HOW THE COMMON BARN-OWL (Tyto alba)

HUNTS IN DARKNESS BY HEARING

by H. Christian Floyd, Lexington

How do owls find and catch prey in darkness? Their large, frontally oriented eyes suggest keen night vision as a popular explanation. Owls do indeed have excellent night vision. Large pupils and retinas very densely packed with rods (light-sensitive cells) enable them to see in very dim light. The frontal orientation of their eyes gives them binocular vision - and, presumably, the accompanying advantage of depth perception - over a wide field of view. However, it is keen hearing that affords some owls their greatest sensory advantage for nocturnal hunting.

In experiments with the Common Barn-Owl (Tyto alba), Roger S. Payne, and later Masakazu Konishi and Eric I. Knudsen, demonstrated that this owl can determine the direction of sound produced by potential prey with an accuracy of one or two degrees in both azimuth (angle right or left) and elevation (angle up or down). Payne's observations showed as well how the barn-owl makes full use of auditory information in performing a strike. Konishi and Knudsen identified precisely the hearing mechanisms that permit such accuracy.

In this article, I will attempt to summarize and integrate the findings of these researchers as reported by Payne in The Journal of Experimental Biology and by Knudsen in Scientific American.

Location of prey by hearing alone.

Even before the work of these researchers, naturalists had evidence that owls must sometimes depend upon a sense other than vision in order to hunt. Calculations had shown that natural light levels must often be too low for an owl to see its prey, and rodents are often invisible targets for reasons other than lighting, e.g., the cover of snow or grass over their pathways. However, the capability of an owl to locate and strike prey in total darkness was first rigorously demonstrated in 1958 by R. Payne and W. H. Drury in researches begun at the Massachusetts Audubon Society in Lincoln.

The demonstration was performed in a light-tight room measuring twenty-five by twenty feet, with a seven-foot-high perch at each end and a two-inch layer of dry leaves on the floor. A Common Barn-Owl was introduced into the room and allowed to become familiar with the surroundings over a period of five weeks. The room was dimly lit during this period except for daily twelve-hour periods of total darkness during the fifth week. At the end of this time, the owl was deprived of food for two days. Then, with the room totally darkened, a mouse was released into the leaves. Although the mouse rustled about in the leaves, the owl made no attempt to strike, and the mouse was removed after an hour. Similar results were obtained twenty-four and forty-eight hours later, but on the fourth trial, the owl attempted its first strike and promptly captured the mouse. In each of sixteen trials, the owl made a strike at a mouse at least twelve feet away. It missed in only four of these strikes and then by no more than two inches.

That the owl was not using senses other than hearing to locate its prey was demonstrated by variations on this experiment. When the live mouse was replaced by a mouse-sized wad of paper that was dragged through the leaves, the owl successfully struck that too. This demonstrated that the owl did not depend upon some characteristic of the living mouse such as odor or infrared radiation to locate its target, even assuming it could detect these stimuli. In another variation, the owl's hearing was impaired by placing a small cotton plug in one ear. The owl flew toward the mouse but landed short, showing that it depended upon intact ears for accurate location of the prey. Inasmuch as earlier experiments had demonstrated the inability of the barn-owl to avoid obstacles in darkness by echolocation, the experimenters concluded that the owl was relying on ordinary passive hearing.

Payne continued experimentation with barn-owls over a four-year period in another light-tight room, forty-two feet long and twelve feet wide. To observe the owl's behavior in total darkness, he illuminated the room with an infrared source, watched through an infrared viewer (sniperscope), and photographed experimental sequences with infrared film. Payne argues convincingly that the infrared illumination did not enable the owls to see the prey. As evidence, he exhibits a sequence of infrared photographs including a frame in which an owl directly faces a mouse just eight inches away. He recounts how the owl, which had just missed in an attempted strike, showed no interest in the prey until the lights were turned on, whereupon the owl immediately reacted and caught the mouse.

<u>What the owl determines by hearing with respect to direction and distance</u>.

Exactly what information about prey can the owl determine in darkness from what it hears? In order to fly to and strike a variably placed target, relying solely on hearing, an owl must be able to determine the direction to the sound source. Can the owl also determine the distance to the target by means of hearing only? Common sense suggests that the owl could not successfully conclude a strike without some perception of proximity to the target during the terminal portion of its flight; otherwise, the owl would merely collide with its prey. Given this, an owl's flight behavior in making a strike should reflect how well it perceives the distance remaining to the target. An owl making a successful strike in adequate light, i.e., when it can see, may judge the distance to the target visually. Therefore, comparison of strike behavior under conditions of light and total darkness may suggest how well an owl perceives distance by means of hearing alone. Payne made just such a comparison and his observations are summarized below.

