SOUND-SOURCE LOCALIZATION
BY THE RED FOX

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ABSTRACT

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By

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When prey animals must vocalize but must not reveal their position, natural selection has favored nearly pure-toned calls which are more difficult to locate than calls of complex tones. In a controlled test I determined how well nine red foxes located 13 different frequencies of pure sound. Using food as a reward, the foxes were trained to choose the correct location of a sound signal emitted from one of two possible loudspeaker positions. The foxes located 3.5 kHz better than all other frequencies and had the most difficulty locating frequencies less than 900 Hz and greater than 14 kHz.

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INTRODUCTION

Red foxes (*Vulpes vulpes*) respond to certain sound signals in their predatory habits as indicated by their approach behavior to artificial and recorded distress calls of their prey (Morse and Balser, 1961; Busnel, 1963). The acoustical detection used by foxes would be maximized if all audible calls of the prey species could be readily located; however, some vocalizations of the prey species seem not to be useful in directing the fox toward their sources. Certain birds signal the presence of a predator by giving a continuous and nearly pure-toned call which is difficult for humans to locate (Marler, 1955).

According to Marler and Hamilton (1967), vertebrates locate sound sources by binaurally comparing differences in intensity resulting from the sound shadow of the head, differences in arrival time, and differences in phase. They state that differences in arrival time are independent of the frequency and are best determined if the sound contains abrupt discontinuities, whereas detection of phase differences requires a continuous sound. Locating a sound by detecting differences in phase is possible for low frequencies with wavelengths greater than twice the distance between the ears, but at higher frequencies wavelengths are shorter and phase differences are difficult to detect. At higher frequencies the head acts as a sound shadow so that locating a sound by intensity differences is possible only when the wavelengths are less than the distance between ears.

Locating a sound by detecting differences in intensity and differences in phase depends upon the head configuration and may, because the two sound-locating mechanisms do not overlap, result in an interval of sound frequencies more difficult to locate than sounds of higher and lower frequency. It would probably be especially difficult for a predator to locate the source of a nearly pure-toned call if it were pitched too high for locating by phase differences but yet not high enough for locating by intensity differences. Predators, on the other hand, can presumably best locate a particular call of nearly pure tonal quality if their head configurations are such that detecting differences in either phase or intensity is maximized at that frequency.

This experiment was designed to determine how the ability red foxes have for locating pure-toned sounds varies as a function of the frequency.

METHODS

Experimental Design

The ability that a sample of nine foxes had for locating 13 frequencies of pure sound ranging from 300 Hz to 34 kHz, was estimated in a controlled test situation. Also controls with no sound were tested to insure that the foxes were locating by audition. The nine experimental subjects and thirteen treatment levels were then analyzed in a cross classified design with the number of correct choices as the dependent variable.

