

ACOUSTIC LOCATION OF PREY BY BARN OWLS (*TYTO ALBA*)

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INTRODUCTION

The external ears of many species of owls are asymmetrical (Ridgeway, 1914; Stellbogen, 1930). Although the asymmetry may involve the modification of different structures in different species (Stellbogen, 1930) the result is usually the same: one ear has its opening above the horizontal plane, the other below it. Though Pumphrey (1948), Southern (1955) and others have suggested that the asymmetrical ears of owls may be useful in hunting, prey location by hearing was first demonstrated by Payne & Drury (1958). Work prior to that time had suggested that, in the wild, light levels must often fall below that at which owls can see their prey, thus forcing them to rely upon some non-visual sense in hunting. Dice (1945) calculated the minimum intensities of light required by the barn owl (*Tyto alba*), the long-eared owl (*Asio otus*), the barred owl (*Strix varia*), and the burrowing owl (*Speotyto cunicularia*) to see a dead mouse from a distance of 6 ft. His rough calculations of the reduction of light due to the absence of the moon, the shade of trees and shrubs, and various degrees of cloud cover led him to conclude that '...in the natural habitat of owls the intensity of illumination must often fall below the minimum at which the birds can see their prey'. Measurements of the minimum amount of light necessary for a barn owl to avoid cardboard barriers placed in its flight path (Curtis, 1952) seem to support Dice's contention that owls cannot see their prey under the conditions of poor illumination frequently encountered in the wild. There are also doubtless many occasions when mice are not visible regardless of the amount of light available since they routinely keep to the protection of litter on the forest floor or, as in the case of field rodents, spend much of their time abroad in the protection of covered paths which they have cleared among the bases of the grass stems.

Vanderplank (1934) proposed that owls could see warm-blooded animals by the infra-red they radiate. However, this theory has long been discredited, since the lens and vitreous humour of the eye are practically opaque to infra-red radiation and the small amount of infra-red coming from a mouse-sized object at physiological temperatures would be far below any usable level by the time it reached the retina (Matthews & Matthews, 1939). Hecht & Pirenne (1940) found that infra-red at an intensity 'millions of times greater than that of green light which easily elicits a pupil change' produced no iris contraction in owls. They concluded that 'the owl's vision thus corresponds to the predominantly rod structure of its retina and the idea that nocturnal owls have a special type of vision sensitive to infra-red radiation for seeing in the woods at night is erroneous'.

Although it is generally conceded that most birds have a poorly developed olfactory sense, recent anatomical studies (Cobb, 1960; Bang, 1960; Bang & Cobb, 1968) as well as field studies on turkey vultures (Stager, 1964) and electrophysiological evidence for odour sensitivity (Tucker, 1965; Wenzel, 1965) all suggest that, among others, tube-nosed marine birds, turkey vultures and several echolocating species may possess a useful olfactory sense. Thus one must consider the possibility of owls finding their prey by olfaction even if it seems unlikely that an olfactory system could operate at a useful range or be accurate enough to direct a strike unless strongly supported by other senses. Although I know of no study of olfaction of owls, Dice (1945) working with captive owls searching for prey at low light intensities noted that 'In very dim light and in darkness several of the owls at various times actually touched with a wing, or stepped upon a mouse carcass without seeing it. If these owls use the sense of smell at all in locating the general position of their prey, its value to them for the purpose must be very slight.' My observations of owls in the dark (under infra-red illumination) confirm his view that prey must be touched first before it is taken.

It has also been postulated that owls may 'echolocate' as do some species of bats, birds and porpoises (for a review see Griffin, 1958). However, Curtis (1952) found a direct correlation between light intensity and the ability of barn owls to avoid a series of barriers placed in their flight path. Had they been echolocating, their performance should have been independent of available light.

Taken together the above observations suggest that in the sort of dimly lit places frequented by owls in search of near-invisible prey, it is unlikely that they can locate prey by seeing it in available light, or as a self-luminous infra-red source; or by homing on its smell; or by echolocating it. One strong possibility remains: passive acoustic location, i.e. homing on the noises made by the prey. The work reported here concerns that ability. *Note:* since most of my research was done with barn owls (*Tyto alba*) the term 'owl' will be understood to apply to that species unless otherwise stated.

