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HOW THE BARN OWL LOCATES PREY BY HEARING

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It has long been known that the ears of many species of owls are asymmetrical, usually one ear opening above and the other below the horizontal plane. Several investigators, intrigued by this asymmetry, have suggested the possibility of its being associated in some way with the ability of owls to locate prey. As indicated by Dice (1945), the vision of owls is inadequate for seeing mice moving in the leaf litter of a heavily-shaded forest floor when the nights are cloudy and moonless. Since many such nights normally occur during the year, it seems probable that owls, to survive, must hunt their prey by still another means, which may be based on hearing, perhaps associated in some way with the asymmetry of the ear openings.

To determine whether hearing is involved, I tried the following experiment on a Barn Owl *(Tyto alba)*. At the Laboratory of Ornithology, Cornell University, I constructed a light-tight building (floor, 12 by 42 feet; height, 6 to 8 feet) with a perch at each end, spread dry leaves over the floor, and introduced an owl. Turning out the lights to achieve total darkness, I put a mouse on the floor where it rustled the leaves whenever it moved. This experiment, done many hundreds of times during a period of four years, showed that a Barn Owl is capable of locating and striking a mouse in total darkness with an accuracy of at least one degree in both the vertical and horizontal planes.

The figure of "one degree" is only approximate and I do not have space here to discuss the various conditions and assumptions on which it is based. More data will be needed before I can state confidently the exact degree of accuracy of a Barn Owl. I can only say that I have made every effort to disprove what seems to be truly incredible accuracy and I now have sufficient data to suggest that the accuracy is much greater than one degree — on the order of a few minutes of arc.

Proof That Sounds Alone Are Sufficient

The Barn Owl need only hear the sound of a mouse rustling in leaves in order to locate and strike the animal. This fact I determined in the following way. A mouse-sized wad of paper was tied to a thread, thrown into the leaves on the floor of the room which was in total darkness, and dragged through them. The owl immediately caught the wad of paper. Because the lights were out, the owl could not use vision. Because the paper had no heat above that of its surroundings, the bird could not use infrared sensitivity. Because the paper had no mouse-like odor, the owl could not use a sense of smell.