Subjects

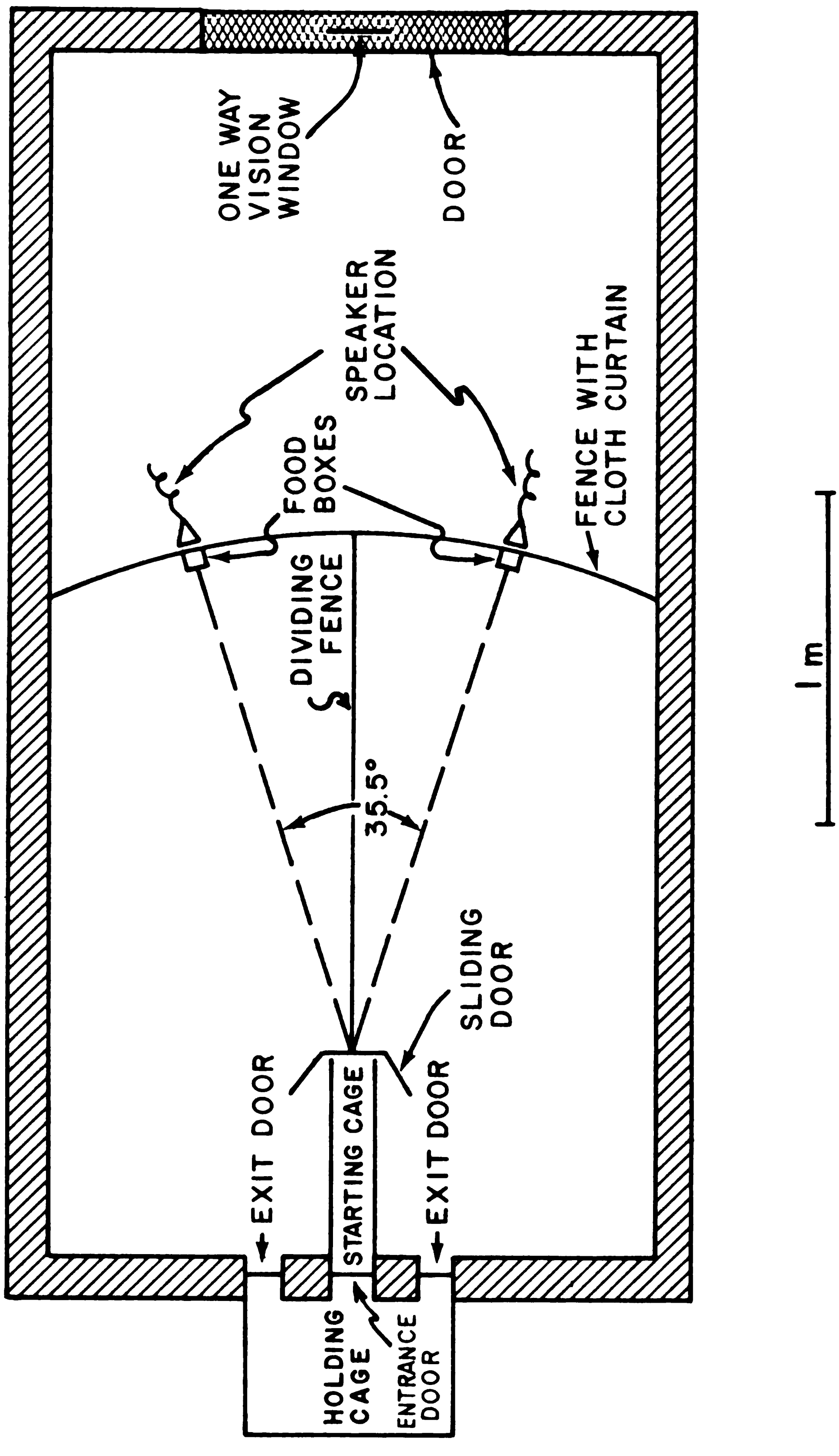
Five male and four female foxes were taken as pups from four areas and raised in captivity at Michigan State University where the experiment was conducted. The normal diet consisted mainly of commercial dog food except during testing when raw meat was used as a reward. The foxes were tested at nine months of age.

Procedure

Experimental Chamber

The interior dimensions of the experimental chamber were 1.8 m wide, 1.8 m high and 3.6 m long (Figure 1).

Figure 1.--Test apparatus.


ONE WAY VISION WINDOW
DOOR
SPEAKER LOCATION
FOOD BOXES
FENCE WITH CLOTH CURTAIN
DIVIDING FENCE
35.5°
SLIDING DOOR
EXIT DOOR
STARTING CAGE
EXIT DOOR
HOLDING CAGE
ENTRANCE DOOR
1 m

The door, located at one end of the chamber, had a 15 by 30 cm one-way vision window horizontally mounted 1.5 m above the floor. The walls and ceiling of the chamber were carpeted on both sides and egg flats were fastened on the inside of the walls and ceiling to suppress echoes. The floor of the chamber consisted of a 5 cm layer of fiberboard and three layers of carpeting. The steady-state ambient noise level in the chamber averaged 53 ± 3 db (re 0.0002 dynes/cm^2) when measured on the linear scale of a Brüel and Kjaer type 1613 sound level meter. The room was illuminated by a 300 watt incandescent light bulb.

Sound System

Thirteen test frequencies (0.3, 0.6, 0.9, 2.0, 3.5, 5.0, 6.5, 8.5, 10, 14, 18, 26, and 34 kHz) were generated by a Hewlett-Packard model 0-10/APA-6X audio oscillator and fed into one of two transducers. The accuracy of the frequencies generated were checked with a Tektronix 502A dual beam oscilloscope. A University model T-202 sphericon super tweeter was used for the frequencies 6.5 kHz and higher and a JFD model ALC-1 speaker was used for the frequencies 10 kHz and lower. This allowed a comparison of the two speakers at 6.5, 8.5, and 10 kHz. The frequencies used were all within the range of hearing for red foxes (Peterson, 1969).

Calibration

The system was calibrated with the B and K sound level meter located at various positions in the starting cage. The intensity of all but the highest two test tones and from both speaker locations was kept at 74 ± 4 db (re 0.0002 dynes/cm^2) when measured on the linear scale. The highest two frequencies were calibrated with the frequency response curve supplied by the manufacturer of the University speaker. A VO Matic 360 volt meter was used to insure the voltage output of the signal generator remained constant.

