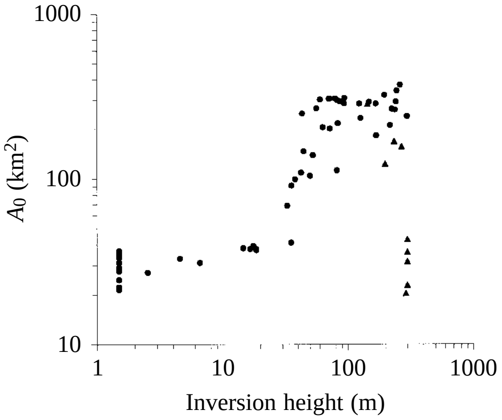


Fig. 2. Zero-wind, –67 dB calling area (A_0) as a function of inversion height, for 65 tethersonde runs. Surface inversions and non-inversion profiles are shown by circles, elevated inversions by triangles.

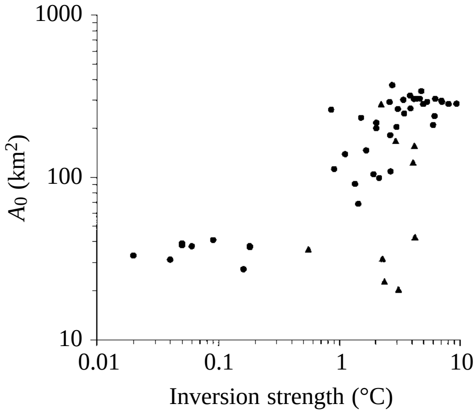


Fig. 4. Zero-wind, –67 dB calling area (A_0) as a function of inversion strength, for 65 tethersonde runs. Symbols are as for Fig. 2.

height. Near-surface temperature inversions typically disappear soon after sunrise as the ground heats up. Under inversion conditions, acoustic energy is refracted downwards and near-ground sound levels consequently increase.

Fig. 2 depicts the relationship between inversion height and A_0, where the inversion height is defined as the height of the highest temperature value recorded (cut-off at 300 m) and A_0 is the calling area computed from the temperature profile alone, neglecting wind. If there is no inversion present, the height is defined as the starting height of the tethered balloon for each sounding (1.5 m). A_0 contours are, of course, perfect circles, since wind effects are neglected and therefore cannot induce directionality. Each data point represents one of the 65 soundings (tethersonde runs).

As inversions increase in height from 1.5 to 20 m, A_0 increases slowly. Above 20 m, the inversion begins to trap the ground mode (Lee *et al.* 1986) and A_0 increases rapidly to 300 km^2 at 80 m. An A_0 value of 300 km^2 corresponds to a circle with a radius (calling range) of 9.77 km. A_0 remains near 300 km^2 as inversion height increases from 80 to 300 m. The exceptions to this trend, the five points in the lower right of Fig. 2, are all *elevated* inversions. Four other elevated inversions fit the general trend. Fig. 3 depicts an elevated inversion (solid line) and a standard ground-level inversion (dashed line) for comparison. The temperature profile below an elevated inversion can explain the low values of A_0 for those points in Fig. 2. From ground level to the base of an elevated inversion, temperature can decrease with height, refracting sound upwards and diminishing sound pressure levels. Although an elevation of as much as 20–50 m can enhance low-frequency sound propagation by reducing ground attenuation, sound pressure levels (SPLs) will decrease and become more erratic for greater elevations.

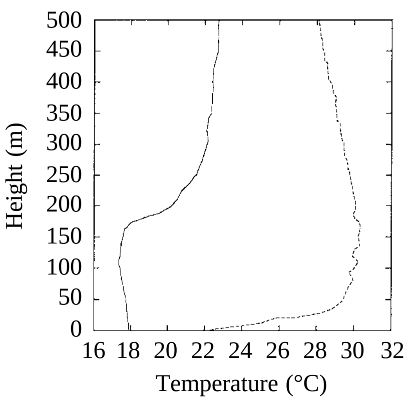


Fig. 3. Example of an elevated inversion (solid line; 05:00 h local solar time, 20 September 1992) and a ground-level inversion (dashed line; 20:08 h, 18 September 1992).

Fig. 4 shows the relationship between inversion strength (defined as the difference between the maximum temperature in the first 300 m and the surface temperature) and A_0. As reported in Garstang *et al.* (1995), the range and therefore A_0 increase with inversion strength. The exceptions, the four outliers in the lower right of Fig. 4, are among the most elevated of inversions recorded during the experiment, with the zone of positive temperature gradient beginning more than 100 m above the ground. An inversion that is growing in strength will increase the calling area smoothly if it is near the ground. If it is highly elevated, as many of the strongest inversions are, attenuation and enhancement plots oscillate as a result of mode trapping (Garstang *et al.* 1995). Figs 2 and 4 indicate that calling areas are likely to be degraded if an inversion is elevated. Range prediction is also likely to be less accurate for elevated inversions (Larom, 1996).