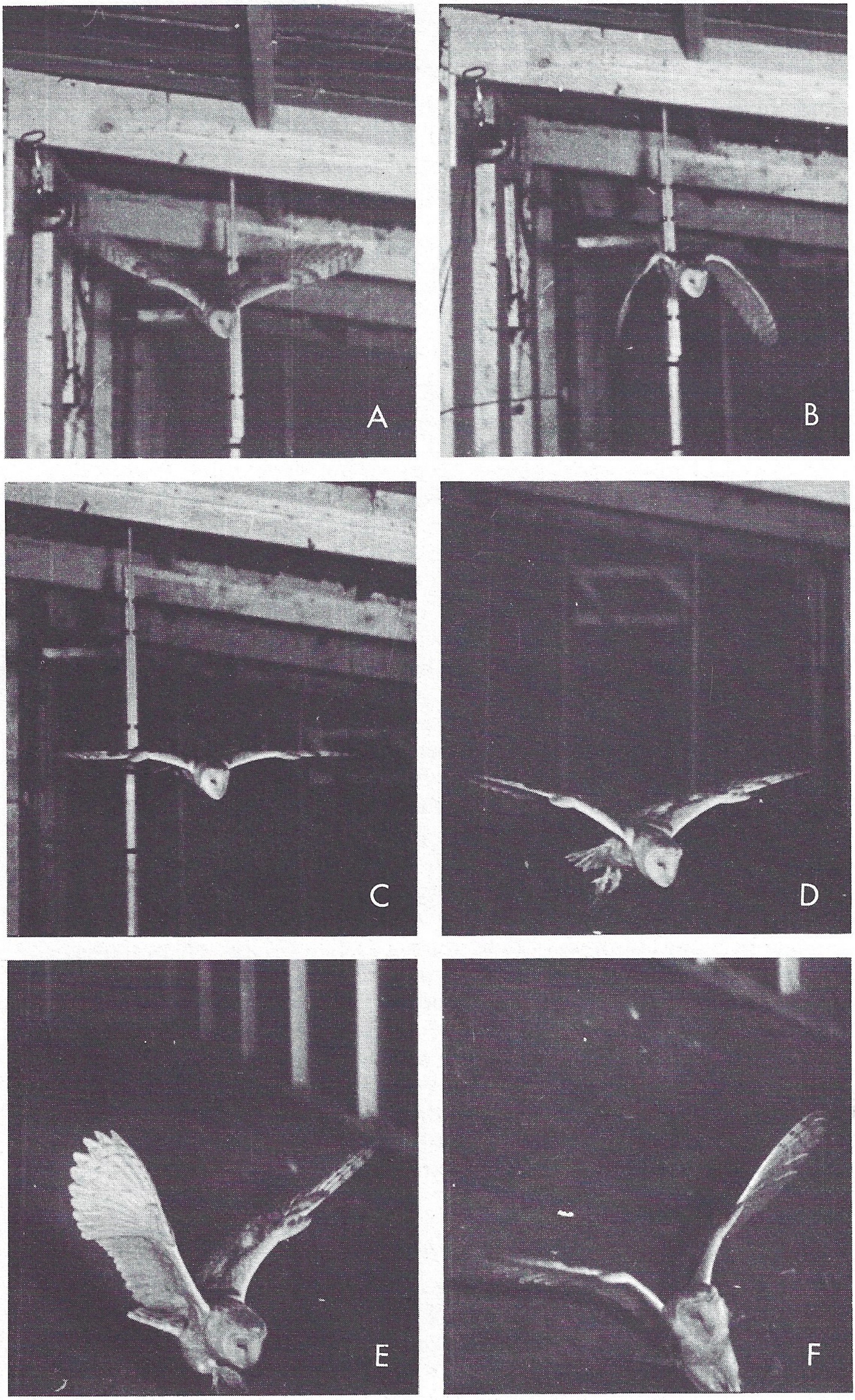

Figure 1. Barn Owl striking at a mouse in light. Leaving the perch, the bird takes one stroke with its wings (B) and then glides toward the mouse (C,D). Just before striking, it raises its wings and brings its feet forward (E). At the moment of impact its eyes are closed (F).

How then did the owl locate its prey? There are two possibilities: 1. Echolocation (the technique of producing sounds and locating objects by means of the echoes from them). 2. Homing on the source of the sound. Curtis (1952) was unable to detect that Barn Owls have any ability to echolocate. As further evidence against echolocation, I noted that Barn Owls regularly struck at a loudspeaker which broadcast mouse-like sounds while buried under two inches of leaves. This leaves the second possibility, namely, that the owl locates its prey by the sounds made by the prey.

Dependence of Owl on High Frequencies

In attempting to prove that sounds made by the prey are used by the owl, I wanted to be sure at the outset that the owl did not receive addiional information after leaving its perch — in other words, that the owl could not make corrections by using sounds heard during flight. Consequently, I buried in the leaves a loudspeaker which broadcast a recording of leaf-rustles. A switch on the owl's perch turned off this loudspeaker when the owl flew. Responding to the broadcast, the owl located its source as it did the wad of paper described above. When I filtered out frequencies above 8,500 cycles per second (the highest audible octave for humans), the Barn Owl's angular accuracy in locating the sound source was only about five to seven degrees in both the vertical and horizontal planes. When all frequencies above 5,000 cycles per second were removed, the owl refused to attempt to strike. This showed that the Barn Owl's accuracy in locating a sound source depends upon the presence of high frequencies.

Behavioral Differences Between Strikes in Light and Darkness

I photographed the owl flying at mice in the light. Then, by aiming the camera with a sniperscope (a device for transforming invisible infrared light into visible light) and taking motion pictures on infrared sensitive film, I photographed the flight of a Barn Owl in "total visible darkness." When I compared these two films, some extremely significant differences were noted.

Let us first look at the flight of an owl in the light (Figure 1). When the owl first saw or heard the mouse, it turned its head to face the mouse. The bird then crouched down and leaned forward. It pushed off from the perch while taking one stroke with its wings and then glided towards the mouse without further wing flapping. Its feet were held well back. Just before striking, it raised its wings, brought its feet forward, and threw its head back. At this point it presented the appearance of a projectile with its claws as the tip of the projectile. At the moment of impact its eye were closed. On long glides, the owl sometimes accelerated just before impact by means of a single hard stroke with its wings.

The same owl, striking in the darkness (Figure 2), performed somewhat differently. When the mouse first rustled the leaves, the owl turned its head towards the mouse exactly as it did when it could see the mouse. Once the owl faced the mouse, it had to hear at least one additional sound before striking. It again leaned forward and flew. However, this time it did not glide smoothly but, instead, flapped its wings quite violently and continuously all the way to the mouse and, with each stroke, its feet swung back and forth beneath it like a pendulum. When it was just over the mouse, it again brought its feet way forward and threw its head back, thus bringing its widely spread talons into the same path that its head was taking a moment before.