Training and Testing

The foxes were trained to choose one of two possible positions from which the sound source was coming then to approach and open the door of a food reward box located below and in front of the loudspeaker. A correct choice was rewarded with a 10 gram piece of raw meat. The apparatus, similar to the one used by Neff *et al*. (1956), consisted of an intertrial holding cage, located outside of the chamber, a starting cage where the animal received the sound stimulus, a 1.22 m high separating fence, and a cloth curtain attached to a fence behind the two food boxes (Figure 1). The food boxes were 15 cm wide, 12 cm deep and 22 cm high with 11 by 14 cm hinged doors and were open in the back to facilitate placement of the meat. The speakers were centered 8 cm above the food boxes and were positioned behind the cloth curtain to avoid visual cues. The speakers formed a 35.5 degree test angle with the starting cage as the apex.

At the beginning a preliminary control test was conducted to determine if the animals could locate the meat by odor alone. With the food boxes one m from the starting cage and a 58 degree test angle, the foxes could not locate the meat.

Training started at three months of age by conditioning the foxes to associate food with the sound stimulus. At five months of age the foxes were consistently responding in the test apparatus. Pilot studies then indicated that a test angle of 35.5 degrees elicited a less than perfect response from the foxes.

A trial consisted of putting the speaker and food in place while a fox waited in the holding cage, turning on the stimulus, letting the fox into the starting cage, five seconds later releasing the fox from the starting cage, and turning the stimulus off after the fox had reached the food box and eaten the meat or after he made an error. The dividing fence extended above the starting cage and prevented the animals from reversing their choice. The appropriate exit door was opened and the foxes were trained to exit and wait in the holding cage until the next trial. Speaker location was determined by the Gellermann series (Gellermann, 1933) which is different combinations of left-right choices. During the speaker and meat placement all movements were kept constant to avoid giving the animals additional cues. Intertrial time was kept a constant one minute.

When the actual testing began, each animal received 10 trials daily of a randomly determined frequency until all 13 frequencies and a control of no sound had been tested twice. The control was identical to the other treatments except the sound stimulus was not turned on. The frequencies 6.5, 8.5, and 10 kHz were tested twice with each speaker for comparison between speakers.

One final control was used to insure that the animals were not locating the sound while they were yet in the holding cage. Each day after testing every fox, an additional trial was given where the sound stimulus was turned on and off before the fox entered the starting cage. The rest of the trial was identical to the regular trials.

RESULTS

The data for the entire testing period are presented in Appendices A and B. For the statistical analyses a response is defined as the correctness of choice made by a fox.

χ^2 goodness of fit tests indicate the foxes responded randomly to both the daily control trials ($P > 0.70$) and to the replicated control test ($P > 0.80$). Therefore, the test situation allows making the assumption that a better than random response may be attributed to the foxes locating the sound source.

The speaker used at 6.5 kHz was randomly determined for each fox since a Mann Whitney U test shows that the foxes did not differ in their response to the two speakers at 6.5 kHz ($P > 0.10$). The University speaker was used for all frequencies higher than 6.5 kHz because at 8.5 and 10 kHz the foxes responded significantly more accurately to it than to the JFD speaker ($P < 0.05$). The data used for the final analyses of treatment and animal differences appear in Appendix C.

There are highly significant differences between frequencies ($P < 0.001$) but the foxes do not differ significantly ($P > 0.10$). A Friedman two-way analysis of variance was used to test for frequency and animal differences because the data are skewed toward complete accuracy in response. The mean response of each fox at all of the 13 frequencies is given in Figures 2 and 3 and the mean response of all foxes at all of the 13 frequencies is given in Figure 3.

The following trends are apparent from Figure 4. Starting at 0.3 kHz the foxes show a gradual increase in their response until 3.5 kHz where all foxes reach a peak response. As the frequency increases from 3.5 kHz, the foxes show an average decline in response with slight dips at 8.5 kHz and 18 kHz. Mann Whitney U tests show that the foxes differed significantly in their response at 8.5 kHz and 18 kHz when compared to the next higher frequencies respectively ($P < 0.05$).

Figures 2 and 3 show that the foxes were not identical in their response. Some of the fox X frequency interactions might be attributed to one poor test out of the two tests for each frequency. Examples of this are fox numbers four and six when tested at 2.0 kHz. Fox number four got 5 out of 10 and 10 out of 10 correct responses during the two tests at 2.0 kHz. Fox number six got 5 out of 10 and nine out of 10 correct responses during the same two tests. Foxes seven and nine show a definite increase in response at 34 kHz whereas the rest of the foxes remain unchanged or fall off in their response.

Figure 2.--The mean response in 20 trials for foxes one through five.