The preceding argument suggests that the temperature gradient ($\delta T/\delta z$, where z is height above ground and T is temperature) in the first 100 m above the ground is an important control on A_0. Fig. 5, based upon observed temperature profiles, confirms the predicted relationship between range, area and vertical temperature gradients. For each sounding, the temperature gradient is computed by a linear least-squares fit to the first 100 m of temperature data. A_0 increases rapidly from 20 to 200 km^2 as $\delta T/\delta z$ increases from –0.02 to 0.04 °C m^{-1}. Above a $\delta T/\delta z$ value of 0.04 °C m^{-1}, increasing $\delta T/\delta z$ has no effect on A_0.

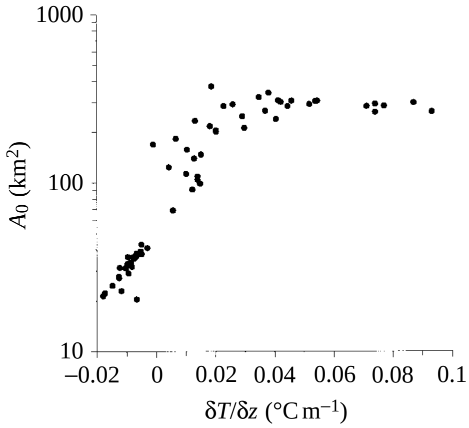


Fig. 5. Zero-wind, −67 dB calling area (A_0) as a function of temperature gradient $\delta T/\delta z$, for 65 tethersonde runs.

Combined effects of wind shear and temperature gradient

Low-level wind shear (change of wind vector with height) has pronounced effects upon the range and direction over which low-frequency sound will be propagated at the surface. In an isothermal atmosphere ($\delta T/\delta z$=0), with wind direction constant with height but with wind speed changing as shown in Fig. 6, a 15 Hz signal is transmitted over markedly different ranges in the downwind, crosswind and upwind directions. Downwind propagation is mildly enhanced and upwind propagation is markedly degraded.

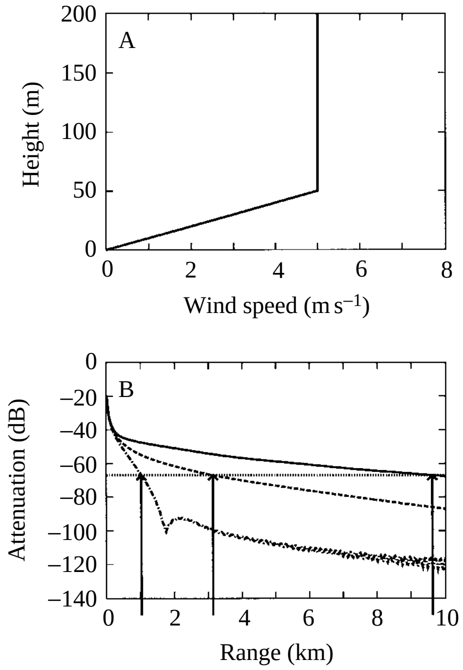


Fig. 6. A simple model of low-level wind shear (A) and the 15 Hz attenuation (B) predicted by the Fast Field Program (FFP). The atmosphere is assumed to be isothermal ($\delta T/\delta z$=0). Downward attenuation is shown by the solid line, crosswind by the dashed line and upwind by the dash–dot line. The hypothesized elephant low-frequency calling range for a −67 dB difference between call strength and hearing threshold, as in Fig. 1 (horizontal line), is shown for each wind condition by a vertical arrow.

Wind-generated noise from intrinsic atmospheric turbulence increases greatly with wind speed and is greater at low frequencies than in the audible range (Morgan and Raspet, 1992). Induced turbulence from flow around the receiver (the receiving elephant's ear) also adds to the perceived wind noise. Nocturnal wind noise is lower because winds near the surface are generally low at night and turbulence is almost absent. The range estimation method used in the current study does not take wind noise into account and may therefore overestimate daytime calling ranges and areas while underestimating the remarkable increase in calling range and area from day to night.

The calling area A is defined as the area contained within the −67 dB contour when wind velocity profiles are used as well as temperature profiles as input for the FFP. The Richardson gradient number, R_i, which combines temperature and wind gradients in the form:

$$R_i = \frac{\boldsymbol{g}}{T_0} \frac{\delta T/\delta z}{|\delta u/\delta z|^2} ,$$

where $\boldsymbol{g}$ is the acceleration due to gravity, T_0 is surface temperature and u is wind speed, is employed to examine the complex effects of temperature gradients and wind shear by suggesting that the calling area A may scale with R_i. Fig. 7 shows A *versus* R_i. R_i was computed using temperature and wind gradients over the first 100 m above the ground. For R_i<–5, A is usually less than 50 km^2. For R_i>3, A>150 km^2. Between theses values, A increases in proportion to R_i.

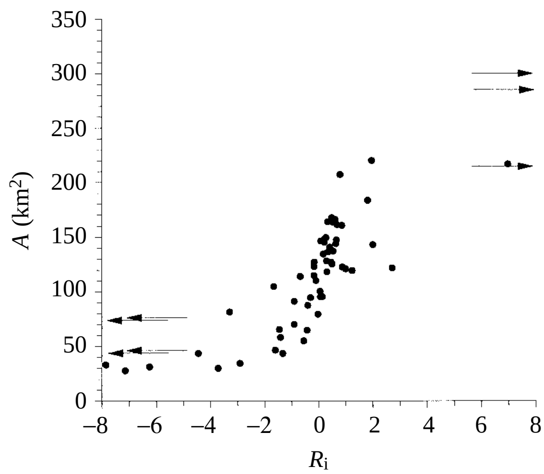


Fig. 7. The −67 dB calling area A as a function of the Richardson gradient number R_i (based upon temperature and wind speed gradients from linear fits to tethersonde data for the first 100 m above the ground) for 65 tethersonde runs. Arrows indicate where values at these heights extend beyond the x-axis scale.

