Barn Owl screams when held in hand, showing size of strong beak. Feathers forming facial disk are evident.

Part II

MARKSMAN OF THE DARKNESS

Experiment shows how *Tyto alba* can locate its quarry in the night

By Roger S. Payne and William H. Drury, Jr.

Any bird that sings, if we stop to think about it, should be able to hear its song. Biologists have shown that this is true: not only can a bird hear its own song, but the tones that it hears best are those near the middle range of all the various notes it utters. This seems to be a general avian rule—but, like most rules, it has exceptions, and a notable exception is found in the case of owls. J. Schwartzkopff has shown that the Long-eared Owl (*Asio otus*), for example, can hear about the same tones that humans do: it is, however, most sensitive to tones high above the middle range of its own voice—even above the normal middle tone of most small songbirds' songs.

Why do owls have this strange specialization to best hear notes that are so much higher than their own calls? It seems that there must be some reason, important in the lives of owls, which has made it necessary for them to hear high-pitched sounds.

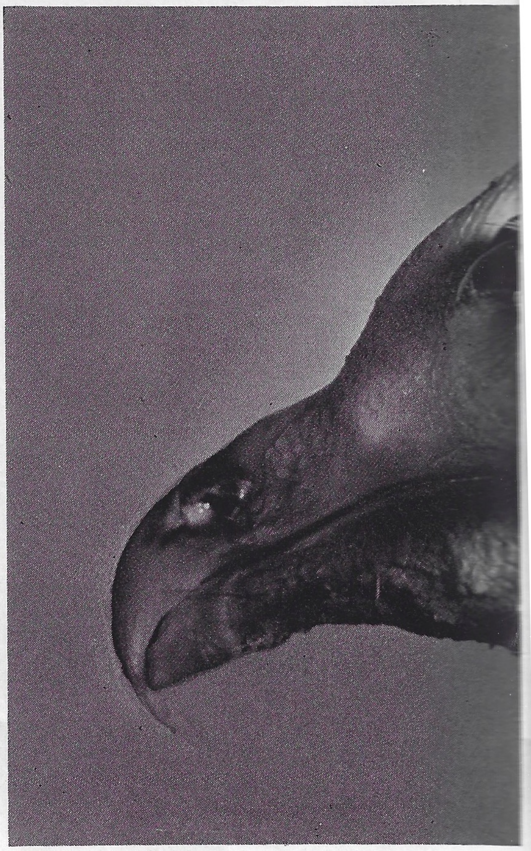
We know, for example, that mice (which are important prey for many owls) squeak at about the same pitch at which owls hear best. Although mice probably do not squeak often enough to allow hunting owls to track them all down this way, they do make rustling and crackling sounds as they move through ground litter, and some of the component frequencies of these sounds are high-pitched. Can it be that owls, hunting in darkness, use their ears to locate mice? When the light is poor, even the best eyes would have difficulty seeing a mouse moving about in the leaves or grass. But what about the ears?

If we examine an owl's ears, we find them quite different from the ears of other birds—for instance, a sparrow's—and with many modifications for sensitive hearing. Starting at the outside of a bird's head and working inward to the middle and inner ear, we find that the structure of these three parts differs from the parallel three-part mammalian structure. In birds, the outer ear is a chamber that ends flush with the surface of the head, without any external, sound-concentrating device, such as the funnel-like external ear of mammals. In the middle ear of birds we do not find three bones (hammer, anvil and stirrup); instead, there is one large bone called the columella. Finally, in place of the spiral, snail-shell-like cochlea of mammals' inner ears, the birds' cochlea is almost straight. Now, how do owl's ears differ from this general avian design?

First, an owl's head is large and wide, so that its ears are set fairly far apart. In the case of the larger owls, this separation means that the time difference between the arrival of sound at one ear, and then the other, of an owl would be greater than in the case of a songbird—perhaps great enough to provide a clue concerning the sound's direction. Second, the ears of many owls are asymmetrical. In some, the size of the opening differs between right and left ears. In others, the external ear cavity is divided into two compartments; one a blind alley, the other going to the eardrum. The blind alley is a different compartment on each side of the head. Owls which have no visible structural differences between their ears, may possibly use flaps of skin in front of their ears to change the effective sound path to each ear and make reception different for the two ears. It seems from theory (which we will not discuss here) that such differential reception is necessary in determining distance to a sound source. The Barn Owl (*Tyto alba*) has symmetrical ears, but the highly-developed flaps of skin in front of the ears are asymmetrically placed. They are shown on page 319.