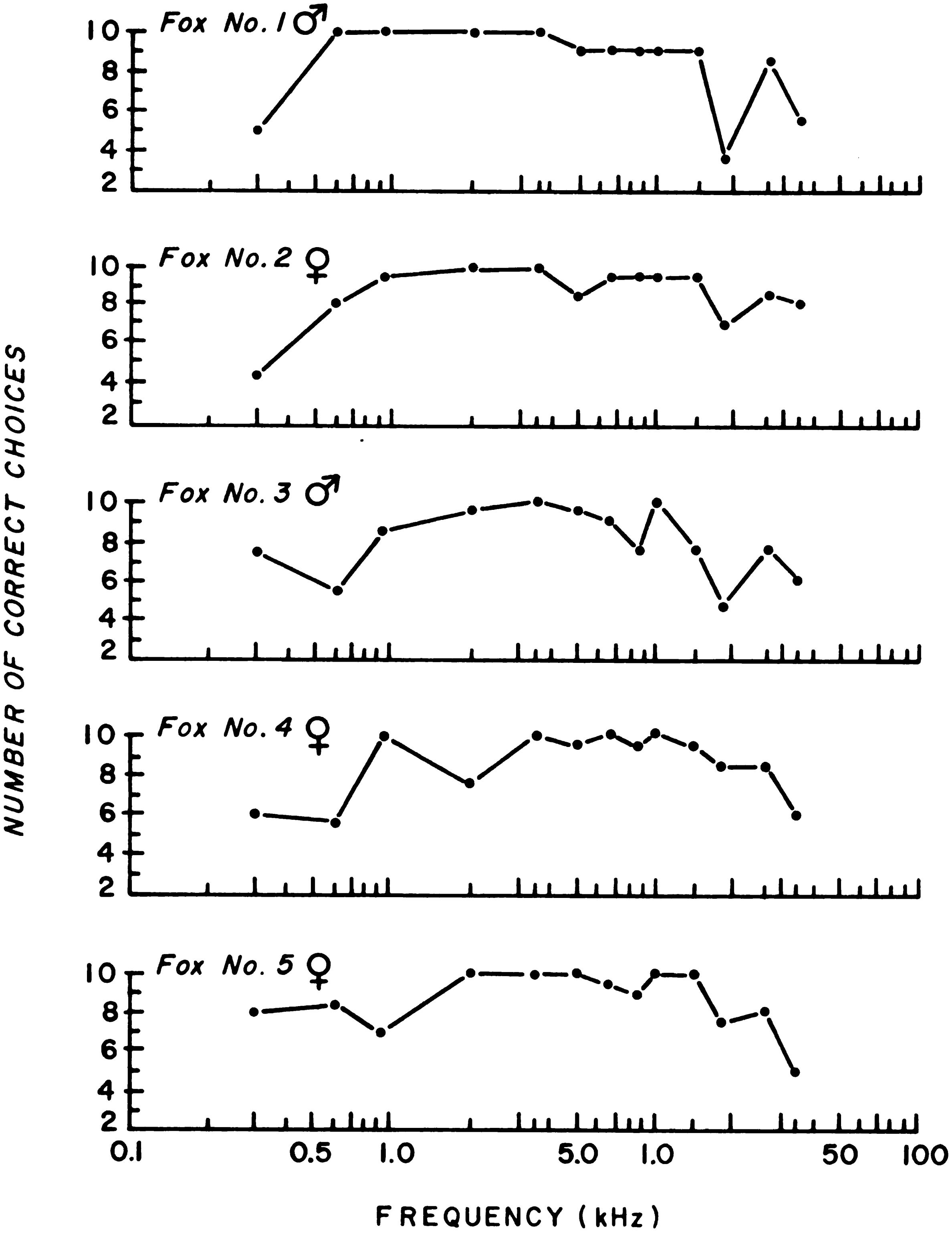

Fox No. 1 ♂
Fox No. 2 ♀
Fox No. 3 ♂
Fox No. 4 ♀
Fox No. 5 ♀
NUMBER OF CORRECT CHOICES
10
8
6
4
2
0.1
0.5
1.0
5.0
1.0
50
100
FREQUENCY (kHz)

Figure 3.--The mean response in 20 trials for foxes six through nine.

