THE IMPORTANCE OF DIRECTIONAL SOUND RADIATION IN AVIAN VOCALIZATION

STEVE R. WITKIN

Many studies show the importance of frequency structure and timing characteristics for acoustical signals (e.g., Thorpe 1961, Hinde 1969), but we know little about the sound pressure levels and spatial radiation patterns of such signals. Here I offer evidence for directional radiation of certain calls of the Black-capped Chickadee (*Parus atricapillus*) and discuss ways in which selection may favor directional beaming.

Most of the scant literature on radiation patterns concerns sounds produced by echolocating bats (e.g., Möhres 1953, Griffin 1958, Simmons 1969) rather than sounds used for communication among individuals. Gerhardt (1975) found that a treefrog (*Hyla chrysoscelis*) and a toad (*Bufo americanus*) produce directional mating calls, whereas the spring peeper (*H. crucifer*) produces omnidirectional calls, but he did not discuss reasons for this difference. Although Archibald (1974) demonstrated directional radiation for Ruffed Grouse (*Bonasa umbellus*) drumming sounds, this report is the first study for avian vocal signals.

METHODS

This study was part of a larger investigation of sound pressure levels (Witkin 1975), in which I analyzed more than 750 calls and 2,510 call-notes from 21 color-banded chickadees. The study was conducted over a 3-month period (9 February–27 April and 15 November–12 December, 1974) at a winter feeder at the University of Wisconsin-Milwaukee Field Station in Ozaukee Co., Wisconsin.

Because chickadees readily vocalize at feeders, I placed a microphone (Brüel & Kjaer 4145) 100 cm from the centers of two landing perches which were attached to either side of the feeder. The distance between the perches was 25 cm. I mounted the microphone on a tripod, and used a windscreen (B & K UA0207) to reduce noise from air turbulence. Because the microphone is designed for perpendicular incidence, I aimed it directly at the feeder. The microphone was connected to a B & K sound level meter (2704), set for A-scale weighting, which in turn connected to the line input of a Nagra IV.2L tape recorder. Recordings were made on Scotch 203 tape at a speed of 19 cm/s.

Prior to recording chickadee calls, a 94 dB calibration tone of 1 kHz was recorded, using a B & K sound source (4230). I analyzed the tapes with a B & K sound level recorder (2305), set to measure the root-mean-square (RMS) sound pressure levels of the calls in decibels (re 0.0002 dynes/cm^2). Writ-

ing speeds of 250–500 mm/s were used to maximize the stability of the level recorder writing system. I used a Kay sonagraph (6061B), fitted with a 150 Hz band-width filter, to measure the midpoint frequency of each call-note to the nearest 0.1 kHz. When harmonics were present, I measured the midpoint of the darkest harmonic (i.e., the harmonic containing the most energy). Mean midpoint frequencies were calculated by averaging all midpoint values for each note-type. For further details of analysis see Witkin (1975).

To determine whether the radiation patterns of chickadee calls were uniform or directional, I scored individuals calling from a landing perch as facing either toward or away from the microphone. Instances in which I was unsure of the direction (over 65% of all call-notes recorded) were excluded from analysis. I estimate the degree of accuracy in determining whether an individual was facing toward (0°) or away from the microphone (180°) to be ±30°.

