THE UPPER FREQUENCY LIMITS OF HEARING IN THE EUROPEAN STARLING

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The upper limit of hearing (ultrasonic limit) has been determined with reasonable accuracy for only fourteen species of birds; in general, it lies between 12,000 and 20,000 cycles per second (Schwartzkopff, 1955*a*, 1955*b*; 1956; Frings and Slocum, 1958). Schwartzkopff (1955*a*) alone, using electrophysiological methods, has reported responses of the ear above 20,000 c.p.s. It would seem fair to conclude, therefore, that the hearing ranges for birds do not generally extend to higher frequencies than those for man. The frequencies of greatest sensitivity seem, as for man, to be from about 1000 to 5000 c.p.s. The audiograms of the very few species of birds that have been studied seem to rise more steeply above 5000 to 6000 c.p.s. than does the audiogram of man (Schwartzkopff, 1949, 1952; Heise, 1953; Schleidt and Schleidt, 1958). As Schwartzkopff (1957) has pointed out, however, the data necessary for secure generalizations about hearing in birds remain to be gathered.

The present paper reports information on the upper limit of hearing for the European Starling (*Sturnus vulgaris*). The ultrasonic limit for this bird has been reported by Brand and Kellogg (1939) to be about 15,000 c.p.s. and by Trainer (MS, thesis Cornell Univ.) to be about 10,000 c.p.s. The last figure is almost certainly too low and may have resulted from the nature of the sound system used. The results here presented are a contribution to this neglected field of avian physiology. They may have further interest because of the appearance of a phenomenon not previously noted in tests on hearing in birds. These studies were made while the authors were at the Pennsylvania State University.

MATERIALS AND METHODS

The adult Starlings used in these experiments (14 males, 9 females) were captured in barns in Pennsylvania between September of 1953 and March of 1954 and kept in captivity for from 4 to 10 months before the experiments began. During that time they became adapted to caged life but were seldom handled. A number of foods recommended in the literature were tried, until we found that water and dog biscuit (Milk Bone, Tiny Bits) alone kept the birds healthy and active. The birds were held inside a building under artificial conditions of heat and light. The hours of light and darkness corresponded with those of the outside. In colder months the temperature remained at approximately 16° C.; in warmer months it followed the outside.

The birds were trained and tested in a cage (36 × 18 × 24 cm.) built over an electric grid floor, with back and roof of acoustic board. The ends were electric grids, constantly charged. The front had a window of glass (23 × 18 cm.) set in a plywood and acoustic board frame. The roof was attached with adhesive tape, permitting easy removal for servicing. A perch 9 cm. above the floor was supplied with two wires for shocking. An inductorium, producing sufficient voltage to make the bird jump, activated either the floor grid or the perch wires through a switch.

"Pure" tones of known frequencies and sound pressures were produced by a Hewlett-Packard Model 200 AB audio-oscillator driving an Altec Model 633A microphone used as a loudspeaker. A switch in the line was used to turn the sound on and off. The experimental cage was enclosed in a small anechoic chamber, with the microphone 4 cm. from the end of the testing cage (fig. 1). The usual position of the birds on the floor of the cage was about 20 cm. from the speaker; the perch was about 30 cm. from the