Still a third contrast is found in the owl's eardrum. It is very large—proportionally, far larger than in other birds. With a larger area of sensitive surface exposed to sound waves, a larger amount of the waves' mechanical force is available to owls than to most other birds. This means,

Barn Owl strikes. All photographs were taken by David G. Allen in re-enactment at Cornell of original experiments. Windows were boarded to exclude the light and owl struck by ear as prey moved, rustling dry leaves strewn on floor.



Owl's head is seen in three states, *above*: feathered, plucked to reveal hidden skin-flap, and bare skull. *Below*, ear is seen from two views: *left*, outside and *right*, inside the skull. The drawing shows enlarged eardrum (ex-

other things being equal, that an owl can hear a less intense sound than other birds can. As we look at the middle ear, we find that, while in most birds the columella is attached to the center of the eardrum, in owls, it is attached off-center. The center of the eardrum moves farther than the edge, because the edge of the eardrum is attached to the skull and the eardrum bulges inward when a sound wave strikes it. If we consider just one radius of the eardrum, we see that it is acting as a lever with fulcrum at the outside edge of the eardrum. The force that the moving eardrum can exert upon an off-center columella is multiplied, just as force is multiplied as we move closer to the fulcrum of a lever. Thus, although the columella moves a shorter distance as a result of this off-center attachment, force is gained, and the owl has achieved what is probably another advantage over other birds in hearing soft sounds.

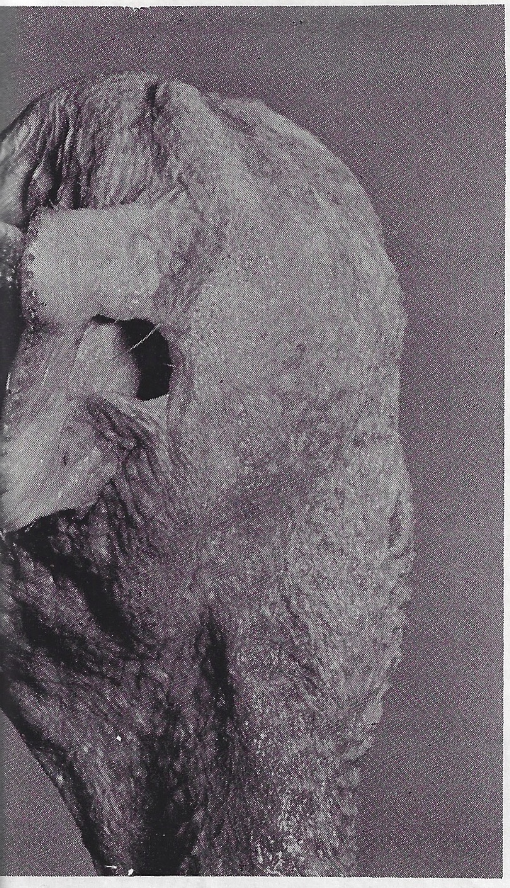
The columella, itself, fits into the cochlea at a spot called the "oval window," acting somewhat as a piston on the liquid inside. The motion of this liquid disturbs the nerve endings in the cochlea. The nerve endings transform mechanical impulses into electrical ones that travel to the bird's brain. Because the cochlea is a blind alley, the liquid inside it has no place to flow: but when the columella pushes on the liquid, this pressure must be relieved. The "round window," a hole in the cochlea, covered by a thin membrane, provides for this. As force is applied, the round-window membrane swells out. Within limits, the larger the round window, the less will be the resistance to liquid being moved by the columella. By now, it should not be surprising that, in owls, this round window is proportionally larger than it is in other birds.