ANATOMY

External ear

It is generally stated that the ears of the barn owl are asymmetrical (e.g. Kaup, 1862; Ridgeway, 1914; Schwartzkopff, 1962). However, I have found that the placement of the two ear flaps (operculi) lying directly in front of the openings to the ear canals is grossly asymmetrical (Pl. 1 D-G). (This has probably been overlooked in the past because these flaps are normally hidden beneath an overlying veil of auricular feathers, the removal of which ruins a specimen as a study skin.) The asymmetry is such that the centre of the left ear flap is slightly above a horizontal line passing through the eyes, while the centre of the right ear flap is slightly below that line. As shown in Pl. 1 F, G, the angle between the edge of each ear flap and the line of closure of the bill is also different by about 15° on the two sides of the head. I found this asymmetry to be consistent, both in extent and sense, in all six barn owl heads available to me for examination.

A frontal view of a live barn owl's head is shown in Pl. 1 B. Eight parallel rows of feathers, the outermost of which are dark-tipped, form the heart-shaped periphery of the face. The opening of each ear lies at the focus of one-half of this heart, a curving wall of feathers which is almost, but not exactly, parabolic. The feathers in each

curving wall are highly modified, having reduced webs and rachises which, for their size, are unusually thick (Pl. 1A). They are also more densely packed than any other feathers on the owl's body. If they are removed the array of holes formed by their empty sockets shows 'hexagonal closest packing' indicating that they are as close together as is physically possible. The skin from which they grow is likewise thickened into a ridge (Stellbogen, 1930) further increasing the available surface area for feather attachment without sacrificing density of packing. These adaptations suggest that there have been strong selective pressures favouring a curving wall that reflects sound—the usual sound-absorbent properties of feathers having been circumvented by emphasis of those surfaces which could act as reflectors, and orientation of them normal to incoming sound waves.

The entire area of the face enclosed by the heart-shaped rows is filled with auricular feathers—a sort of feather which in other birds covers little more than the ear orifice (Pycraft, 1898). Auricular feathers are filamentous, having slender shafts, long barbs and no barbules (see Pl. 1C). Pumphrey (1948) suggests that they 'ensure laminar flow across the orifice of the auditory meatus and subdue the whistling of the wind'. I found that in barn owls the auricular feathers do not reduce the intensity of incoming sounds measurably. (Complete removal of the auricular feathers yields less than 1 db difference in the intensity of tones between 3000 and 20,000 Hz as received by a calibrated microphone implanted at the site of an owl's ear drum—the technique used in these measurements is described more fully in the discussion of directional sensitivity, see below.) Acoustically speaking, the auricular feathers are really 'not there'. Thus to get a better idea of those features of an owl's head that *are* of acoustic significance it is perhaps best to see the head with the auricular feathers removed (Pl. 1D-G).

The heart-shaped band of densely packed feathers we have been discussing is one of the chief features of a barn owl's appearance—along with frontally directed eyes it is one of the things that makes any owl look 'owlish'. Another characteristic feature is that when an owl looks along a horizontal line its bill points downwards into its breast feathers rather than pointing horizontally, as in most birds. Since the longest dimension of the feather 'parabolas' is between the occipital region of the skull and the tip of the bill, selection for a downward tilting head would enable owls to capture sound waves over a wider area than if the head were held horizontally (and thus, perhaps, to hear fainter sounds too) by sampling more of the energy in a sound field.

One can conclude from these observations that asymmetrically placed ear flaps, feathers that are modified to reflect sound and held in a tightly packed and almost parabolic wall, and even the characteristic position in which the head itself is held, are all adaptations involved in hearing. Indeed some of the chief features of an owl's appearance seem principally to be adaptations for hearing.