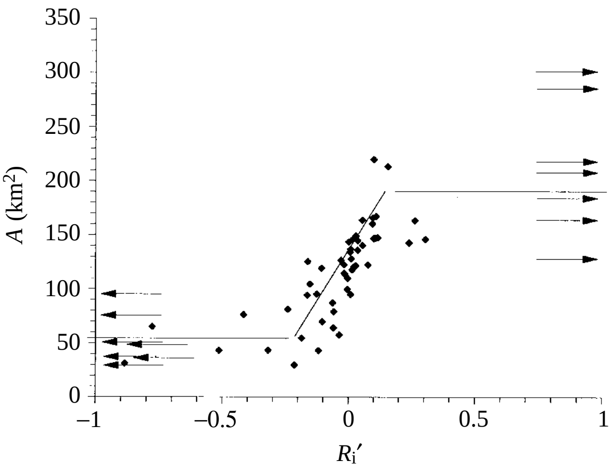


Fig. 8. The –67 dB calling area A as a function of the Richardson gradient number R_i' (based upon temperature and wind speed gradients from tower data taken at the same time as 65 tethersonde runs). The A values of points falling outside the x-axis range are indicated by arrows.

Determination of calling area size

Range predictions using simpler measurement systems can now be suggested, based upon two primary influences on low-frequency propagation: wind shear and temperature gradient. Field biologists and park personnel wishing to estimate calling range will not have access to tethersondes or other highly specialized instruments, but wind and temperature observations at two levels near the ground may be available. To facilitate range prediction using such a method, data from the 5 and 10 m levels on a tower at Etosha are compared with the area predictions made from the tethered balloon soundings. Details of the tethered balloon flights may be found in Larom *et al.* (1996). Fig. 8 shows the calling area A as a function of the Richardson gradient number, R_i' (derived from the 5 and 10 m data instead of from a sounding as for R_i in the previous section). R_i' was calculated as 1 h running means, using tower data originally stored as 5 min averages. The data cover values of R_i' from –10.8 to 54.0, and straight lines have been fitted in three sections: (R_i'<–0.2), (–0.2<R_i'<0.2) and (R_i'>0.2). The calling area A averages approximately 50 km^2 in highly unstable atmospheres (R_i'<–0.2) and 190 km^2 in highly stable atmospheres (R_i'>–0.2), but displays considerable variability. The transitional zone is well modelled by a least squares fit (r^2=0.60, P=<0.0001).

In Fig. 9, calling area is computed over the entire period of the field experiment, using the 5 and 10 m tower data and the R_i' correlation shown in Fig. 8. Calling area size changes on two time scales; over 24 h periods (horizontal axis) and from day to day (vertical axis). Both the diurnal and interdiurnal variations are weather-dependent. Large-scale influences on the weather of southern Africa can be simplified into five circulation types (Garstang *et al.* 1996; Garstang and Tyson, 1996). Four of these weather types occurred during the Etosha study. These may in turn be simplified into two basic categories; undisturbed (UD) and disturbed (D). Undisturbed (anticyclonic) circulations occurred on 63 % of the field study days, generally producing cloudless skies. On undisturbed days, strong daytime heating and nocturnal cooling occur, and inversion formation and decay is marked. Under disturbed weather conditions, in contrast, the strong diurnal cycle of surface heating and cooling is greatly diminished. Partially cloudy or cloudy and rainy weather (D) occurs with travelling easterly or westerly waves. These conditions occurred on 37 % of the experimental days.

Maximum calling areas occur predominantly during undisturbed periods (e.g. 9–20 September 1992) and at night. Minimum calling areas occur during the day, but without clear coincidence with disturbed weather. The diurnal cycle in calling area size is, however, diminished on disturbed days and most pronounced on undisturbed days. In general, Fig. 9 shows early evening and early morning maxima in calling area size except during a few disturbed days.

The complex interaction between wind and temperature profiles and low-frequency sound transmission makes daytime conditions more difficult to predict. Minimal calling areas are caused by a combination of strong sun and low wind speeds. When high-pressure systems prevail (undisturbed), conditions are sunny but strong northeasterly surface winds prevail; this enhances the daytime calling area somewhat owing to a moderation of the daytime super-adiabatic temperature lapse rates by mechanical mixing. Disturbed conditions can also increase the daytime calling area, moderating the negative temperature gradient by increasing the cloudiness and absolute humidity. Minimal calling areas can occur during either disturbed or undisturbed conditions whenever there is both enough sunlight for significant surface heating and wind speeds low enough to prevent mixing. Under these conditions, ground heating is unmoderated by mixing, moisture or cloud cover, and $\delta T/\delta z$ is strongly negative ($\delta T/\delta z$<–10 °C km^{-1}).