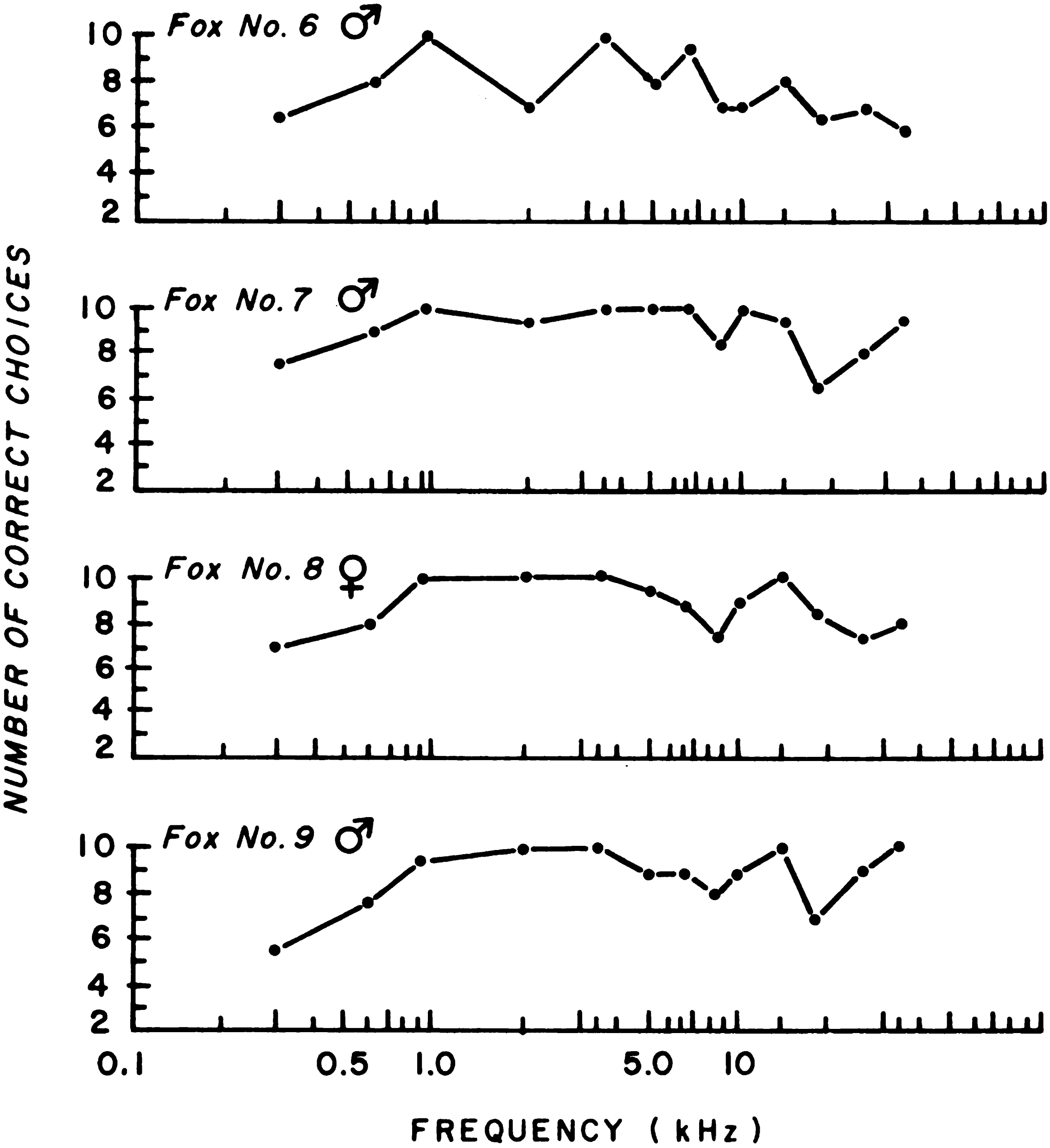
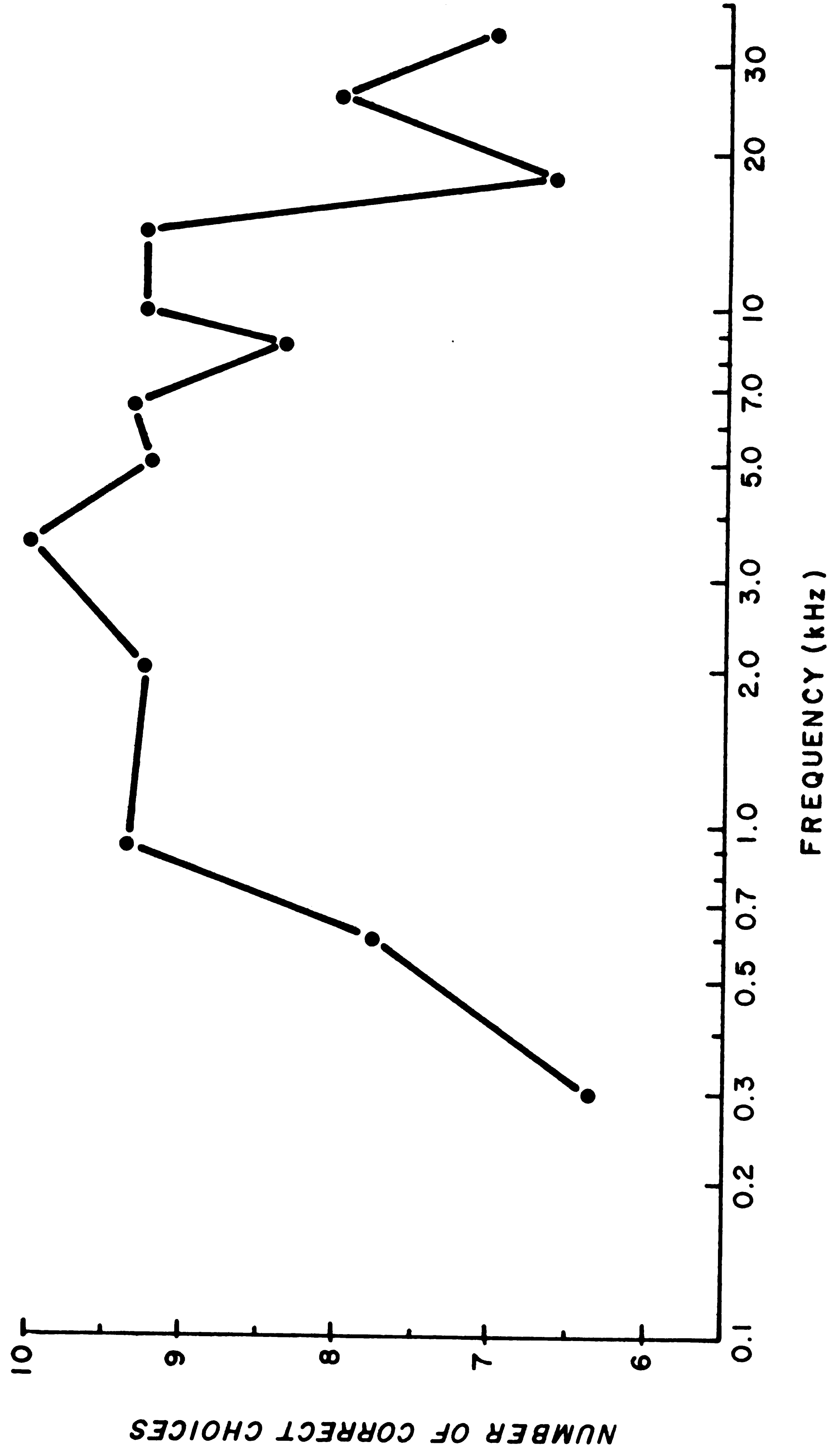