Both in darkness and in light, the owl usually turned to face the mouse directly as soon as the mouse rustled the leaves. Then the owl remained motionless on its perch for several seconds. Just before taking flight, it leaned forward, lowered its head, raised its wings, and, near the point of falling, pushed off from the perch with its feet. From this point on, the manner of flight varied with the light conditions. In light, the owl took a single wingstroke and then glided along a direct path toward the mouse. During the glide, only small balancing and steering motions were made using the wings; the feet remained tucked beneath the tail. In darkness, however, the owl flapped its wings rapidly all along the flight path to the target. The resulting speed of flight was half the speed of the owl's direct glide when it could see, and the feet swung "back and forth like a pendulum," giving the owl "the appearance of being constantly prepared to collide with an object or to land on the ground." Although it could see nothing, the owl constantly faced the area from which the sound had come and kept its eyes open until just before impact.

The movement of the feet just prior to impact was the same in light as in darkness. The owl brought its feet forward to a position just beneath the bill, then pulled its head back and turned "in mid-air, end for end, placing the talons so that they follow[ed] the trajectory formerly taken by the head." The spreading of the talons for the actual strike, however, occurred much sooner in the dark than in the light. The open talons were usually observed in the photographic sequences of strikes in darkness but were never caught on film in the sequences of strikes in light, not even in a photograph showing the feet just six inches away from the mouse.

<u>How does the barn-owl perceive proximity to the target</u>?

Payne's observation that the owl always brings its feet forward just before impact confirms the common-sense deduction that the owl must, even when it cannot see, have some perception of proximity to the mouse. However, the bird's slower, flapping flight in darkness with the feet dangling and the talons opening earlier suggests that its perception of nearness to the target is less certain in the absence of light. Awareness of approach to the target in darkness must be mediated by one or more of the following: by hearing, continually updated by the owl's kinetic sense of how far it has moved since it last heard the mouse; or by perception of closeness to the ground (where owls normally find prey), based on a sensation of increased back-pressure from wingstrokes close to a surface; or by familiarity with the surroundings in combination with a kinetic sense of vertical displacement from the perch.

Payne performed some experiments to test whether the owl could judge the distance to the sound source by auditory means. He stretched a narrow strip of mist net horizontally between two supports. On this surface, the height of which he could vary, he placed a dead mouse with a leaf glued to it. By twitching a long string tied to the mouse, he made the leaf rustle until the owl took flight for a strike. The ability of the owl to judge distance accurately by means of hearing would be proven by a significant number of successful strikes at different heights. In the twelve trials performed, the position of the net was changed for each trial. In six trials, the owl flew past the net and struck the floor within six inches of the correct line of flight. In five trials, the owl alighted on the floor short of the mouse, and in one trial, the owl captured the mouse (perhaps due to an accidental collision with the net). The results were inconclusive.

<u>What is the role of hearing in directional accuracy in strike tests?</u>

To test this, Payne observed the accuracy of the owl's strikes in darkness. The error in the owl's perception of direction to a sound source should be no greater than the directional error of its strikes. Payne's experimental technique for determining the directional error of a strike was to locate the bird's impact point on the floor, measure the displacement of this from the target sound source, and compute from this displacement the azimuth and elevation errors. Azimuth error is the angular error right or left of the true direction to the target. Elevation error is the angular error above or below the true direction and is calculated from the position of the impact point beyond or short of the target. In the calculation of these angular errors, the displacement errors are divided by the strike distance, i.e., the distance to the target from the original position of the owl's head. For example, a one-inch miss of the target over a strike distance of ten feet produces the same angular error as a two-inch displacement over a distance of twenty feet, assuming that the angle of the owl's approach to the floor is the same in both instances. In the calculation of the strike elevation error, the angle of approach to the floor must be considered, because for near-horizontal angles, small errors above or below the true direction to the target result in large errors in impact beyond or short of the target. A familiar analogy is the stretching of our shadows when the sun is low in the sky.