The transition from the dry to the wet season occurring towards the end of the field experiment period appears to influence calling area. Nocturnal enhancement (A>190 km^2) diminishes after 25 September 1992, as incursions of moister air from the north and increased cloud cover become more common.

On any given day, the calling area undergoes an expansion and contraction which may be as large as an order of magnitude. Fig. 10 shows one such 24 h period at Etosha (18–19 September 1992). One hour before sunset (17:00 h LST), the calling area is 58 km^2 and is contained within the 6 km radius. The range is as low as 2 km in the upwind direction. Rapid expansion occurs during the next hour; A is 217 km^2 at 18:00 h LST, and by 19:00 h LST reaches 302 km^2. At 19:00 and 20:08 h LST, the –67 dB attenuation contour is nearly symmetrical, with a radius of approximately 10 km. After 20:08 h LST, the calling area contracts and becomes asymmetrical in response to increased winds. Around sunrise (06:05 h LST), A has fallen to 161 km^2. Two hours later (08:00 h LST), the calling area is highly directional and restricted in the upwind direction, with an area of only 31 km^2.

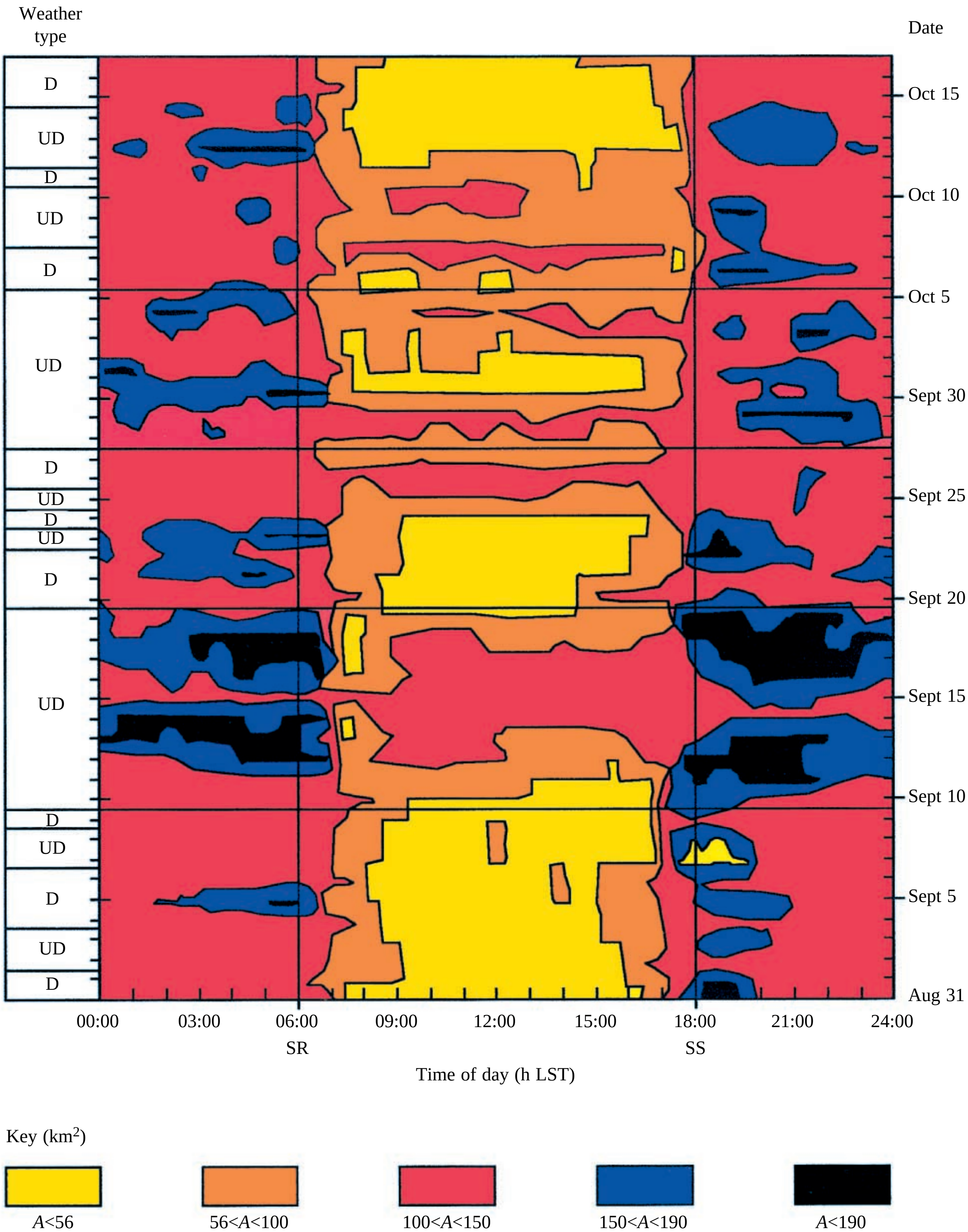


Fig. 9. The –67 dB calling area A predicted from 5 and 10 m tower data using R_i' correlation shown in Fig. 8. The key shows intervals of calling area A in km^2. The horizontal axis is time of day in local solar time (LST) with sunrise (SR) and sunset (SS) shown by vertical lines. The left ordinate is the weather type with undisturbed or fair weather shown as UD and disturbed, cloudy or rainy weather shown as D. The right ordinate is experiment months and days in 1992. Horizontal lines enclose two periods of continuous UD weather from 9 September to 20 September and from 27 September to 6 October 1992.