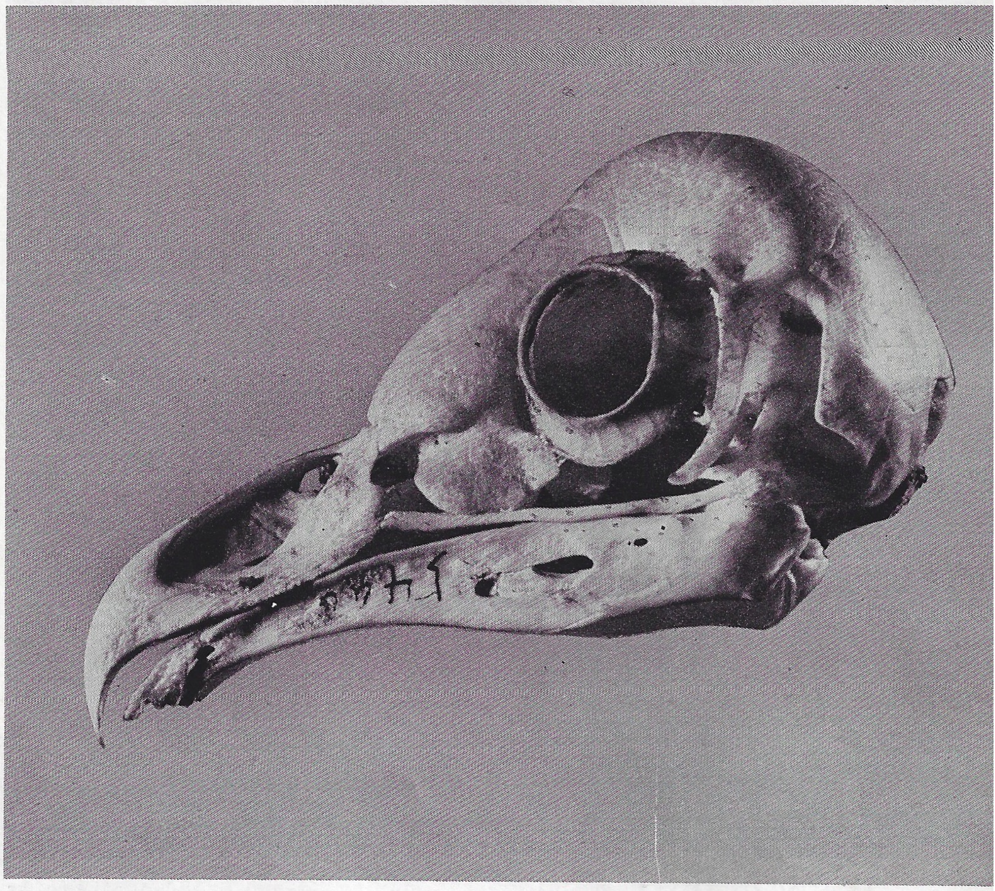
In all birds, the eardrum is many times larger in area than the footplate of the columella (the end of the columella that inserts in the oval window). This disproportion in size multiplies pressure on the liquid of the cochlea, and the amount of multiplication is determined by the ratio between the area of the eardrum and the area of the footplate. As pressure is multiplied, sensitivity to slight sounds is increased. An example of the owl's advantage here is the following: in the house sparrow (*Passer domesticus*), this ratio is about twenty-two to one; in the Long-eared Owl, it is forty to one.

Finally, a widely accepted theory (not yet proven experimentally) holds that the length of the cochlea is directly related to the ability of the ear to analyze complex sounds. Whether or not this theoretical function of cochlea length is correct, the fact remains that owls have longer cochleas than would be expected in birds of their size.

We are faced here with a great deal of evidence, all telling us that owls must have extremely exceptional hearing. The next question seems to be: "Why?" In September, 1956, while Payne was at the Louise Ayer Hatheway School of Conservation

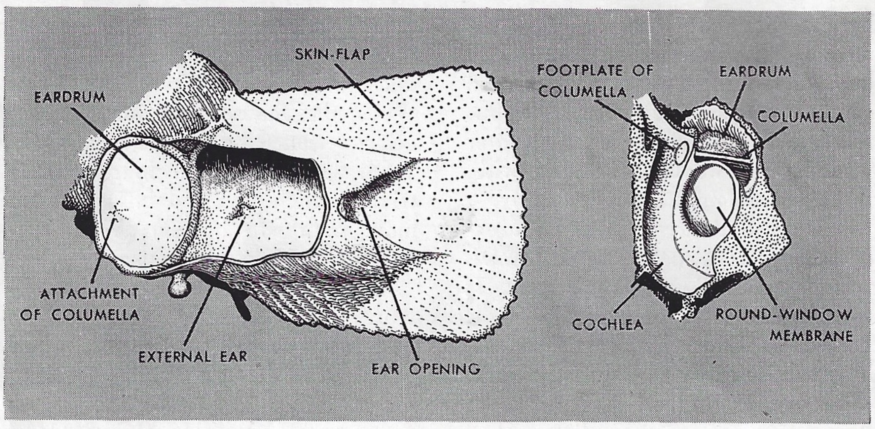
Mr. Payne, now engaged in graduate work at Cornell, and **Dr. Drury**, Director of the Massachusetts Audubon Society's Louise Ayer Hatheway School of Conservation Education, were both trained in zoology at Harvard. **Mr. Payne** is continuing the research here described at Cornell.