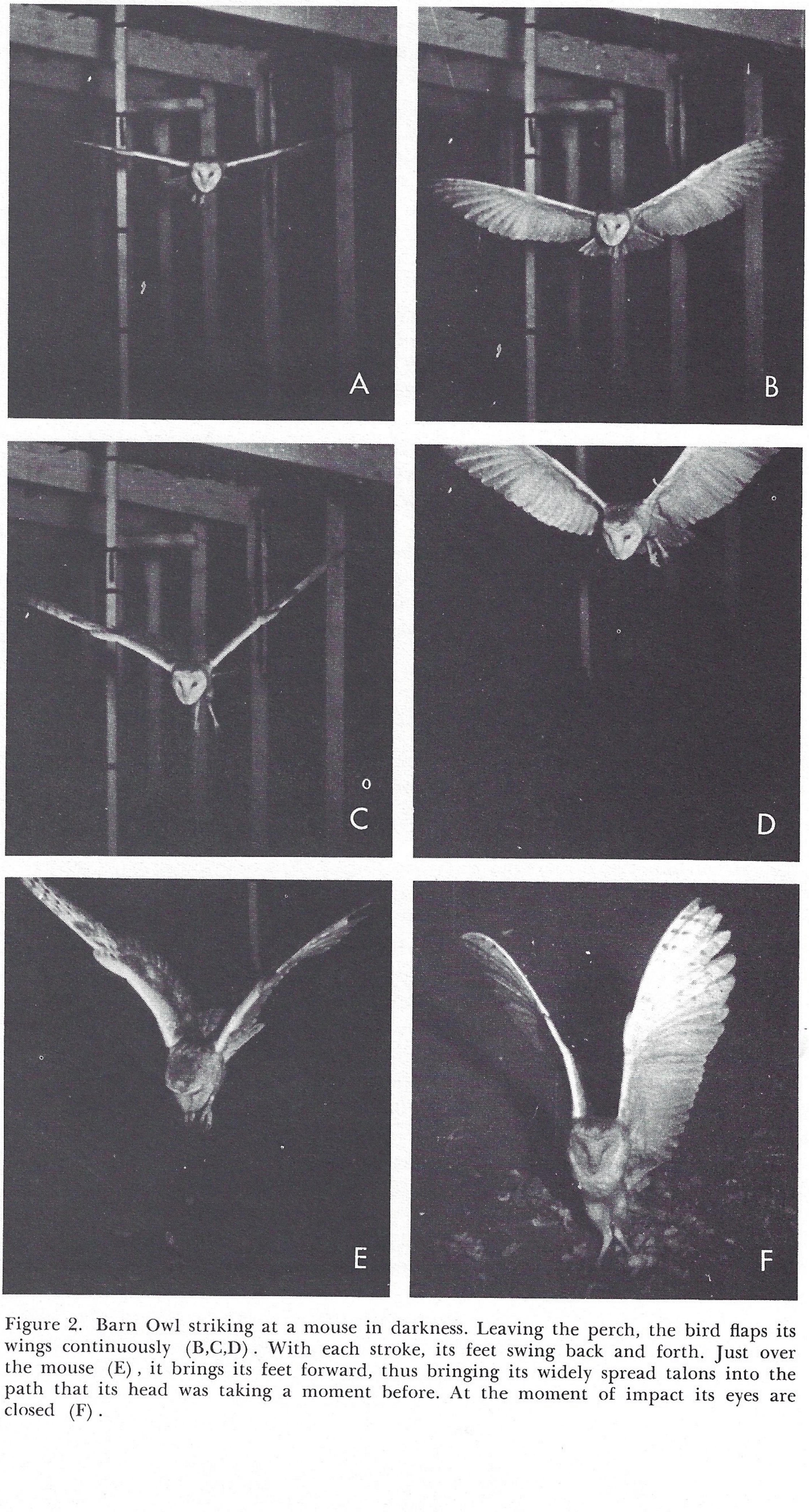

Figure 2. Barn Owl striking at a mouse in darkness. Leaving the perch, the bird flaps its wings continuously (B,C,D). With each stroke, its feet swing back and forth. Just over the mouse (E), it brings its feet forward, thus bringing its widely spread talons into the path that its head was taking a moment before. At the moment of impact its eyes are closed (F).