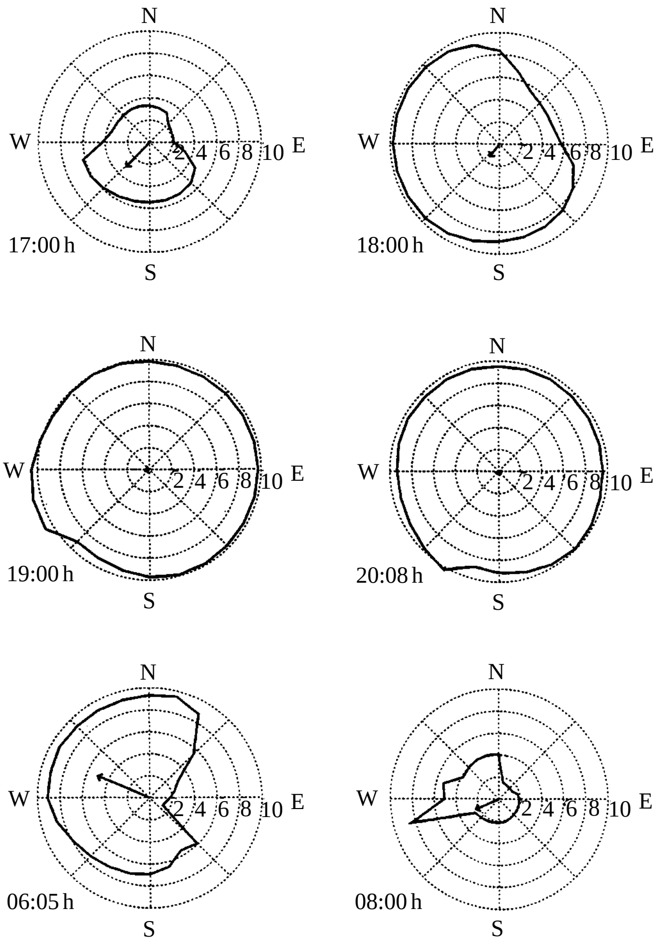


Fig. 10. The −67 dB attenuation contours of calling range calculated using the Fast Field Program (irregular solid line) and mean wind in the first 300 m above ground (vector arrow). Circular rings (broken lines) depict both range (in km) and wind speed (in m s^{-1}). Data from tethered balloon soundings made on 18–19 September 1992. Cardinal points of the compass are shown to indicate wind direction and directional dependence of calling range. Time of sounding in local solar time (LST) is given at the lower left of each plot.

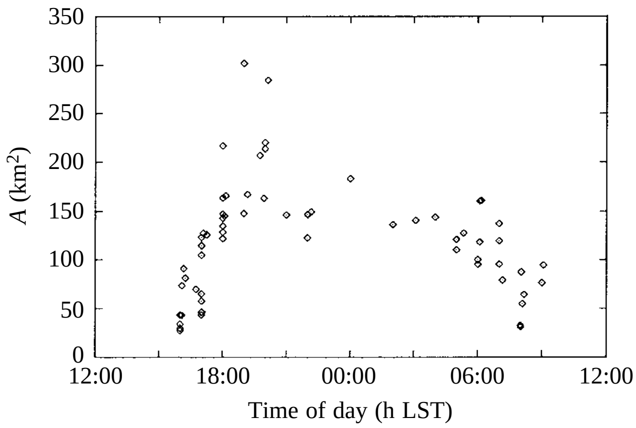


Fig. 11. Area (A in km^2) covered by the −67 dB attenuation contour as a function of time of day, for 65 tethered balloon soundings from 16 September to 4 October 1992.

Soundings were not taken during the day, but the calling area would probably be below 50 km^2 owing to the strong negative temperature gradient and high winds.

Fig. 11 shows the distribution over 24 h of the predicted calling area for all 65 soundings of temperature and wind. Following Larom *et al.* (1996), the following temporal regions can be identified: (1) 16:00–18:30 h LST, rapid growth in A; (2) 18:30–20:30 h LST, optimum calling time, with A as high as 300 km^2; (3) 20:30–06:00 h LST, A declines with the formation of a nocturnal wind maximum (details of this nocturnal jet may be found in Larom *et al.* 1996); (4) 06:00–09:00 h LST, rapid decrease in area with sunrise; (5) daytime, low calling area, A probably often below 50 km^2.

Discussion

For sounds at the very low frequencies used by the African elephant, the calling area varies markedly over 24 h periods in the dry savanna habitat of Etosha National Park. Low-frequency calls will be restricted in range during the day and the range will expand at night. Because calling area is optimized by strong positive temperature gradients and low winds, there is an early evening maximum in calling area (Fig. 11). Regional weather systems influence this diurnal cycle. The cycle is most pronounced during clear weather conditions (Fig. 9), which occur more than 60 % of the time in the dry season. The cycle is somewhat suppressed under partly cloudy, mildly disturbed conditions and is almost absent on overcast days. Seasonal controls are also manifest; the diurnal cycle lessens with the transition from the dry to the wet season. Longer-term (climatic) variations are a distinct possibility.