Fox No. 6 ♂
Fox No. 7 ♂
Fox No. 8 ♀
Fox No. 9 ♂
10
8
6
4
2
NUMBER OF CORRECT CHOICES
0.1
0.5
1.0
5.0
10
FREQUENCY (kHz)

Figure 4.--The mean response in 10 trials for all nine foxes.


NUMBER OF CORRECT CHOICES
10
9
8
7
6
FREQUENCY (kHz)
0.1
0.2
0.3
0.5
0.7
1.0
2.0
3.0
5.0
7.0
10
20
30

DISCUSSION

The foxes responded best between 0.9 and 14 kHz with a high response at 3.5 kHz and a low response at 8.5 kHz. If frequencies lower than 8.5 kHz are located by phase difference detection and frequencies higher than 8.5 kHz are located by intensity difference detection, then the low response at 8.5 kHz could be attributed to the two locating mechanisms not overlapping. The tympanic membranes in adult red foxes are approximately four cm apart so phase differences should become difficult to detect above 4.2 kHz and intensity differences should be difficult to detect below 8.4 kHz.

Österholm (1964) reported that a single fox located 700 Hz more accurately than all higher frequencies. The reason his results differ from the results of this study may be because he used a different test situation and because his fox was tested at a younger age.

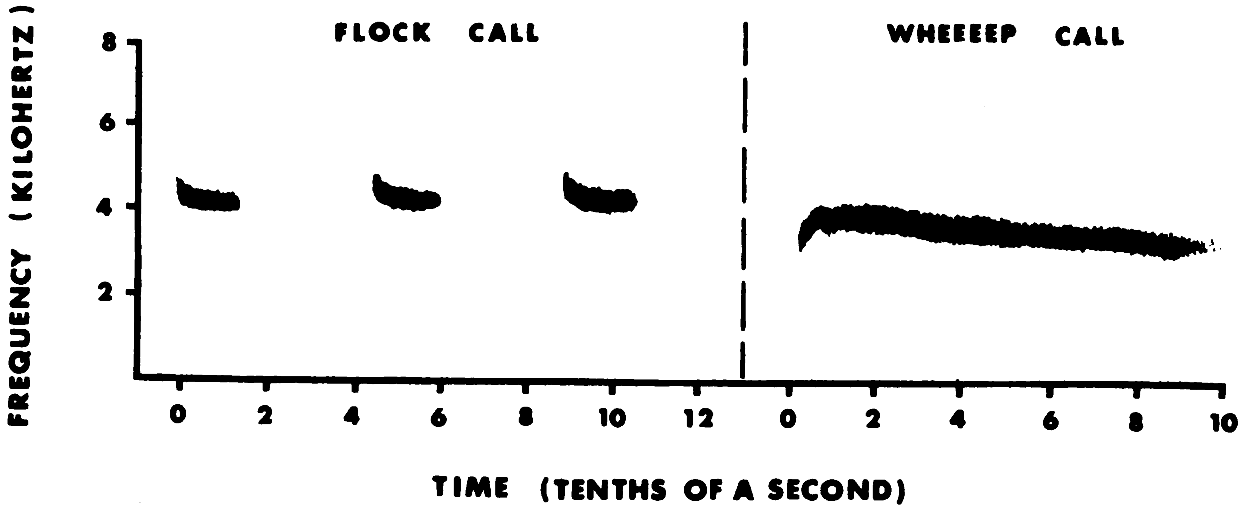
The pinnae might enable foxes to binaurally detect phase differences at frequencies higher than those predicted by the theory. Batteau (1967) contends that the human pinna has a significant role in auditory localization by temporarily delaying the incoming auditory signal as a function of the pinna position relative to the sound source.