Middle ear

In owls with modified external ears almost every structure of their middle ears shows some departure from the general avian pattern. Schwartzkopff (1955a, 1963) has reviewed many of these modifications, so I will only summarize them here. The eardrum is proportionally larger in owls than it is in other birds. The significance of

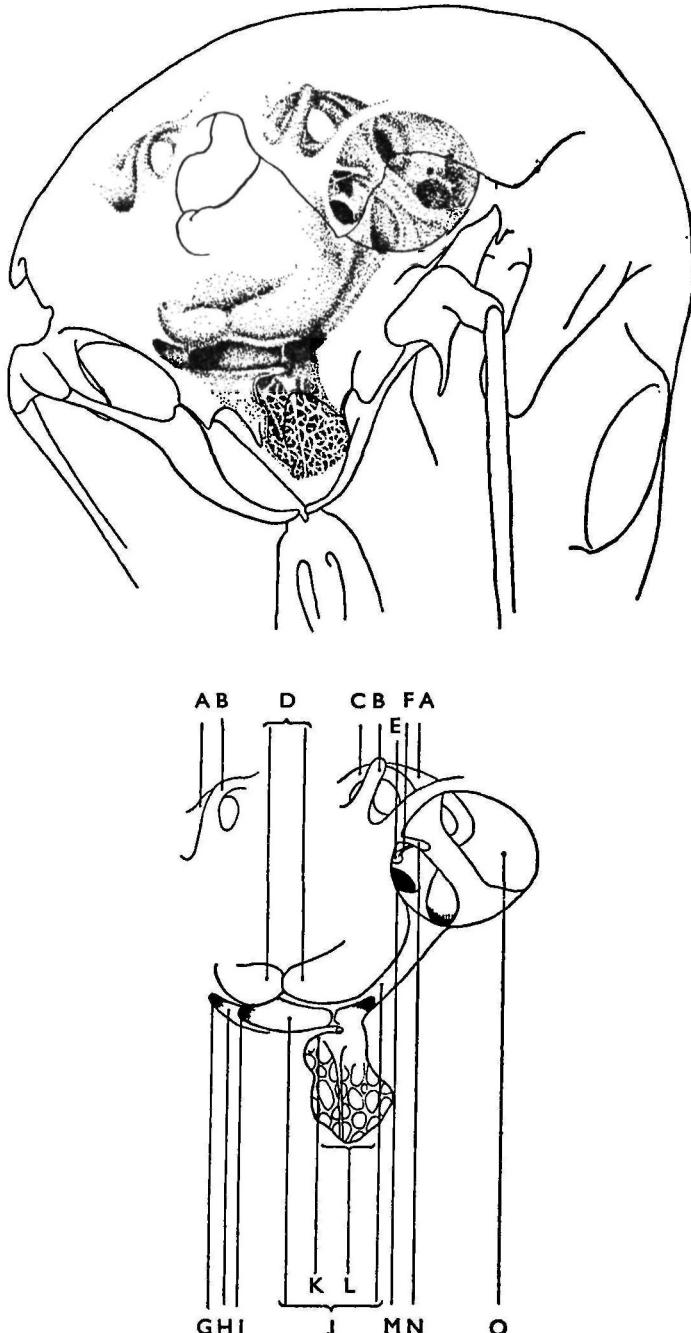
this becomes apparent in view of the fact that the eardrum, columella, and stapes footplate offer an impedance-matching device, to transform airborne vibrations of large amplitude and small force to cochlear-fluid-borne vibrations of large force and small amplitude. Other things being equal, this is most effective if the ratio of the area of the eardrum to the area of the stapes footplate is large. This ratio is 21 in the domestic chicken (*Gallus gallus*), for example, while in the long-eared owl (*Asio otus*) it is 40.

The columella attaches at or near to the centre of the eardrum in most birds, but off-centre in many owls. Krause (1901) showed that the footplate of the columella (flat in most birds) bears, in the case of owls, a knob which projects into the cochlear fluid. Schwartzkopff (1955 a) points out that the motions of the columella in owls are not only piston-like (as in other birds which presumably hear less well), but also like a lever, and that, 'since the movements of this lever produce considerable turning moments at the remarkable velocity of the sonic vibrations, the pressure upon the hinge, namely, the elastic connexion with the footplate in the oval window (*annulus fibrosus*), must be reduced. This is done through "mass equilibration".' He explains that mass equilibration is achieved by the knob on the footplate of the columella, which also reduces eddy formation in the perilymph of the inner ear.