The strike distance is a critical factor in the above calculations. The directional error varies approximately in inverse proportion to the strike distance. Because the

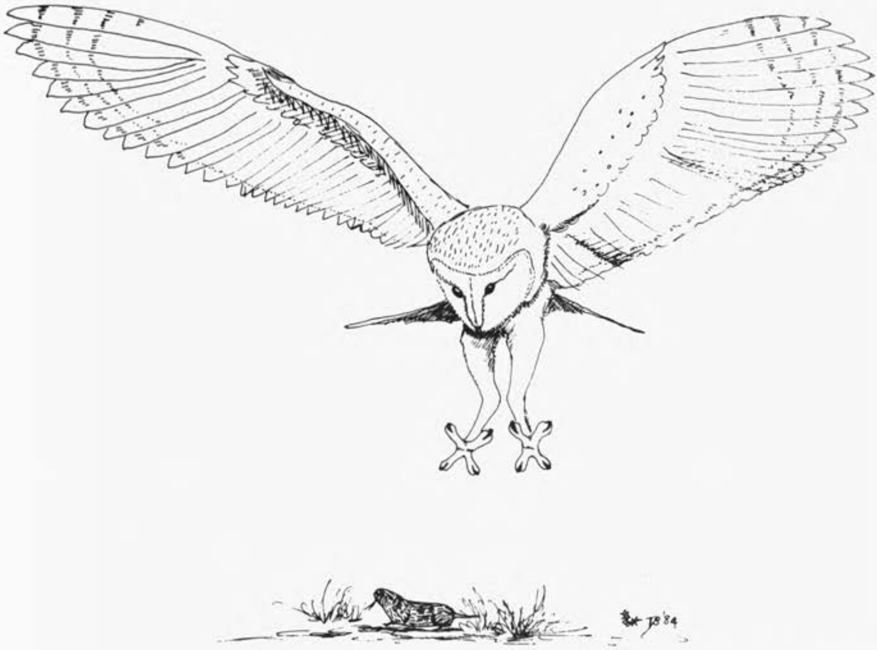

Illustration by Denise Braunhardt

original position of the owl's head when perched was the reference point for the calculation of direction, Payne had to design these directional accuracy experiments to prevent the target sound source from providing the owl with any additional information once the owl takes flight. To compute the mean error for a series of trials, Payne used only the data from strikes in which the owl missed its target and justified doing this "in order to exclude any trials in which the owl may have gained additional information during flight." In any case, as Payne points out, his averages probably overestimate the true error characteristic of the owl's strike. He further found that the owls would not strike at all beyond a distance of twenty-three feet. Instead, they would fly closer, alight on the floor, and listen for another sound from the intended prey.

Payne used two different setups for measuring strike accuracy. In one experiment, the target sound source was a small loudspeaker hidden under a layer of leaves. Recordings of leaf rustlings were played over the loudspeaker to induce the owl to strike. The error of the strike was determined by measuring between the center of the loudspeaker and the center of the owl's talon strike-pattern recorded on a sheet of Plasticene under the leaves in the vicinity of the loudspeaker. For one series of forty-four trials in which the owl missed

23 times, the experimenters reported the mean error of the misses as 2.9 ± 2.0 degrees in azimuth and 2.5 ± 1.6 degrees in elevation. Payne expressed some doubt about the results because of the poor quality of the loudspeaker, particularly at high frequencies. Generally, the owl waited longer to strike at recorded leaf noise. However, as we shall see later in another article, the speaker setup provided information on how the frequency composition of the sound affected the accuracy of the owl's directional perception.

In the other experimental arrangement, the target was a dead mouse with a leaf tied to its body. The mouse was pulled by a thread tied to its tail over sand once every ten seconds for a period of one second. As the owl left the perch, a switch was thrown to signal the experimenter, who instantly stopped pulling on the thread and thus minimized the chance of an additional sound being heard by the owl during its flight. The location of the owl's strike was determined by imprints in the sand. In a series that included more than 200 successful strikes, the mean error of a set of just five misses analyzed was 0.8 ± 0.5 degrees in azimuth and 0.5 ± 0.3 degrees in elevation.

The directional error being measured in the above experiments has two sources: the error in the owl's hearing-based perception of direction to the target and the deviation of its flight path from a straight line toward the target. In total darkness and without additional sounds to guide it, the bird's ability to fly along a straight line to the goal would depend on flight motor skills, sense of direction, and a kinetic sense of deviation from a straight path. Therefore, these tests demonstrated that the Common Barn-Owl has not only a remarkably accurate perception of direction based on hearing alone but also an extraordinary ability to fly a straight line.