Avoiding Correction for Parallax

Since the owl makes the calculation of the position of the sound with its ears and yet must strike it with its feet, it should have to make a correction for parallax. The owl's accuracy is sufficient to warrant such a correction — particularly at short distances. The owl neatly avoids having to make this correction by flying at a mouse along the line between ears and mouse and then replacing the path taken by the ears with its widely spread talons at the last moment.

Maximizing the Strike Pattern

The owl also maximizes the chances of getting a talon into a mouse by maximizing the area which its talons cover. Figure 3 shows a constellation of dots made by light shining through eight holes punched in a piece of paper that had been laid over a loudspeaker. The holes were made by the talons of a Barn Owl at the moment of impact. The resultant oval pattern, if bisected perpendicular to the long axis, shows four holes to the left (the talon marks of the left foot) and four holes to the right of the line of bisection (the talon marks of the right foot). The spacing between the holes is quite uniform. This implies that the spacing between the feet is held the same as the spacing between any two talons. The resulting oval, encompassing a mouse-sized area, also maximizes the strike pattern.

To insure getting the maximum number of talons into a mouse, the owl should strike with the long axis of the oval of his strike pattern parallel to the long axis of the mouse, and this is exactly what it does. The strike is so oriented even in total darkness. In other words, the owl can determine the direction in which the mouse is headed and orient its strike accordingly. He makes this calculation acoustically by hearing the mouse move from one place to another.

The Owl Cannot See in Infrared

I include Figure 4 (taken like those preceding it from an infrared motion picture film) as proof that the owl could not see under the conditions that I was using to observe and photograph it. I used sand instead of leaves in this case in order to be able to track the exact point of impact of the owl in relation to the mouse. On the mouse's tail I fastened a leaf to make a sound when the mouse moved. The owl struck at the mouse and missed. This was a good indication that the owl did not see the mouse because never once did I observe a Barn Owl miss a mouse in light though I have watched hundreds of such strikes. The owl actually hit the leaf and knocked it off the mouse's tail. During the next few seconds the mouse moved away and in so doing collided with another leaf. The owl's back was turned. The bird whirled to face the sound but the mouse had then cleared the leaf and was running noiselessly on sand. The owl now faced the mouse directly from a distance of a few inches (Figure 4C) but could not see or hear it, as is evidenced by the fact that it did not strike. The mouse moved on with impunity (Figure 4D). The owl turned away (Figure 4E), searched the few leaves that were on the floor (Figure 4F), and then stopped all searching. Following this, I turned on the lights and the owl struck the mouse immediately.

Information Available to Owl from Sounds Made by Prey

We have seen something of what the owl can do. The next question is: How does the owl do it? In other words, what information is available to the bird from a complex sound, such as rustling leaves, and how does it use this information to determine the position of the mouse?

Figure 3. Holes made in a piece of paper by the talons of a Barn Owl at the moment of striking.

Because of the peculiar asymmetry of the external ears of the Barn Owl, one might guess that sounds on their way to the eardrums are affected by the external ears. If this were true and one could calculate the effect of the external ears, some clue might be gained as to the means used by an owl in locating the position of a sound source. Since the owl has no control over the sounds which it uses for acoustic location and can never predict their form, we can assume that there are only three types of information which the ears can extract from a sound wave: 1. Component frequencies. 2. Relative time of arrival or phase differences between the sounds at each ear. 3. Relative intensities of sounds in each ear.

Since reflection or refraction from, or by, solid structures, stationary in relation to a sound source, cannot change frequency, the first, frequency changes by the external ear structures, need not be considered. Because the Barn Owl must face the mouse directly before making a final orientation, and because, in that position, differences in time of arrival or phase would be too slight for an owl to appreciate with enough accuracy to explain his minimum angle discrimination, the second, differences in time, is probably useless to an owl in making final fine calculations, though such differences may be of help in initial, rough location. The third possibility — changes in intensity varying with the angle from which the sound is received — seems fruitful.