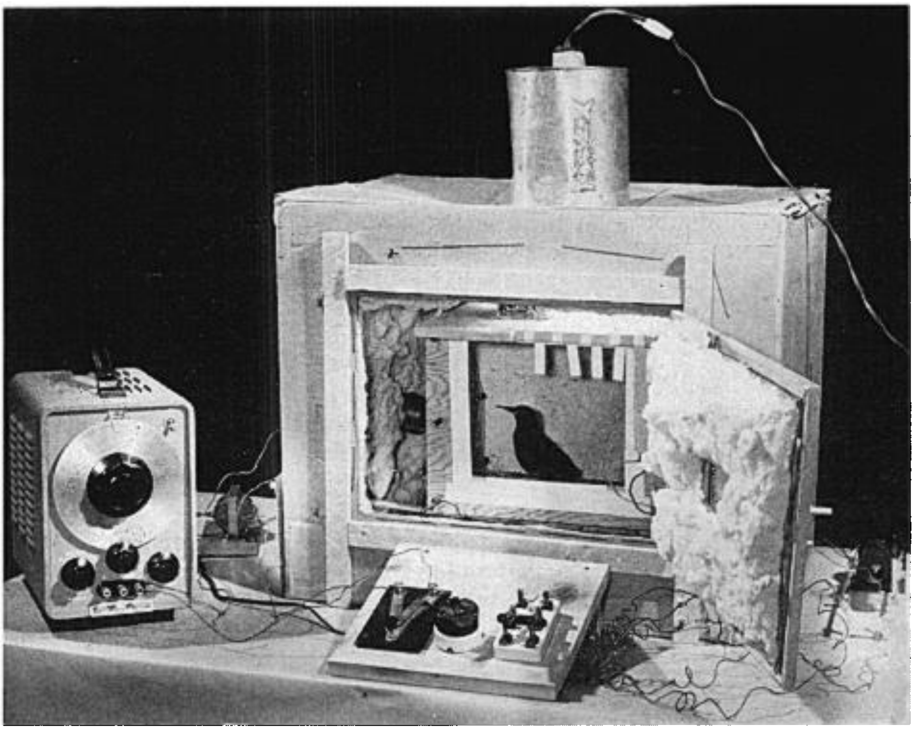

Fig. 1. Experimental set-up used for training and testing Starlings.

speaker. The birds could not see the experimenter's hands on the switches, so no visual cues were available to them to indicate when the sound was turned on. The frequencies and sound pressures of the sounds used for training and testing are given in table 1. These were determined by E. Ackerman and R. Berger of the Physics Department, using a calibrated system.

Training for the first nine birds began July 11, 1954, and for the remaining 14 at various times between then and October 4. A bird was given 20 trials at each daily training period. A trial consisted of a 5-second exposure to the sound followed by a shock, if the bird failed to respond. The trained response was jumping from a resting position on the floor to the perch, or vice versa, when the sound was turned on. If the bird responded before the shock, the reaction was considered positive. If it did not

TABLE 1

INTENSITIES IN DECIBELS (*re* 0.0002 DYNES/CM.^{2}) FOR VARIOUS FREQUENCIES OF SOUND USED IN TRAINING AND TESTING STARLINGS

Frequency (cycles/sec.)	Sound pressure (decibels)	Frequency (cycles/sec.)	Sound pressure (decibels)
7000	113 ± 5	15,000	106 ± 5
8000	112 ± 5	19,000	96 ± 5
11,000	103 ± 5	20,000	97 ± 5
12,000	114 ± 5	25,000	120 ± 5
13,000	115 ± 5	30,000	112 ± 5
14,000	113 ± 5	35,000	103 ± 5

respond until shocked, the reaction was considered negative. The frequencies used in training were selected at random between 7000 and 14,000 c.p.s. Times between tests were varied so that the birds could not learn to respond at set intervals. The birds were considered to be trained when they responded positively in more than 10 out of 20 trials.

When the Starlings responded regularly to the sound, they were tested for their ultrasonic limit. A bird was first exposed to the frequencies used for training and then to frequencies above 14,000 c.p.s. until it no longer responded. Tests were also made by starting at frequencies above the highest one eliciting positive responses and progressively using lower frequencies. The total number of tests for the 23 birds was 16,180.

There was sometimes a click when the switch was closed too quickly. To eliminate possible response to this sound, a series of clicks without shocks was occasionally produced.

RESULTS

Noise in the room or even in an adjoining room disturbed the Starlings and interfered with training and testing. This effect was described by Schwartzkopff (1949) for other species. The Starlings appeared alert and less "nervous" in the morning shortly after the lights were turned on and were usually tested then.

The birds learned at a satisfactory rate and were good experimental subjects. Once they had learned, they retained the pattern for several weeks without further training. When testing was halted for 14 weeks and then resumed, six birds out of seven responded positively within six days.

There were no significant differences in rate of learning between the sexes. Learning time varied among individuals from four to 20 days. Trainer (1946) stated that Starlings trained at one frequency did not respond at other frequencies. However, the Starlings in these experiments responded without further training to frequencies outside the range used for training. Apparently, they have the ability to generalize.