One of the most striking features of the middle ear of the barn owl is its connexion with the cranial air chambers, which are very large owing to the extreme pneumaticity of the skull. Three cavity systems are regularly distinguished in birds, as is a communication between left and right middle ears via these cavities. In the barn owl the courses of the first two cavities agree with Stellbogen's description (1930) of their courses for the tawny owl (*Strix aluco*). I found, however, that the connexion between the Eustachian tube and the canal leading from the middle ear to the third air chamber (in the sphenoid bone) is more extensive in the barn owl than the oval passageway through which this communication takes place in the tawny owl. In barn owls, at a point about one-third of the way towards the midline of the skull from the middle ear, the Eustachian tube and the tube leading to the third air chamber join and widen into a single passageway (Text-fig. 1). This passageway meets its mirror image companion from the other ear at the midline of the skull, two or three spicules of bone affording the only occlusion to an otherwise free communication. The chamber thus formed astride the midline is caudally and rostrally flattened. It is bounded dorsally by a portion of the floor of the brain cavity and ventrally by the cochleae; rostrally, it communicates with the third air chamber via two, large, nearly circular openings, one on each side of the midline.

The air chamber itself is a network of bony spicules. It is so large (one-fourth or more of the skull volume) that one is sure to break into it by dissecting downwards from the top of the skull at any point between the eyes.

The fusion of the Eustachian tubes not only with each other (at the midline just before they enter the mouth cavity), but also with the canals leading to the third air chamber, suggests that there has been a strong selective pressure towards an open connexion between left and right middle ears. This connexion could only be more complete if there was no dividing wall separating the Eustachian tube and canal to the third air chamber as they emerge from the middle ear cavity. Stresman (1927, as quoted in Stellbogen, 1930) proposed that connexion of left and right middle ears



Text-fig. 1. Semi-diagrammatic drawing. Lateral view of partly dissected barn owl's skull. The outline drawing identifies features on the drawing above. A, B and C, semicircular canals. D, cochlea. E, footplate of columella. F, columella. G, opening of the Eustachian tube into the middle-ear cavity. H, bone partition between the Eustachian tube and the canal leading to the third air chamber. I, opening into the middle-ear cavity of the canal leading to the third air chamber. J, cavity formed by fusion of the Eustachian tube and the canal leading to the third air chamber. K, position of the communication between the air chamber in the sphenoid bone and the cavity formed by the Eustachian tube and the canal leading to the third air chamber. The point of communication in this view is partially covered by an overlying bone lamella. L, portion of the third air chamber in the sphenoid bone of the skull (showing spicules of bone). M, Round Window. N, attachment of columella to eardrum: observe that it is off centre. O, tympanum.

serves to equalize pressure in the two ears. I would add that without some such connexion, precise comparison of sound pressures received in the two ears would be impossible. As it is my contention that owls are not concerned with absolute measurements of sound pressures, it seems to me that a special mechanism to equalize pressure in the middle ear with the environmental atmospheric pressure would be unnecessary. Indeed, I have found no such special modification in owls.

The possibility that the canal connecting the two middle ears may allow sounds entering one ear to be heard by the ear of the opposite side has worried me considerably for reasons which will become clear later. Wada (1923) has shown that in birds deflexions of one eardrum will cause deflexions of the eardrum of the opposite side, but his experiments employed long-term pressure fluctuations and were not concerned with rapid fluctuations perceived as sound. Observations by Schwartzkopff (1952) and Schwartzkopff & Bremond (1963) are considered below.

Inner ear

The round window of the cochlea is much larger in owls than it is in other birds. Since the cochlea is encased in bone and since the perilymph within it is, for all practical purposes, incompressible, pressures created in the fluid must be relieved if the fluid is to move the basilar membrane. In all birds relief is provided by the round window, a hole in the wall of the cochlea covered with an elastic membrane. Within obvious limits the larger the round window the less the resistance of the fluid to vibrations. In owls the round window is about five times greater in area than the oval window (Schwartzkopff, 1955a).

The cochlea is longer in owls than it is in other birds and it is also conspicuously curved (Schwartzkopff, 1955b). The cochleae of barn owls meet at the midline and their bony walls touch (see Text-fig. 1). Without changing course or curving more, they could be no longer than they are. Since length of cochlea seems to relate to ability to discriminate frequencies it is likely that owls discriminate frequencies well. It is also possible (as suggested by Pumphrey, 1948) that long basilar membranes may give owls extraordinary intensity discrimination—a factor that fits well with my theory of how they locate sound sources (see below).