posing wide surface to sound waves), off-center columella that fits into cochlea at the "oval window"—against which columella moves like a piston— and "round window," affording relief for fluid thus compressed in cochlea.

Education, in Massachusetts, the authors decided that it would be worthwhile to look into this question. The late James L. Peters, of Harvard's Museum of Comparative Zoology, had suggested to Drury in 1947 that the reason for specialized ear structure in owls be investigated. A Barn Owl (*Tyto alba*) was donated to us by Dr. Winthrop W. Harrington of Lexington, Massachusetts, who had raised it from the age of a few days. This exceptionally tame bird was known, with apologies to A. A. Milne, by the name of "WOL."



WOL had the instincts to hunt and pounce, but being hand-raised, he did not know *what* to hunt, or pounce upon. He would peer at a picture on a newspaper page, and glide down and strike it with his talons. He seemed to be striking at any small object that differed from its background. This well-developed hunting activity, before he "knew" what to hunt, was an interesting aspect of animal behavior in itself. We set out to show him prey.

"WOL's House," as it was called, was in a kennel where the late Mrs. Hatheway, who left her estate and a generous endowment to the Massachusetts Audubon Society, had formerly bred and trained Welsh terriers. It was a room about twenty-five feet by twenty feet, empty except for a seven-foot-high perch, a bathing trough and a table in one corner, where we fed WOL when experiments were not going on.

The first time WOL saw a living mouse he flew down onto the floor near it. The mouse ran. WOL finally caught it, but only after a long chase—half-flying and half-running over the floor. The same pattern of chasing the mouse persisted for the next several trials until, one day, he flew from his perch and struck a mouse directly. This, a more normal hunting method, stayed with him, for he struck the mice directly thereafter.

Having satisfied ourselves that WOL was capable of catching mice in true owl fashion, we set up the equipment for our hearing experiments. We spread dry oak leaves on the floor. This meant that anything moving through the leaves on the floor could be heard. We boarded up the windows, with painstaking precautions, to make sure that the room was light-tight. We checked ourselves

Grasping its prey, Barn Owl keeps wings and tail raised to spill the supporting air and maintain balance, as talons are used to secure bird's catch.

by exposing hypersensitive film for an hour when the lights were turned out: the film was developed and showed no trace of exposure. We thus felt safe in assuming that, no matter what animal we were working with, there was no light for it to see by.

The preliminary to our next experiment was to make sure that WOL was "at home" in his quarters. It was very important for him to know the whole room "by heart," so that he would later fly round in the dark. We gave him about five weeks to "memorize" his surroundings. During this time, we left a small night light on in the room, turning it off occasionally. During the last week before we started our experiments, and off and on during them, WOL was left in complete darkness.

OUR first experiment was to release a wild-caught Deer Mouse (*Peromyscus leucopus*) on the leaf-strewn floor of the room, with the lights off. The mouse moved about, "exploring" the room and rustling in the leaves. When the mouse stopped and was silent, we heard WOL leave his perch, fly down and strike in the leaves. Quickly we turned on the lights and found WOL, standing motionless, holding the mouse in his talons. We tried this seventeen times. When the mouse stopped (and, in our experience, *only* when it stopped) WOL flew. In all but four of these trials (which involved misses by no more than two inches), WOL successfully struck the mouse.