Three Dimensional Polar Diagrams

The problem is how to get an owl to tell us how loud it hears a sound in each ear when a sound of constant intensity is presented from different angles relative to it. I approached this problem by implanting a microphone in each of the owl's ears and measuring sound intensities at the site of the eardrum while broadcasting sounds of constant intensity from various angles to the owl. When such experiments are performed on other animals, data on intensity variations versus angle of presentation are usually taken only in the horizontal plane. The graphs from such data are called polar diagrams. Barn Owls, however, unlike most animals, are capable of at least equal accuracy of location in the vertical and horizontal planes. Therefore, one must construct polar diagrams in three dimensions by presenting sounds not just from a loudspeaker running on a horizontal, circular track but from a loudspeaker that can broadcast sounds from any point on the surface of a sphere. Without going into either a lengthy description of my procedures, or a detailed examination of the rather complicated graphs which resulted, I will merely mention some of the trends I observed and conclude by presenting a theory to explain how Barn Owls may use these three dimensional, polar-sensitivity patterns to locate a sound source.

Nulls in Relation to Frequency

Perhaps the most striking features of the Barn Owl's polar-sensitivity plots are the sudden drops in intensity which occur over narrow angles as one gets within about one octave of the owl's high frequency limit of hearing. Such sudden drops are called "nulls." Rough tests in which I implanted electrodes on each inner ear and recorded the cochlear microphonic response of the Barn Owl showed that the upper frequency limit of hearing is about 20,000 cycles per second. At about 5,000 cycles per second each ear has a broad region of maximum sensitivity directed forward with the sensitivity falling off gradually as a sound is directed at either side of the head. As the frequency is raised the region of maximum sensitivity becomes narrower and then is divided into two regions by a horizontal, equatorial band of poor sensitivity. At the same frequencies a crescent-shaped region of poor sensitivity, half circling the line of sight on the same side of the head as the ear being tested, begins to appear. By 11,000 cycles per second crescent-shaped and horizontal null regions are very pronounced in each ear and they have moved closer to the line of sight. Any further increase in frequency makes the null regions more extreme. In other words, the rates of cut-off, or the rate of change of intensity versus angle of presentation, are more extreme. As frequency is increased to about 15,000 cycles per second and beyond, a host of additional null regions appear at various angles, scattered about seemingly at random with the crescent-shaped and horizontal nulls still present and moving closer to the line of sight.

Throughout the spectrum of the frequencies audible to the Barn Owl, one area surrounding the line of sight will always receive sounds at maximum intensity. The general trend is for this area of maximum intensity to become smaller and smaller due to the movement towards the line of sight of the bordering null regions. Thus, if the owl adjusted the position of its head to hear all the frequencies in a complex sound at maximum intensity, either simultaneously or in sequence, it might get the following results: Let us assume for the sake of simplicity that the owl is listening to one frequency and then another. At a frequency of 5,000 cycles per second, it could make a rough and rather hazy location of the sound by turning the head to receive a maximum intensity in both ears. Should the owl then switch its concentration to some higher frequency and maximize its reception by adjusting the head position, the owl would improve its previous location of the sound source, since higher frequencies have narrower regions of maximum sensitivity due to the impingement of the bordering null regions. The owl could continue to concentrate on ever higher frequencies and further refine its location of the sound source with each new frequency by continuing to orient its head to hear equal and maximum loudness in each ear. By the time the limit of its hearing range is reached, the owl would be confined to listening in sufficiently small regions of maximum sensitivity bounded by sufficiently abrupt cut-offs to give it a theoretical minimum angle of sound location of a fraction of one degree.