Several efforts by various investigators have been made to find asymmetry in the inner ears of owls, but they have all met with failure. Since the external ears of many owls are asymmetrical, sounds reaching each of the cochleae will be different, and the finest of frequency and intensity discriminations are necessary to expose these differences. In order to take advantage of the maximum information that can be extracted from such differences, all adaptations internal to an owl's eardrum should contribute to faithful reproduction, equivalent in the two ears, with all variables held constant. In the light of this argument one can expect to find less (rather than more or any) individual variation between the left and right middle and internal ears of owls than in most other birds. It is not surprising, then, to find that the largest connexions between middle ears (allowing for fastest equalization of pressure between the two ears) are found in birds which have the best hearing (Tiedemann, 1810, as quoted by Schwartzkopff, 1952).

BEHAVIOURAL EXPERIMENTS

First demonstration of a barn owl's ability to orient acoustically

The work cited in the introduction indicates that owls must rely heavily on some non-visual sense to locate prey if they are to survive. The anatomy of owls' ears indicates that they are significantly different from the general avian pattern. The question now seems to be, are these differences associated with location of prey?

The first experiments showing that a barn owl can strike a mouse directly in total darkness were performed by Payne & Drury (1958) in a 25 × 20 ft room made light-tight by taping large sheets of 'Masonite' over the windows with opaque electrician's tape.

After entering the room when there was full sunlight out of doors and allowing 40 min for dark adaptation, all light leaks were carefully patched until no more could be seen. As a further precaution all experimentation was carried out at night. As a final test of darkness a sheet of Kodak *Royal Pan Press* film was cut in half and one-half of it was placed on the floor of the room for 1 h. Exposed and unexposed portions of the original sheet were then developed for twice the recommended time and compared. There was no visible difference between the two halves of the original sheet.

Once it was clear that the room was light-tight, 2 in of dry leaves were spread on the floor, a perch 7 ft high was placed at each end, and a hand-raised barn owl was freed in the room. In this room the owl lived in dim light for about 5 weeks, during which time it presumably became familiar with its surroundings. During the last week, the room was kept completely dark, 12 h of each day and during the last two days of that week the owl was given no food. Then, a live-caught deer mouse (*Peromyscus leucopus*) was released in the leaves on the floor. After about 20 min the mouse began to rustle the leaves and continued to make rustling noises intermittently for about an hour, until it was removed. The owl made no attempt to strike the mouse on the first three nights in which this experiment was repeated. On the fourth night the owl struck the mouse directly and successfully on the first trial. During the next few days, in 16 more trials, the owl made 16 strikes at a mouse at least 12 ft away, missing only four times and never by more than 2 in. In each case the owl left its perch only after the mouse stopped rustling the leaves.

The fact that the owl was using the sense of hearing and not olfaction or infra-red sensitivity to locate prey was established by an additional experiment carried out twice during this period and dozens of times since. With the lights turned off, a mouse-sized wad of paper was dragged through the leaves on the floor. The owl successfully struck the paper wad. The paper wad and the leaves through which it was dragged were at the same temperature. Therefore, the owl could not have located it by any infra-red contrast with its surroundings. The paper wad put out no mouse-like odour, so homing on scent would be of no value. Because the lights were out, the owl could not see the wad. It is unlikely the owl echolocated it since the work of Curtis (1952) shows that barn owls have no ability to echolocate and experiments which I have carried out since are in agreement with his conclusions. The only possibility left, as I see it, is that the owl was orienting acoustically to the sounds made by the mouse.

At this time we performed another experiment which also indicated that hearing

was what the owl had been relying on to locate prey in total darkness. The owl's hearing was impaired by blockage of first one ear then the other with a small cotton plug. In both cases the owl flew, in darkness, directly towards the mouse but landed about 18 in short of it. After each trial the cotton was removed, and the owl was allowed to try in total darkness to catch the same mouse it had just missed. In both cases the owl then struck successfully.