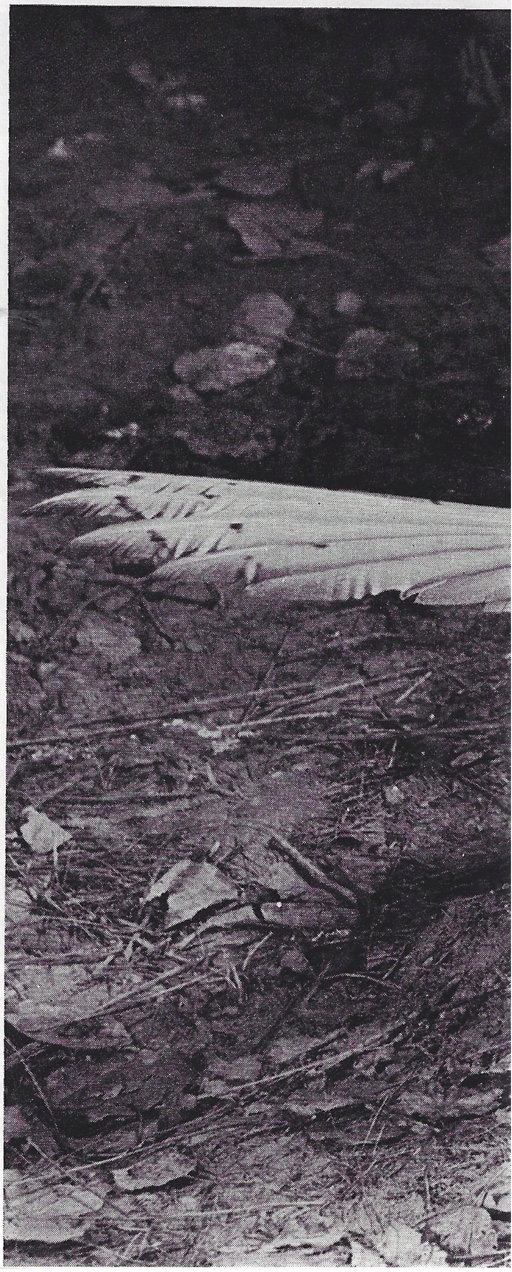
With no light available, WOL obviously was not using his eyes to find the mouse. This left four other possibilities. I: He could be using his ears, and homing on the sounds the mouse made. II: He could be homing on the odor of the mouse. III: He could be making his own sounds, using the echoes to guide him (echolocation), as some bats are known to do. IV: He could be "seeing" the mouse by means of radiation in wave lengths invisible to us—in other words, the infrared heat waves given off by the mouse. Although evidence suggests that owls are insensitive to infrared radiation, we could not ignore the possibility.

To test the heat, odor and homing-on-sound hypotheses, we proposed to see whether WOL could find an object that had no smell and gave off no heat greater than the heat of the leaves on the floor, but which made a sound like a mouse rustling through the leaves.

A crumpled wad of paper (mouse-size), dragged through the leaves on a thread, seemed just right. We turned out the lights and dragged the paper wad through the leaves. We heard WOL leave his perch and strike. We snapped the lights on; he held the wad of paper in his talons.

Since the paper wad had neither smell nor heat (above the heat of its surroundings), we interpreted this to mean that he could only have been using his ears to direct him to our fake mouse. Fortunately, since W. E. Curtis (1952) had shown that Barn Owls have no ability to echolocate, we could discount this possibility.

Theory suggests that an owl would



need both ears to determine distance to a sound source, but we wanted to make sure. We plugged one of WOL's ears with cotton, turned out the lights and released a mouse. We heard WOL leave his perch and strike in the leaves. We turned on the lights and saw both animals standing motionless, WOL about eighteen inches short of the mouse, but on the right line from his perch. We removed the plug and tried him again. This time, WOL caught it. We repeated this experiment with the cotton plug in WOL's *other* ear, with the same result.

WITH this array of evidence before us, we now felt sure that WOL was using his hearing to guide him to the mice in the darkened room. L. R. Dice was the first worker to find that Barn Owls (and Long-eared and Barred Owls, as well) could catch mice in total darkness. Dice's primary interest, in his experiments, was to determine the value of protective coloration in mice. To do this, he released two Deer Mice (*Peromyscus maniculatus*) of different color strains on the floor of a room in dim light: one mouse matching the color of the background, and the other contrasting to it. Dice then released an owl and recorded which mouse the owl caught. After many such trials—using four species of owls, including a Barn Owl—protective coloration was definitely shown to possess advantages for survival in mice.