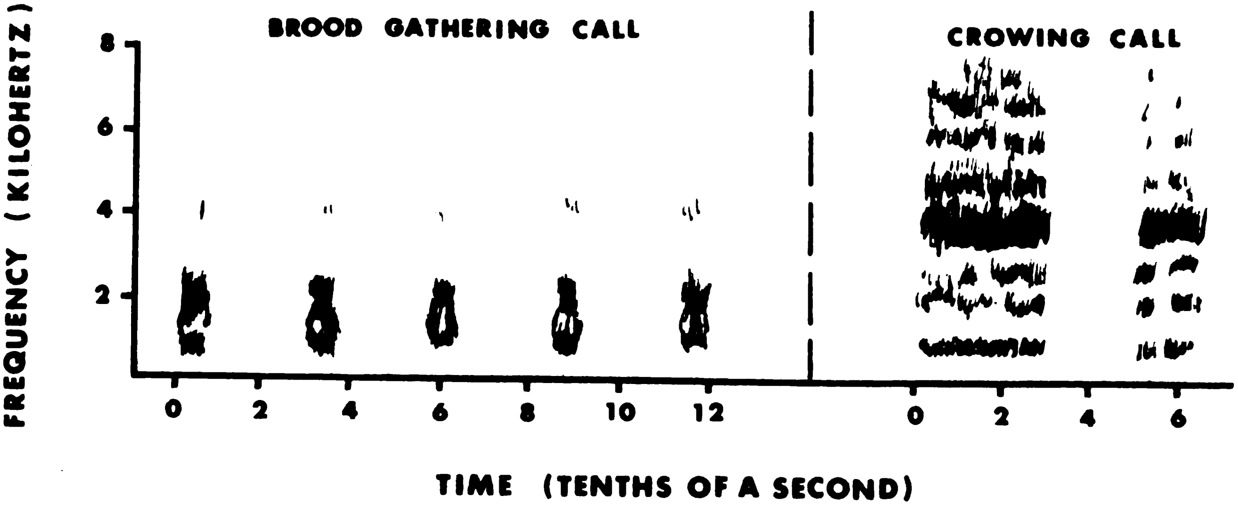
An animal must emit sounds which provide a minimum of locating cues if revealing its position is disadvantageous. This is done by avoiding abrupt discontinuities, hence minimizing binaural detection of differences in time of arrival, and also by using a nearly pure tone minimizing binaural detection of differences in phase and intensity. Examples of such calls are the flock call of ring-necked pheasant chicks (*Phasianus colchicus*) and the wheeeep call (Sheldon, 1967) of a lost woodcock chick (*Philohela minor*) (Figure 5). The flock call is emitted by pheasant chicks under stress and is difficult for humans to locate (Heinz, personal communication). The wheeeep call of woodcock chicks is also difficult for humans to locate (G. A. Ammann, personal communication).

Human beings have more difficulty in locating the frequencies of sound between 2.0 and 5.0 kHz than the immediate higher and lower frequencies (Stevens and Davis, 1938; Marler, 1955). These frequencies are too high to locate by binaurally detecting phase differences and too low to binaurally detect intensity differences. Although a call can be structured to offer a minimum of locating cues, humans and foxes probably do not have the same ability for locating the call. The juvenile woodcock wheeeep call and the juvenile pheasant flock call are examples of calls that foxes might locate better than human

Figure 5.--Calls having the characteristics for being difficult to locate. (Spectrograph of flock call after Heinz and Gysel, in press.)

Figure 6.--Calls having the characteristics for being easy to locate. (Spectrographs after Heinz and Gysel, in press.)