The experiments described above were repeated many times in another light-tight room at Cornell University 42 ft long and 12 ft wide, with a single-pitch tin roof. One of the long walls was $8\frac{1}{2}$ ft high, the other $6\frac{1}{2}$ ft high. A permanent blind occupied the last 4 ft of one end of the room; it was equipped with two viewing ports of one-way glass and a single window of plate glass 4×6 ft. To prevent the owl from attempting to fly through the glass, it was kept covered, except when observations were being made.

During the first 2 years the floor was spread with a 2 in layer of leaves. During the third and fourth years the floor was spread with sand on which, in some experiments, small piles of leaves were placed. In other experiments the mouse's movements were made audible by the rustling of a leaf tied to its tail or glued to its body.

Using this room several lines of experimentation were followed: (1) comparisons of the barn owl's behaviour when striking in light and in darkness, with the hope of finding out what conditions are necessary for accurate acoustic orientation; and (2) attempts to determine (a) whether the owl can judge distance as well as direction; (b) what information the striking owl uses to adjust its final body position to the orientation of its prey's movements; and (c) the limits of the owl's angular accuracy in locating prey acoustically.

The description of the barn owl's behaviour when striking in the light is based on a careful analysis of thirty ciné sequences of the flights of two different owls, and supplemented by observations made during many hundred unfilmed flight experiments. As far as I have been able to ascertain, the introduction of cameras and lights made no difference to the owl's behaviour in striking mice once it had become accustomed to them, i.e. after 2 or 3 weeks.

In order to observe the owl's hunting behaviour in darkness, I illuminated the room with infra-red and watched through an infra-red viewing device. Two such devices were used during the course of these experiments: a World War II Sniperscope, and a 'Nite-eye'. ('Nite-eyes' are no longer made but infra-red viewers can be obtained from Varo Optical Inc., 215 East Prospect Avenue, Mount Prospect, Illinois 60057.) A satisfactory illumination for direct observation with these instruments was an incandescent light bulb held in a light-tight housing behind a standard war surplus sniperscope filter. I took motion pictures in total darkness with a 35 mm 'Eyemo' camera loaded with Kodak 'Hi Speed Infra-Red' film and aimed with a Sniperscope attached alongside it on the same tripod. The camera triggered a multiple flash stroboscopic unit which produced a 70 watt-second flash. When filtered through a Kodak No. 87 Wratten filter there was sufficient infra-red to photograph an owl at distances under 25 ft with the camera set at $f\ 3.5$. Plates 2-5 were made using this apparatus. The longest consecutive period that the stroboscopic lights could be operated was about 3 sec. Since the full 3 sec were necessary for filming the strike, none of my sequences shows the take-off from the perch.

In total darkness, facing the reflector directly, I was able to see with the naked eye a deep-red image of the filament of the strobe bulb itself when it was fired. However, I could detect no red colour, not even a vague sensation of redness, from the light reflected off any object in the room, including the wall right next to the bulb unit.

I have slim evidence that a barn owl, too, could see the strobe filament; for twice, when pursued in darkness by a person, it flew towards the strobe bulb and collided with the filter. I doubt that the owl was orienting to the sounds made by the shock-heating of the bulb during firing since the owl flew away from the strobe the first time I turned it on. Unless the owl flew in the direction of the strobe merely by chance, I suspect it was flying towards the only light it could see: the dim red glow of the strobe filament.

In spite of the fact that the owl probably could see the strobe filament, I have proof that a barn owl could not see a mouse even at a distance of a few inches under the conditions of infra-red illumination I used when taking motion pictures in the dark. Plate 2 shows 8 frames (Q-X) from a motion-picture sequence in darkness in which an owl struck at and missed a mouse. That it missed is a strong indication already that it did not see the mouse, for, in all the many hundred strikes I have by now watched in enough light so I could be sure the owl could see if it chose, no owl has ever missed. In the Plate 2 sequence when the owl missed it hit a leaf that I had tied to the mouse's tail, and knocked the leaf off (frames Q-T). Between frames T and U the mouse started to move away but collided with another leaf (several frames are omitted from the sequence in efforts to abridge it for reproduction here, thus frame U is taken from a second starting-up of the camera about 10 sec after the owl struck). The owl whirled to face the mouse (frame U shows the owl facing the mouse directly from a distance of about 8 in) but apparently this one sound was insufficient for the owl to locate the mouse as it did not attempt to strike. The mouse avoided further collisions with leaves as it moved silently across the sand away from the owl, and the owl then raised its head (frame V). A few seconds later the mouse was several feet away from the owl (frame W) which was stamping about in the leaves as though searching there. Finally, the owl raised its head again (frame X). Since it appeared to have lost interest, I turned on the lights. Immediately the owl saw the mouse, flew over and struck it.