Directional accuracy of the barn-owl's hearing measured by head orientation in response to sound.

In Payne's experiments, the barn-owl revealed its perception of direction by means of a complex sequence of motions that contributed their own errors to the measurable result. Might the owl accurately reveal its perceived direction of a sound source by some simpler behavior? In fact, the owl does this in its very first movement in response to a sound from potential prey: it turns to face directly toward the source of the sound. Since the eyes of an owl are fixed in position in its skull, movement of the entire head is necessary to align the eyes in the direction of the prey and also, as we shall see in a second article on this subject, to bring the target into the region of the owl's best auditory reception. We might reasonably expect that a movement so simple yet so essential to the optimal use of the owl's senses should be executed with an accuracy at least as good as that of the strike itself.

On this basis, Konishi and Knudsen investigated the directional accuracy of the Common Barn-Owl's hearing by measuring the head orientation of a perched owl in response to variably placed sounds. The measurements were taken in a totally dark chamber lined with materials to eliminate echoes. The direction faced by the owl was determined precisely by means of signals from a lightweight electromagnetic "search" coil mounted on top of the owl's head. The procedure was as follows. First, a sound was generated from a stationary "zeroing" speaker located directly in front of the owl's perch. This initial sound caused the owl to face precisely the same spot at the start of each test. Then, a sound was generated from a movable "target" speaker, and the direction that the owl turned to face was measured and compared to the actual direction of the target speaker. This speaker was arranged on a semicircular track so that it could be rotated about a horizontal axis and positioned in almost any direction relative to the owl's head but always at the same distance from it. A computer was used to control the position of the target speaker and to record the head movements of the owl. Thus Konishi and Knudsen could conveniently and rapidly perform a large number of precise tests without disturbing the bird unduly.

The results obtained by Konishi and Knudsen in these head-orientation tests agreed with Payne's findings; all three researchers demonstrated that the barn-owl is "capable of locating the source of a sound within a range of one to two degrees in both azimuth and elevation." However, Knudsen describes the barn-owl's accuracy in enlightening comparative terms: "One degree is about the width of a little finger at arm's length. Surprsingly, until the barn-owl was tested, man was the species with the greatest known ability to locate the source of a sound; human beings are about as accurate as the owl in azimuth but are three times worse in elevation. Monkeys and cats, other species with excellent hearing, are about four times worse than owls in locating sounds in the horizontal dimension, the only one in which they have been tested."

Correlation of directional accuracy with talon spread, prey size, and maximum strike distance.

Several factors determine the limits of angular error allowable if an owl is to be successful in catching prey. A rough calculation involving several parameters - the size of the owl's talon spread, the size of the prey, and the distance beyond which the owl will not strike at all but simply fly closer - can be made to determine quantitatively what these limits are.

From photographs and from holes left by the owl's talons in sheets of paper in the target area, Payne found that the owl strikes with the spread talons of its two feet held in a particular pattern. Both feet are rotated outward so that