FLOCK CALL
WHEEEEP CALL
FREQUENCY (KILOHERTZ)
8
6
4
2
0
2
4
6
8
10
12
0
2
4
6
8
10
TIME (TENTHS OF A SECOND)


BROOD GATHERING CALL
CROWING CALL
FREQUENCY (KILOHERTZ)
8
6
4
2
0
2
4
6
8
10
12
0
2
4
6
TIME (TENTHS OF A SECOND)

beings. Both of these calls are pitched around the frequencies that foxes appear to locate the best and humans experience some difficulty in locating.

To be readily located, a vocalization should contain a wide range of frequencies and abrupt discontinuities providing for binaural detection of differences in both phase and intensity as well as detection of binaural time differences. The brood gathering call of the hen and the crowing call of the male ring-necked pheasant are examples of vocalizations having these characteristics and are shown in Figure 6 for comparison to the calls of Figure 5.

Future research should determine which sound signals, and their properties, red foxes respond to in their predatory habits. Many of the prey species taken by red foxes use sound signals that are pitched within the frequencies that foxes readily locate; however, the young of some rodents can emit high frequency calls, ranging from 17 to 80 kHz, which would be difficult for foxes to locate (Hart and King, 1966; Noirot, 1966; Noirot, 1968; and Noirot and Pye, 1969). It would be interesting to determine which property of a sound signal elicits the response from a fox. Finally, it is yet to be determined how much more readily foxes locate discontinuous sounds, of varying intensity and frequency, than pure-toned sounds. Such a study could be done in this type of test apparatus using different combinations of frequency, intensity, and discontinuities in the sound.

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APPENDICES

APPENDIX A.--Number of correct responses out of 10 trials on each of two replications. [These data represent the entire testing period.]

Fox	Frequency (kHz)																Control
	0.3	0.6	0.9	2.0	3.5	5.0	6.5	8.5	10	6.5	8.5	10	14	18	26	34	
1	5	10	10	10	10	9	10	6	10	8	9	9	8	3	9	7	5
	5	10	10	10	10	9	10	4	10	10	9	9	10	4	8	4	3
2	4	6	9	10	10	7	9	8	10	10	10	10	9	6	9	9	3
	5	10	10	10	10	10	10	9	7	10	9	10	10	8	8	7	5
3	7	5	7	9	10	9	8	6	8	9	7	10	9	4	7	6	5
	8	6	10	10	10	10	10	6	9	10	8	10	6	5	8	6	8
4	6	4	10	5	10	9	10	10	9	10	9	10	10	9	9	6	3
	6	7	10	10	10	10	10	8	5	10	10	10	9	8	8	6	5
5	8	9	8	10	10	10	10	9	10	10	9	10	10	8	8	3	6
	8	8	6	10	10	10	9	6	8	8	9	10	10	7	8	7	3
6	7	8	10	5	10	7	10	7	7	9	8	7	8	7	8	7	4
	6	8	10	9	10	9	9	6	10	9	6	7	9	6	6	5	5
7	7	10	10	9	10	10	10	8	9	10	9	10	9	5	6	10	5
	8	8	10	10	10	10	10	7	10	10	8	10	10	8	10	9	7
8	7	10	10	10	10	10	8	7	8	9	6	10	10	8	8	7	6
	7	6	10	10	10	9	9	7	9	9	9	8	10	9	7	9	5
9	6	7	9	10	10	8	10	8	7	9	8	10	10	8	8	10	3
	5	8	10	10	10	10	10	8	6	9	8	8	10	6	10	10	2
	← JFD Speaker →									← University Speaker →							

APPENDIX B.--Number of correct responses out of 32 trials of the daily control treatment.

Fox	Correct Response
1	19
2	17
3	15
4	14
5	23
6	15
7	18
8	16
9	13

APPENDIX C.--Total number of correct responses for the two replications. [These data were used in the final analyses of frequency and animal differences.]

Fox	Frequency (kHz)												
	0.3	0.6	0.9	2.0	3.5	5.0	6.5	8.5	10	14	18	26	34
1	10	20	20	20	20	18	18	18	18	18	7	17	11
2	9	16	19	20	20	17	19	19	19	19	14	17	16
3	15	11	17	19	20	19	18	15	20	15	9	15	12
4	12	11	20	15	20	19	20	19	20	19	17	17	12
5	16	17	14	20	20	20	19	18	20	20	15	16	10
6	13	16	20	14	20	16	19	14	14	17	13	14	12
7	15	18	20	19	20	20	20	17	20	19	13	16	19
8	14	16	20	20	20	19	18	15	18	20	17	15	16
9	11	15	19	20	20	18	18	16	18	20	14	18	20
Totals	115	140	169	167	180	166	169	151	167	167	119	145	128

← JFD Speaker → ← University Speaker →