I have several other film sequences showing owls missing mice. All of them, I feel, demonstrate that failure to strike resulted from inability to locate the mouse accurately. It might be argued that the owl was merely striking at some other object which it dimly discerned as a small, almost invisible, blur of about mouse-size contrasting with the background. However, as Pl. 2, frame U, shows, the white mouse was in plain viewing range for the owl and was in high contrast to the sand background (even in infra-red). Furthermore, it was moving, and still the owl did not see it, as is apparent from the fact that it did not strike then, but struck at once when the white lights were turned on. All this I take as evidence that it has been possible to observe a barn owl under infra-red illumination without the owl also being able to see its prey.

It should be noted that no deductions depending on exact time intervals between frames can be drawn from any of the sequences printed here. All of the pictures on 35 mm film were taken during the winter when the temperature ranged between

–5 and –20° F. To insure that the room was totally dark I had to turn off the electric heaters in the blind, whereupon the temperature in the blind fell so rapidly that the camera, which had a spring drive, was often too cold to operate or would barely operate at all. Information depending on time between frames can be derived, however, from a series of unanalysed films I made later using a 16 mm Arriflex camera with an electric motor drive which ran at a constant speed.

Plate 2, A–P, is a sequence of frames from a motion picture of a strike in the light. The pictures were taken with the infra-red apparatus described above, but a single white light was left on to allow the owl to see the mouse. In all the rest of the sequences (Pls. 3–5) the room was totally dark.

Comparison of behaviour in light and darkness

(1) *Behaviour in light.* Just after a mouse was thrown into leaves in the light the owl would turn quickly to face it, leaning forward slightly at the same time. After this one motion it would hold perfectly still. The length of time between orienting to and flying at the mouse varied from about 0·5 to 30 sec. The longer waits usually occurred when the mouse did not move after hitting the floor, or on the rare occasions when I was in the room with the owl instead of out of sight in the blind. Just before starting to fly the owl would lower its head and lean forward, at the same time raising its wings. Just as it appeared about to fall it would shove off with its feet, take a single wing-stroke, and glide in a straight line towards the mouse. At the moment of leaving the perch the feet swung forward and then immediately swung back to a position in which they trailed behind, tucked beneath the tail. The only wing motions during the glide were very small, apparently being steering and balancing motions. When about 3 ft from the mouse the owl would suddenly bring its feet forward until they almost touched its bill and then pull its head back. Thus, although it maintained its trajectory, it reversed the position of its body along the trajectory by nearly 180° (its feet, which formerly brought up the rear, were now in front). Then, with its eyes closed for a fraction of a second, the owl would strike the mouse with one foot, landing—and presumably absorbing the major shock of the impact—with the other.

At some point between swinging its feet forward and the instant of the impact, the owl opened its talons. Unfortunately, none of my films of strikes in the light shows the open talons. One, however, shows the feet 6 in or less from the mouse, with the talons not yet spread. The spreading of the talons must occur extremely quickly, for not only is the owl travelling fastest at the end of its flight, but also its feet are travelling faster than the rest of its body as they swing forward. One of the two owls which I photographed striking in the light furnished extra acceleration with a wing stroke at the end of its glide just as the feet came forward. (This occurred in all but two out of the 24 strikes filmed.) This did not occur in any of the six filmed strike sequences of the second owl. However, all six of these strikes, as well as the two in which the first owl did not accelerate, were at short range. Future observations should be made to determine whether the final accelerating stroke is a typical part of strikes performed in the light.

In no case did the strike itself kill the mouse or even stun it enough to keep it from moving. If the mouse struggled or turned its head to try to bite, the owl would tighten its grasp with a pressure apparently sufficient to stop all efforts at retaliation,

for the mouse would instantly hold still (this perhaps explains how owls avoid being bitten by rodents during killing).