Figure 1 shows an audiospectrogram and sound level graph of a chickadee call consisting of six notes (a note is defined here as a discrete sound pulse). Following a nomenclature of chickadee calls developed by Ficken et al. (in press) and Ficken and Hailman (unpubl. data), the call shown in Fig. 1 is termed a "Chick-a-dee call," and consists of A, B, C and D notes. These four note-types occur in many combinations, and together comprise the most common vocalizations in the Black-capped Chickadee vocal repertoire. The analysis presented below concerns only these four note-types, as I lacked adequate samples for other note-types.
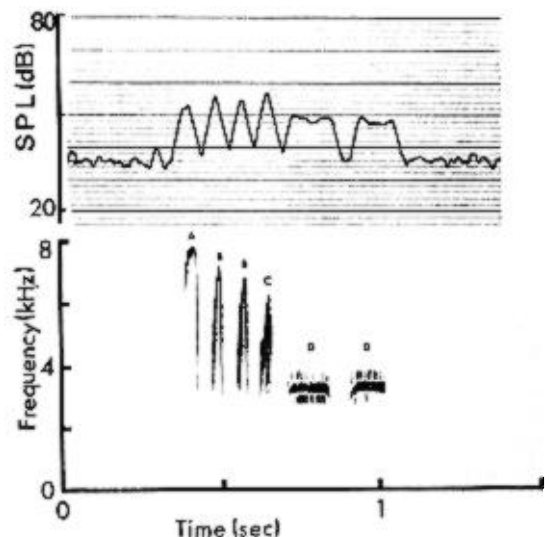

FIGURE 1. Sound level graph (top) and audiospectrogram (bottom) of a Black-capped Chickadee "Chick-a-dee" call, showing the four note-types analyzed in this study.
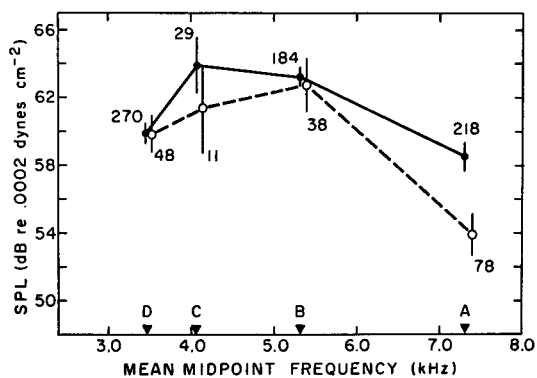
FIGURE 2.   Graph showing mean SPL's and 95% confidence limits for A, B, C and D notes uttered facing toward (filled circles and solid lines) and away from (open circles and hatched lines) the microphone. Sample sizes are indicated above the facing toward data points, and below the facing away data points. Pointers along the abscissa indicate the mean midpoint frequencies of the note-types. The data points are slightly offset to prevent unreadable overlap of the confidence intervals.

RESULTS

Figure 2 shows mean sound pressure levels (SPL's) and 95% confidence limits for the four note-types, uttered facing toward and away from the microphone. Figure 2 also shows the mean midpoint frequencies of each note-type. Although the decibel scale is logarithmic, I calculated means and confidence intervals without converting the dB values to a linear scale (e.g., dynes/cm²). The SPL's of chickadee call-notes are normally distributed when plotted on the dB scale (Witkin, unpubl.). Therefore, one can use parametric statistical procedures if dB values are used. From Figure 2, it is apparent that only the highest frequency note-type (the A note) shows a non-overlap of confidence intervals; therefore, the difference between the means may be considered real.

DISCUSSION

One possible source of difficulty with the experimental design is that SPL's of birds facing the microphone should be greater than SPL's of birds facing away, even without beaming, as the beaks of birds facing the microphone will be slightly closer to the microphone. However, the size of the Black-capped Chickadee (roughly 10 cm total length) is small compared with the measuring distance (100 cm). Applying the inverse square law (loss of 6 dB SPL per doubling of distance) and assuming omnidirectional radiation, I estimate the maximum difference in SPL's between facing toward and away from the microphone to

be about 0.5 dB. This alone cannot account for the observed difference in mean SPL's for the A note (approximately 4.5 dB), and one must conclude that the A note is somewhat directional.

Although Figure 2 shows an overlap in confidence intervals for the B, C and D notes, one must interpret these results cautiously. It may be possible for certain sounds to have radiation lobes separated by 180°; this type of radiation pattern could not be distinguished from uniform radiation with the techniques employed in this study. Therefore, the B, C and D notes are not necessarily omnidirectional sounds.