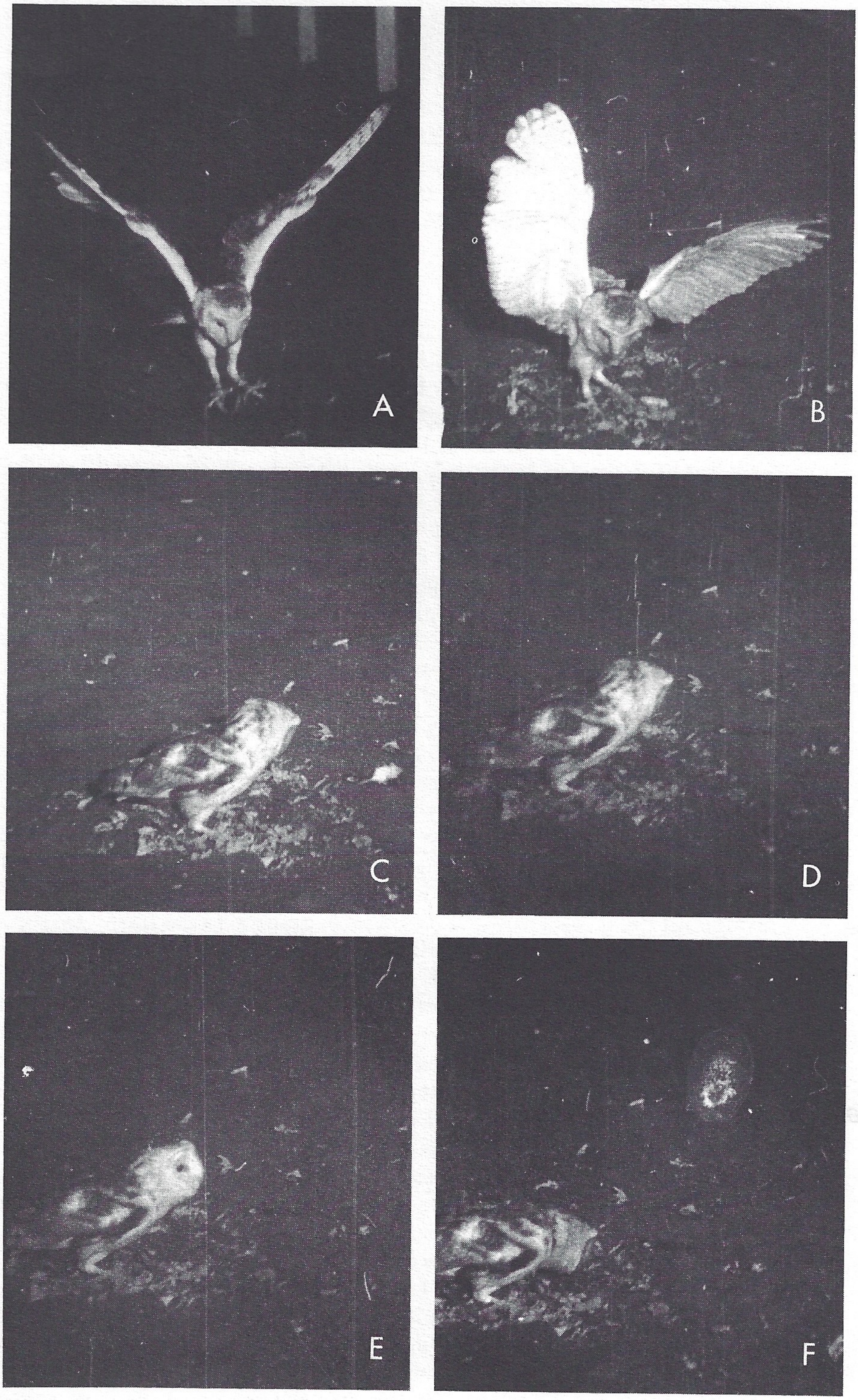

Figure 4. A Barn Owl, striking at a mouse in darkness, fails to see it. Just before striking, the bird spreads its talons (A) to cover as wide an area as possible, but misses the mouse (B). The mouse moves away (C,D,E,F) unseen or unheard by the bird, which finally stops searching.

The technique I have described would also work if the owl moved the head to receive all frequencies at once at the highest intensity in each ear. One might imagine that from the owl's "point of view" it would be moving the head in order to hear with equal loudness in each ear the most "hi-fi" reception possible. Using either technique, simultaneous or sequential treatment of a complex sound, the only position in which the owl could hold the head in the end would be within a fraction of a degree of facing the sound directly.

Further Considerations

There are two important, additional aspects of the polar sensitivity plots which I obtained: 1. Though at first glance all features of polar diagrams at any one frequency appear to be mirror images for the left and right ears, all features in the right ear occur about 10 to 15 degrees higher than their mirror image complements for the left ear. This is undoubtedly linked with the asymmetry of the ears. 2. Since crescent-shaped nulls near the line of sight are semicircular and do not surround the line of sight in either ear and because of the vertical asymmetry of polar patterns just mentioned, a sound, which is moved away from the line of sight while the head is stationary, will decrease with extreme rapidity in one ear while it decreases with extreme slowness or even increases in the other ear.

Thus: 1. Differences due to incorrect orientation of the head are amplified by differential reception in the two ears when the owl tries to match intensities in the two ears. 2. One ear is available (i.e., always available in a region of high sensitivity) to monitor the other ear when its signal at any given frequency is disappearing as the sound is directed at a null region.

Theory

My theory, then, puts only one demand on the owl, namely, that it orient the head in such a way as to hear all frequencies, audible to it in a complex sound, at maximum intensity in both ears. When it has achieved such an orientation, it will automatically be facing the source of the sound with a theoretical accuracy of less than one degree.

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