The evening maximum in calling area is a product of the regional topography near Etosha. Differences in topography, the existence of periods of morning enhancement under certain weather conditions (Fig. 9) and the presence of a secondary stability maximum in the morning (Fig. 7 in Larom *et al.* 1996) all suggest that dawn maxima in calling area will also occur over broad areas of the African and other savannas. At Etosha, dawn maxima are probably suppressed by the formation of a nocturnal jet (a nocturnal wind speed maximum of 10 m s^{-1} or more occurring within the first few hundred metres above the ground) that begins several hours after sunset and persists into the morning. Jets form preferentially over locations of very gentle but continuously sloping topography, such as Etosha (Preston-Whyte *et al.* 1995; Zunckel *et al.* 1996*a*), the South African highveld (Zunckel *et al.* 1996*b*) or the Great Plains of the central United States (Blackadar, 1957; Holton, 1967).

Jets are absent or weaker in areas where the slope is not constant over great distances. In regions of shallow valleys and hills, the dawn maximum should be more pronounced. In these areas, where the wind effects induced by a nocturnal jet are absent, calling conditions may continue to improve through the night as the temperature inversion grows. In areas of higher and more broken relief, topography has a direct effect as sound

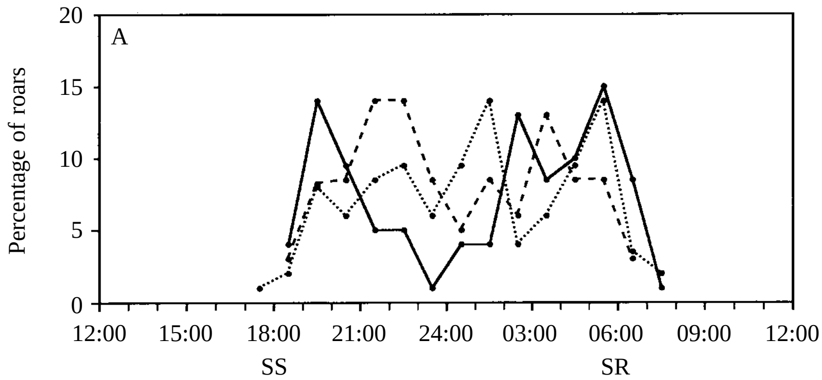
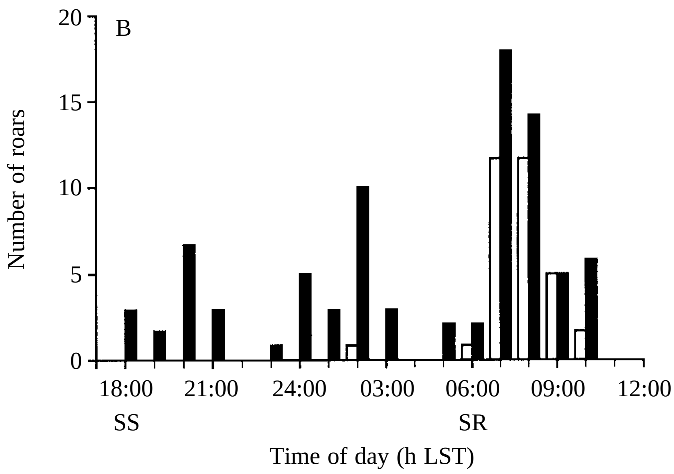


Fig. 12. (A) Time and frequency of roaring by lions (after Schaller, 1972). Solid line, male number 134, daily average over 10 days (N=294); dashed line, male number 159, daily average over 16 days (N=104); dotted line, prides, daily average over 30 days (N=192). (B) Time and frequency of roars by male (filled bars) and female (open bars) lions (after Stander and Stander, 1988). Approximate times of sunset (SS) and sunrise (SR) are indicated. No roars were recorded between 11:00 and 17:00 h.



is channelled around obstacles, and prediction of acoustic fields is greatly complicated. Temperature inversions still form, however, and in all cases nocturnal conditions will be enhanced over daytime.

Optimum near-surface atmospheric conditions, which maximize the calling area, are likely to occur predictably at dusk and/or dawn over a large portion of the African savannas and other areas. A number of species living in these areas specialize in calling during the hours when transmission is best. It seems likely that the predictable atmospheric fluctuations have exerted a selective pressure on the calling behaviour of some of those species. Lions, for instance, roar almost exclusively at night, with dawn and dusk peaks in the number of roars (Fig. 12A, after Schaller, 1972; data from the Serengeti; Fig. 12B, after Stander and Stander, 1988, data from Etosha). Preliminary measurements of a few lion calls in Namibia show them to be similar to those of elephants in sound pressure level (114 dB), although higher in pitch (fundamentals 36–81 Hz, harmonics 129–170 Hz; 100 Hz dominant frequency; K. Payne and C. O'Connell, personal communication). Roaring helps lions to find and avoid conspecifics over distances of several kilometres and functions in territoriality (Schaller, 1972). For animals that announce territorial boundaries vocally, there is likely to be some relationship between territory size and calling area. The long calling ranges predicted for low-frequency sound undoubtedly play a role in the establishment and maintenance of pride areas of up to 400 km^2 in the Serengeti (Schaller, 1972). At these ranges, the same meteorological influences apply for lions as for elephants and may therefore be a factor in the temporal patterning of lion calls.