Two factors may influence directional beaming: the sound-shadow effect of the head and body, and the concentration of sound waves by an acoustical horn. The importance of the first factor depends upon the ratio of the sound's wavelength to the emitting object's diameter; the threshold of directionality occurs at a ratio less than one. The sound-shadow effect is an important factor in echolocating bats, who emit wavelengths much smaller than the diameter of their heads (Griffin 1958). The mean wavelengths of the A, B, C and D notes (as calculated from their mean midpoint frequencies) are approximately 4.5, 6.3, 8.1, and 9.6 cm, respectively (assuming the velocity of sound to be 331.4 m/s at 0°C). Therefore the sound-shadow should have its greatest effect on the A note, whose wavelength is less than half the size of the chickadee's largest linear dimension. The other factor, directional beaming by acoustical horns, affects sounds of horseshoe bats, who possess elaborate nose structures that apparently aid in focusing the beam (Möhres 1953). For this second type of beaming to be effective, the wavelength of the emitted sound should be smaller than the maximum diameter of the horn. The maximum aperture of a chickadee's gape is probably no greater than 1 cm, so an acoustical horn is probably not involved in beaming A notes.

It is easy to conceive of situations where directional beaming would not be advantageous. Two of the several functions commonly attributed to avian song are attraction of mates, and repulsion of intruders. In either situation, it would seem advantageous for the song to radiate in all directions: females from all directions could be attracted, and males in surrounding territories could receive the signal. I have no data for the radiation pattern of Black-capped Chickadee song. However, the D and C notes, which appear to be nondirectional, are roughly the same frequency

as the song (Witkin 1975, Ficken et al., in press). Therefore, the song is also probably non-directional. Recent evidence shows certain other aspects of song structure to be under selection by the acoustic properties of the habitat (Chappuis 1971, Morton 1975, Nottebohm 1975).

There are at least three possible advantages for beaming communication signals: (1) to achieve an effective link between sender and receiver; beaming may help reduce the receiver's equivocation, especially when the channel is permeated with noise; (2) to prevent receivers other than the addressee(s) from obtaining information from the signal; beaming may be effective in preventing predators from using auditory cues to determine the position of the caller; and (3) to increase the transmission distance of a signal; distance may be increased if the energy is concentrated in a beam, rather than spreading out in all directions (this effect could be achieved only if an acoustical horn were responsible for the beaming).

It follows from the above that directional signals in social birds most likely: (1) are used in close-range interactions; and (2) are among the most frequently emitted calls in a species' vocal repertoire, which cause the greatest exposure to predation. Considering the available evidence for chickadee vocalizations, the A note seems to fit the above predictions: as a single note, it is often used at close range, coordinating flock movements (Odum 1941–2, Ficken & Hailman, unpubl. data). Single A notes are also given more frequently than any other call during the non-breeding period (Witkin 1975).

If the sound-shadow effect or acoustical horns are the most important factors in directional radiation, selection should favor the use of high frequency sounds when it is advantageous for the sounds to be directional, for reasons discussed above. The widespread occurrence of ultrasonic bat calls may be due to selection for beaming; beaming might enable bats to select echoes from a narrow angular range in the direction of flight (Griffin 1958, Simmons 1969). However, selection for directional beaming may be only one of several factors selecting for high-frequency avian vocalization. For example, it is known that high-pitched sounds are generally attenuated more rapidly by the environment than low-pitched sounds (e.g., Morton 1975). Therefore, the high frequency of the A note may also result from selection for minimization of transmission distance via attenuation by the habitat, which may also be important in reducing

chances for detection by predators. Morton (in press) recently invoked certain "motivation-structural rules" to explain why avian and mammalian calls used in appeasement and submissive contexts may be high-pitched. Morton's argument, however, does not apply to the chickadee A note, which is not restricted to agonistic situations.