Now, Dice used these species of owls as the predators in his experiments because he had previously found out just how much light these owls needed to see a mouse. Thus, when he adjusted the light in his coloration experiments, he knew whether or not the owl could see the mouse. Since he was interested in a selection of prey based on visual cues, Dice tried to minimize the effect of what he correctly assumed to be the owls' ability to catch mice by hearing alone. In order to do this, he made what he called a mouse "jungle"—a lattice of sticks screwed together and held above the floor by uprights. The "jungle," he hoped, would keep the owls from catching the mice in total darkness, because the owls would not "dare" strike at them through this obstacle.

Dice says that his "jungle" was also probably a closer approximation

WINGS ARE LOWERED, as owl grips mouse. To test theories of prey-detection through odor or heat, authors also used crumpled paper wad, dragged by thread, instead of mouse. Owl caught this, too, proving sound to be determining clue.

Propping body with wings, owl holds mouse in talons, bends to kill it with bill. Propping, like holding wings aloft, is necessary for balance—not, as had previously been thought, to catch the prey by enfolding it in wings.

Dead prey in bill, motionless owl hunches forward some thirty seconds.

of natural conditions, where mice are moving about under shrubs and herbs, than a bare floor would be: a closer approximation of nature, because when he had observed his owls catching mice on the bare floor, they had used their wings to enfold the mouse and pull it within reach of their talons. He assumed that the owls could not do this under natural conditions because the presence of shrubs and herbs on the ground would prevent such behavior.

Our observations showed that WOL, striking his prey on the leaf-littered floor, held his wings over his back after he first struck. Only after he had caught and started to shift the mouse in his talons, did he lower his wings to the floor on both sides and "enfold" his prey. It appeared that WOL used his wings and tail as props when his talons were otherwise occupied and *not* to draw his prey within reach. WOL did this "enfolding" even when he struck a mouse near his feeding table, where table legs were in the way and his feathers disarranged in the process.

The consistency of WOL's enfolding action led us to believe that such behavior occurs in nature, regardless of obstructions, and that the real effect of Dice's "jungle" had been to give painful consequences to the owls' more "natural" hunting method —by hearing—when they came up against the unnaturally rigid stick-lattice in total darkness.

In earlier experiments, testing the vision of owls under various levels of illumination, Dice had used dead mice as bait. They made no sound. He kept reducing the amount of light until the owls could no longer pounce on the dead mice. Then, by measuring that level of illumination, Dice knew how much light the owls needed to seize a mouse. He then measured the amount of light available to night-hunting owls in nature and came to the conclusion that there must be many nights in which owls cannot see well enough to catch their prey. Although R. J. Pumphrey has estimated that an owl can probably see about as well by starlight as men can see by the full moon, we must remember that clouds effect such available light, as do shadows cast by vegetation. Dice measured this light reduction. He found that, under heavy clouds, the reduction may be as great as one-tenth to one-sixteenth of the light from a clear sky, while under trees and shrubs it may fall to between a fiftieth and a 200th of the original light. These reductions may be multiplied in such conditions as forest shadow on a cloudy night, when available light may be no more than a 500th to a 3200th of the normal intensity in the open on a clear night.

What does all this mean in the lives of owls? It means, first of all, that an owl, hunting by vision, goes hungry on cloudy, moonless nights, if he hunts his prey in the woods. Is it not possible that, under such circumstances, the owl will use his remarkable hearing to lead him to a mouse? It has often been suggested that owls do use their ears to locate the general position of their prey, and then switch over to their eyes for the final strike. But WOL's ability to locate mice by hearing alone leads us to suggest just the reverse.

In our hypothesis, the owl's eyes would be used to avoid obstacles, such as branches and twigs, while its ears would lead it to the final strike. Field observation supports this. Watch an owl hunting through the woods: he flies down from a branch, swoops low, and then rises to a perch. This pattern is repeated over and over again. Is he not perhaps getting close to the ground while he flies, in order to see branches as silhouettes against the relatively bright sky? On dark nights, he needs all the information his eyes can provide in order to avoid collisions with branches, while his hearing is valueless for this purpose. We do not mean to exclude the eyes completely from the owl's final "run in." Probably, in nature, owls use either ears or eyes, or both, according to the opportunity afforded. But from our work with WOL it seems clear that hearing, alone, will permit an owl to strike accurately on the darkest night.

Raid completed, owl turns to fly back to perch. Although owl usually holds prey in bill during flight, in present instance he holds it in talons.