Elephants use the long-distance potential of their calls in a variety of ways. A female elephant in oestrus announces her condition through a sequence of powerful low-frequency calls which she repeats periodically until such time as the highest-ranking male arrives to guard and mate exclusively with her. Other calls appear to coordinate the behaviour of widely separated elephants. In a large-scale radio-tracking program in Zimbabwe, Rowan Martin noted evidence of complex coordination between the movements of family herds as they foraged during the dry season. This coordination occurred over distances of several kilometres and at times when visual or olfactory communication was not possible (Martin, 1978). In 1990, W. R. Langbauer, R. Charif, K. Payne, R. Martin and L. Wilson (in preparation) also documented coordinated behaviour while recording the vocalizations of one or more females in 13 separate herds. These animals wore radio collars in which voice-activated audio transmitters were embedded. All of their loud calls were received at a base station. Finding little evidence of active communication between distant herds, these researchers proposed that elephant family groups maintain this coordination by listening for each other's calls and moving in such a way as to keep within earshot of each other for days or weeks at a time (as well as using olfaction in the absence of adverse wind direction).

Fig. 13 shows the distribution over 24 h of all loud low-frequency calls recorded from 14 radio-collared Zimbabwean elephants during a 2.5 month period. These elephants, all adult females, called very little between 02:00 h LST and 09:00 h LST and frequently between 10:00 h LST and 20:00 h LST. The peak calling period is centred around 17:00 h LST. Sound transmission at this time would tend to be much better than at midday. The 17:00 h LST maximum may be a combined response to water stress, avoidance of predation and near-optimum transmission conditions. Late afternoon is when elephant families typically make treks out of the woodland to water (K. Payne, S. Payne, M. Irinaga, L. Leland and A. Masarirevhu, in preparation). Areas near water tend to be clear

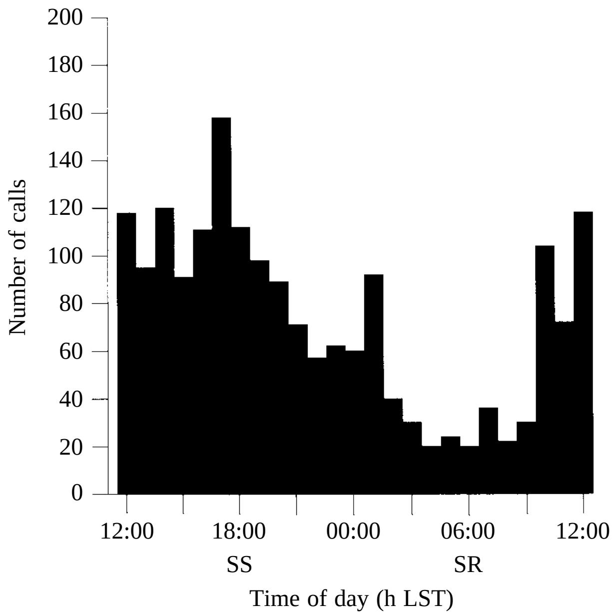


Fig. 13. Diurnal variation of the number of calling bouts for 14 Zimbabwean elephants. Time is in LST. SS, sunset; SR, sunrise (after W. R. Langbauer, R. Charif, R. Martin, K. Payne and L. Wilson, in preparation).

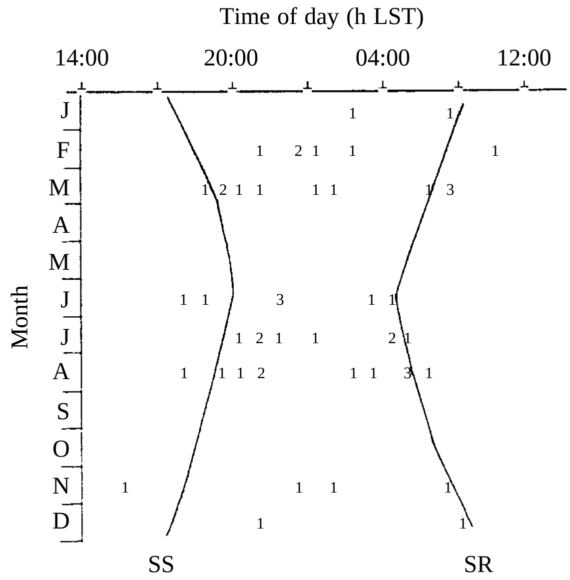


Fig. 14. Distribution of 51 vocalization bouts of coyotes during the day. Numbers indicate how many bouts were heard during any hour (LST). The two lines indicate the approximate times of sunset (SS) and sunrise (SR) (after Laundré, 1981).

of vegetation, and prey animals are maximally vulnerable to attack by predators when coming to drink. Lions are probably the most important predator of elephants; they are known to kill calves. Lions tend to sleep during the day, increasing their activity around sundown; it is therefore beneficial for elephants in family groups to leave the flood plains and waterholes before dark.