The results of the tests for ultrasonic limit are presented in table 2. In July and August, the highest frequencies to which the birds responded were 26,000 to 28,000 c.p.s. In September, the highest frequencies were 23,000 to 25,000 c.p.s. Three additional birds starting in September also responded up to these frequencies. At the beginning of October, the birds responded up to about 20,000 c.p.s., but by the end of the

TABLE 2

NUMBERS OF BIRDS, TESTS, AND POSITIVE REACTIONS AT SOUND FREQUENCY RANGES TESTED

Testing period	No. birds	Total no. tests at each range	Per cent positive reactions				
			7–13 kc.	14–16 kc.	17–20 kc.	21–24 kc.	25–28 kc.
July, 1954	3	9	100	100	89	78	78
Aug. 1–15	5	35	100	100	100	100	89
Aug. 16–31	7	84	100	100	98	90	57
Sept. 1–15	9	84	100	100	87	81	54
Sept. 16–30	9	65	100	100	91	75	20
Oct. 1–15	7	43	100	100	67	0	0
Oct. 16–31	9	59	100	93	25	0	0
Nov. 1–7	9	30	100	97	10	0	0
Feb. 14–28, 1955	7	44	100	98	30	0	0
Mar. 2–31	8	105	100	96	9	0	0
Apr. 1–25	8	134	100	100	1	0	0
May 6–June 16	8	44	100	98	0	0	0
June 20–Aug. 4	8	41	100	98	0	0	0

month they responded only up to 16,000 c.p.s. Four more birds first tested in October responded, likewise, only up to 16,000 c.p.s. Testing was discontinued in early November. In February and March of the next year, when testing was resumed, the ultrasonic limit was 16,000 to 17,000 c.p.s. This remained essentially the same through July. The usual ultrasonic limit for the Starling, therefore, is about 16,000 c.p.s., but it can be higher under some conditions.

DISCUSSION

The results of this study are quite concordant with those of Brand and Kellogg (1939), but both of these differ from the report of Trainer (MS), which sets the limit at 10,000 c.p.s. It seems possible, however, that the sounds he used were of lower sound pressures.

This study shows a puzzling situation: a shifting ultrasonic limit. When responses up to 28,000 c.p.s. were found at the beginning, many precautions were taken to eliminate extraneous cues and careful checks were made on the sound fields. Since later tests were run under identical training and testing conditions, this shifting of the ultrasonic limit is almost certainly not a result of experimental error.

There have been many studies showing gonadal changes at various times of the year, and the Starling has been much investigated (Marshall, 1961). Thus, the difference in ultrasonic limits might be related to the gonadal cycle. However, the acoustical tests in the second breeding season gave results that did not correspond with those of the preceding year. Dissections of the birds, however, showed the usual gonadal cycle. It seems unlikely, therefore, that the gonadal cycle was responsible for the changes in ultrasonic limit.

Perhaps nervous or pituitary-adrenal reactions to handling might have altered the responsiveness. Starlings do not readily become accustomed to handling. When one bird is handled, it causes the others to become excited by its distress call (Frings and Jumber, 1954). Thus all the birds are exposed to exciting conditions, even if not handled. As the experiments progressed, the birds showed less evidence of being excited by the presence of the investigator. In the early days of testing, therefore, the birds may have been under greater stress than later. It is not clear, however, how excitement could act through neural or hormonal intermediaries to bring about changes in the ultrasonic limit.

Some understanding of the reasons for the shift might be gained if more complete information were available in reported observations. Other workers reported occasional positive responses in other species of birds to frequencies outside the usual range, but they did not state the time of year or physical conditions. A further investigation of these factors should be made. Certainly, these results show that the dates of testing and degree of handling are essential data in reports of work in this field.

SUMMARY

Caged Starlings(*Sturnus vulgaris*) were conditioned to sound by a shock-avoidance technique, using sounds of known frequencies and sound pressures. Most individuals learned to respond to sounds at 7000 to 14,000 c.p.s. after 20 trials on each of 20 consecutive days. There were no significant differences between the sexes. After being trained, the birds were tested at 14,000 to 35,000 c.p.s. to determine the ultrasonic limit. This varied with the time at which the tests were made—during July and August, it was 26,000 to 28,000 c.p.s.; by the end of October, it was 16,000 c.p.s. and remained at that through the following summer. The most probable stable ultrasonic limit seems to be 16,000 c.p.s. The shift in limit during these tests remains unexplained but may be related to gonadal cycles or adaptation to handling.

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