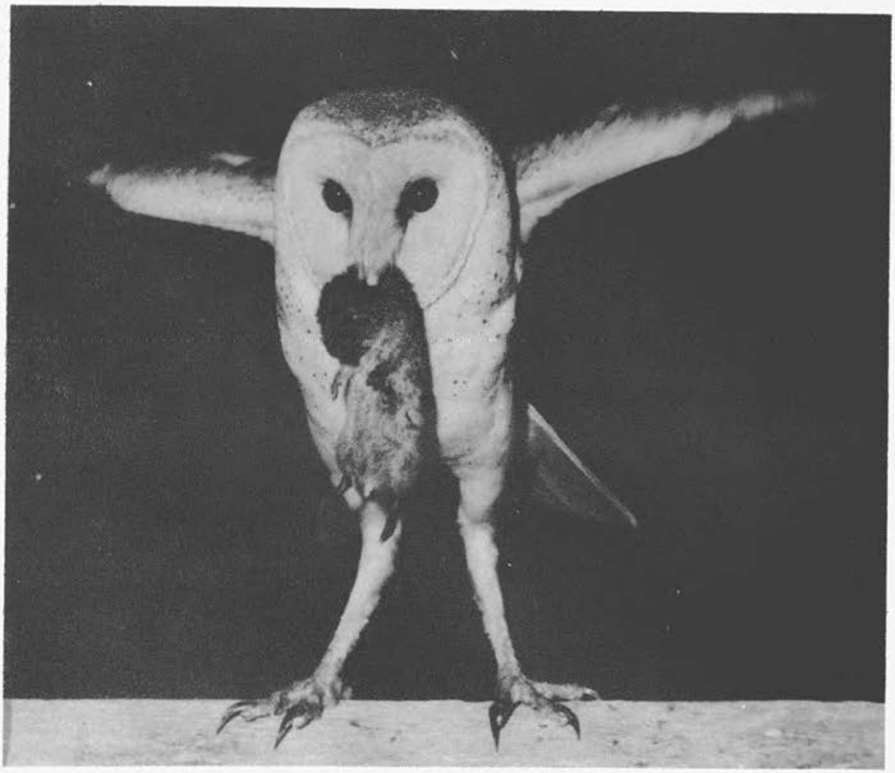

Photo by Hal H. Harrison
Courtesy of MAS

the separation between the two hind toes (halluces) is the same as that between the two inner toes, and the eight talons of the two feet together are spaced at regular intervals around the periphery of an ellipse. This strike pattern measures about six inches from side to side and three inches from front to back. The dimensions of a mouse body are about 3.5 inches by one inch. For the owl to make any contact at all with the body of a mouse, its six-by-three-inch talon strike pattern must intersect the 3.5-by-one-inch mouse. The accuracy required for this depends on the relative orientation between the long axis of the talons' pattern and the long axis of the mouse. Put roughly, the owl's strike pattern approximates a disk 4.5 inches in diameter, and the mouse's body a parallel disk roughly 2.25 inches in diameter. With these approximations, intersection results if the strike displacement perpendicular to the true path is no greater than 3.375 inches. At twenty-three feet, the distance beyond which Payne's owls would not strike, this displacement error results from an angular error of 0.7 degrees, a reasonable value in comparison to the experimentally measured directional errors.

Orientation of the talon strike pattern.

The directional accuracy of the barn-owl's hearing is further revealed in a fascinating manuever that it makes just before impact in a strike, a manuever first described by Payne. As the owl concludes a strike at a moving target, it rotates its body around the line of the strike so as to align the long axis of the talon strike pattern with the direction of movement of the prey, which usually corresponds to the prey's long axis. Payne performed an experiment to establish that the owl was controlling the orientation of its talons in darkness in accordance with a hearing-based perception of motion rather than a perception of prey body orientation based on some other sense.

The target in this experiment was a dead mouse with a leaf glued to its body. Two threads were tied to it so that the body could be pulled either perpendicular to the direction of the owl's strike or parallel to it. The threads were attached in such a way that the mouse would be dragged sideways or tumbling end over end unpredictably. The mouse was dragged only four inches at a time, with a pause of a few seconds before it was pulled back along the same path. This back-and-forth dragging was continued until the owl took flight to strike. In twelve such trials the owl always aligned the long axis of its talon strike pattern parallel to the path of dragging. Specifically, in the six trials in which the dragging path was parallel to the direction of the owl's approach, the owl rotated approximately ninety degrees for the strike; in the six trials with the dragging path perpendicular to the owl's approach, the owl made no detectable rotating maneuver. In some of these trials the mouse was dragged only a distance of two inches. With the owl 140 inches away, this indicates that this bird has the ability to determine the direction of an audible movement over an angle no larger than one degree.

In the orientation of its talons for the strike, the owl exhibits a complex but consistent behavior. The question immediately arises whether such a behavior gives the owl some survival advantage, most likely in this context an increased likelihood of capturing the prey. When the owl can see its prey clearly enough to execute its strike precisely on target, the behavior does seem advantageous, for it results in the owl's completely surrounding prey of mouse size by its talons so that it can grasp the prey securely with one or both feet. However, the advantage offered in a strike in darkness upon prey of uncertain position is not so clear-cut. In fact, the probability of the owl's talon pattern intersecting the body of a stationary mouse is maximized when the long axis of the pattern is <u>perpendicular</u> to the long axis of the mouse. On the other hand, Payne suggests that hitting the mouse with only one or two talons may expose the owl to the danger of being bitten and seriously injured. The parallel strike orientation may achieve the best balance between maximizing the probability of an effective strike and minimizing the chance of injury from a marginal strike. Alternatively, since the mouse may move at the last instant, the probability of making contact may be maximized by aligning the long axis of the pattern with the most likely direction of movement. There seem to be no convincing arguments that the strike orientation behavior gives the owl any advantage at all in darkness.

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