Clearly, many factors work together to shape temporal patterns in calling behaviour. A simple model involving only elephants and lions would suggest that both may respond to the influence of atmospheric conditions on their ability to hear, contact, avoid, join and inform conspecifics. For lions, the reception of information about prey and competitors will be enhanced during periods of optimal transmission; for elephants, their ability to hear, locate and avoid, or to form coalitions to confront, their most dangerous predator – lions – will be increased.

The calling strategy that has evolved probably includes optimum transmission time as one of its considerations. Even if a strategy of calling at times of optimal transmission has not evolved, reception will still be optimized at these times. Females in oestrus, for example, do not withhold their urgent oestrus calls until the hours of best transmission (W. R. Langbauer, R. Charif, R. Martin, K. Payne and L. Wilson, in preparation), yet the reception of these calls by males is nonetheless both temporally and spatially dependent upon atmospheric conditions.

It may prove possible to extend the methods and observations of this paper to other locations and frequencies. Similar atmospheric conditions can prevail in many climates. Similar influences on the propagation of long-range calls will therefore be exerted in many locations. For example, coyotes in the American West respond to sirens at distances of up to 1.6 km (Wenger and Cringan, 1978) and show strong crepuscular (morning and evening) maxima in the number of vocalizations (Fig. 14, Laundré, 1981; Walsh and Inglis, 1989). Walsh and Inglis (1989) and Wenger and Cringan (1978) attempted to correlate coyote calling bouts with atmospheric conditions such as temperature, pressure and wind velocity. The current study suggests that much better correlations will be found with vertical gradients of temperature and wind velocity.

Fig. 15 shows the timing of spontaneous howls given by wolves monitored for 2050 h at two sites in Minnesota. Again, the environment is one in which atmospheric conditions typically enhance sound transmission at dusk and dawn, with better conditions existing at night than during the day. As with lions and coyotes, these wolves concentrated their calling in the hours of best transmission (Harrington and Mech, 1978).

Predictable periods of enhanced sound transmission might also be a factor behind the timing of the calls of birds, frogs and insects. Atmospheric refractivity varies with call frequency and, in general terms, the diurnal change between unfavourable daytime and favourable nocturnal conditions may be even greater for high- than for low-frequency calls. However, high-frequency communication is complicated by a number of other factors, including atmospheric turbulence and ground attenuation, which invariably reduce calling range.

Atmospheric conditions in many savanna and savanna-like environments produce diurnally predictable windows of opportunity for long-distance communication, particularly for animals which use powerful, relatively low-frequency calls. The timing of calling in various large mammals in such

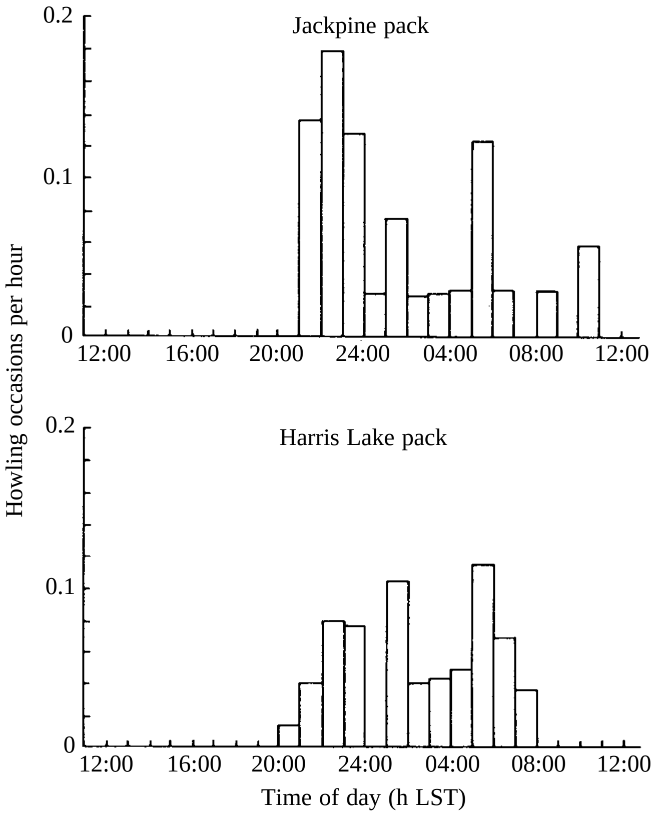


Fig. 15. Time of day when spontaneous howling of wolves occurred around two rendezvous sites in Minnesota (after Harrington and Mech, 1978).

environments suggests that those windows of opportunity may have acted as a selective pressure over long periods, enhancing the ability of a number of species in a number of places to develop social groupings and behaviours that are coordinated over long distances.

Field biologists, whether engaged in observations of behaviour or in acoustic censuses, can take advantage of the prediction of calling range made possible by atmospheric measurements. Field research incorporating such information may add an important new dimension to behavioural studies. There is much to be learned from further investigation of the relationship between meteorological conditions and the behaviour of calling animals.

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