It therefore appears that the high-pitched characteristics of certain avian vocalizations, especially "contact notes" such as the chickadee A note, may result from selection for directional beaming, and for maximal attenuation by the environment. Both factors may combine to decrease greatly the probability of a caller being detected by predators. Low SPL may be another design feature to reduce the transmission distance of a signal; the average SPL of the A note is approximately 54 dB (measured at 1 m), which is among the lowest SPL's of all chickadee calls (Witkin 1975).

The above arguments can perhaps account for the widespread occurrence of high-pitched avian "alarm" calls emitted in the presence of predators. Marler (1955) suggested that the acoustic properties of these calls could be explained by selection for minimization of cues for binaural localization. An alternative hypothesis is that certain features of these calls (e.g., high frequency) could result from selection to reduce the probability of the signal reaching the ears of predators, as seems to be the case for the chickadee A note. It seems clear that we need information on SPL's and radiation patterns for many other species before we can fully understand the selection pressures operating on the acoustical characteristics of avian vocalizations.

SUMMARY

Certain high-frequency calls of the Black-capped Chickadee are directional in radiation pattern. Directional beaming of avian communication signals may be favored by selection for the following reasons: (1) beaming may help to achieve an effective link between sender and receiver, especially in noisy conditions; (2) beaming may prevent receivers other than the addressee(s) from receiving the signal; and (3) beaming may increase the transmission distance of the signal. The two factors influencing beaming (the sound-shadow effect of the head and body, and the concentration of sound waves by an acoustical horn) are most effective for high-frequency sounds. The widespread occurrence of high-pitched avian "alarm" calls may be partially explained by (1) selection for directional ra-

diation; and (2) selection for strong attenuation of the signal by the habitat. Both factors may act to reduce the probability of the alarm call reaching a predator's ears.

ACKNOWLEDGMENTS

LITERATURE CITED

ARCHIBALD, H. L. 1974. Directional differences in the sound intensity of Ruffed Grouse drumming. Auk 91:517–521.

CHAPPUIS, D. 1971. Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: l'évolution des chants en forêt équatoriale. Terre Vie 2:183–202.

FICKEN, M. S., R. W. FICKEN, AND S. R. WITKIN. Vocal repertoire of the Black-capped Chickadee. Auk, in press.

GERHARDT, H. C. 1975. Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. J. Comp. Physiol. 102:1–12.

GRIFFIN, D. R. 1958. Listening in the dark. Yale Univ. Press, New Haven.

HINDE, R. A. [ed.]. 1969. Bird vocalizations. Cambridge Univ. Press, Cambridge.

MARLER, P. 1955. Characteristics of some animal calls. Nature 176:6–8.

MÖHRES, F. P. 1953. Uber die Ultraschallorientierung der Hufeisenmasen (Chiroptera-Rhinolophinae). Z. Vgl. Physiol. 34:547–588.

MORTON, E. S. 1975. Ecological sources of selection on avian sounds. Am. Nat. 108:17–34.

MORTON, E. S. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. Am. Nat., in press.

NOTTEBOHM, F. 1975. Continental patterns of song variability in Zonotrichia capensis: some possible ecological correlates. Am. Nat. 109:605–624.

ODUM, E. P. 1941–42. Annual cycle of the Black-capped Chickadee. Auk 58:314–333, 518–535; 59:499–531.

SIMMONS, J. A. 1969. Acoustic radiation patterns for the echolocating bats Chilonycteris rubiginosa and Eptesicus fuscus. J. Acoust. Soc. Am. 46:1054–1056.

THORPE, W. H. 1961. Bird song. Cambridge Univ. Press, Cambridge.

WITKIN, S. R. 1975. An amplitude analysis of Black-capped Chickadee vocalizations. MS thesis. Univ. of Wisconsin, Milwaukee.

Dept. of Zoology, University of Wisconsin, Madison, Wisconsin 53706. Accepted for publication 13 April 1977.