(2) *Behaviour in darkness.* The behaviour of a barn owl when striking in the darkness (under infra-red illumination) was as follows. The lights were turned out before the mouse was thrown into the leaves on the floor. In most instances the owl turned its head towards the mouse at the first sound of the mouse hitting the floor. After this single orienting movement it remained motionless for 1 or 2 sec, and then flew. There were occasions, however, particularly when the owl had not been starved prior to the experiment, when the owl remained with its eyes closed (apparently asleep) for up to 40 min while the mouse moved noisily about the floor. Not until the sound stopped would it open its eyes, then quite suddenly lean forward, waiting for one or two more rustling sounds before striking. I took these long delays to be signs that the owl was not hungry, for I could make it strike a few seconds after the mouse was offered by depriving it of food 24 h prior to the experiment or by reducing normal rations to half.

During a long wait before striking, the owl often made a series of unusual motions with its head. It would tilt its head at a variety of angles, including upside down with the bill pointed upward; or move it from side to side holding the vertical axis vertical; or move it up and down holding the head tilted 90° to one side. I have also frequently seen such head motions in a lighted room in which there were no sounds audible to me, and such motions can be demonstrated at will by putting a captive owl into unfamiliar surroundings or by placing a large unfamiliar object in familiar surroundings. Both of these observations seem to indicate that the exaggerated head motions are somehow correlated with vision. Pumphrey (1948) suggested that certain head motions in birds are necessary for determining distance visually by the use of parallax, and Southern (1955) suggested that an owl's exaggerated head motions 'are presumably to make the object move across its field of view, even if it is motionless'. Both suggestions depend on the fact that owl's eyes are immobile. It seems to me that these head motions are a fertile field for experimentation, for it seems reasonable that they could serve either a visual function, or an acoustic function, or both. In any case, exaggerated head motions rarely occur in total darkness and they do not have to precede a successful strike. Therefore, although it would be possible to defend almost any theory which linked these extraordinary head motions with an owl's ability to orient to a sound source, such a theory would be, at best, inadequate since an owl can acoustically orient without them.

Whether the owl waited before flying and exhibited the peculiar head motions just described, or flew after the mouse's first few sounds, the remainder of its strike in darkness followed the same pattern. Typically, it left the perch in the same manner in darkness and in light. In darkness, however, it flapped its wings rapidly all the way to the mouse instead of gliding (see Pl. 3). Flying in this way, a barn owl travels at almost exactly half the speed it travels in light. Its feet, which in light are tucked beneath the tail, swing back and forth like a pendulum in darkness. This gives the appearance of being constantly prepared to collide with an object or to land on the ground. Even though its body slightly pitches, rolls and yaws in flight, an owl constantly faces the area from which the sound has come. Although it cannot see, its eyes remain open until just prior to the instant of impact. As it nears the end of its flight, it brings its feet forward until they are level with the tip of its bill (Pl. 3 N). Then, just

as in strikes in the light, it turns in mid-air, end for end, placing the talons so that they follow in the trajectory formerly taken by the head. Spreading of the talons of both feet occurs much earlier in darkness than in light, and was usually photographed.

Distance discrimination experiments

The fact that barn owls can predictably catch mice in total darkness, using sounds that the mice make as their only source of information, indicates that they can orient acoustically in both vertical and horizontal planes. However, whether barn owls can also determine the distance to a sound source is uncertain. An owl's change in position just before impact, i.e. bringing its feet way forward and turning end for end in mid-air, might indicate that the owl judges distance, for it seems to know at what point along a chosen flight path to stop flying and start striking. It is also possible, however, that an owl senses its approach to the ground while flying. For instance, the wing flapping, characteristic of flight in the dark, might serve the function of setting up a series of downdrafts whose increased back pressure would inform the owl of its proximity to the ground. In this case, once having chosen a flight direction in the vertical and horizontal planes, the owl would only have to fly along it until it sensed the ground, at which point it would bring its feet forward for the strike.

To determine whether a barn owl can judge distance to a sound source I allowed an owl to try striking at a mouse suspended in mid-air, i.e. in a free sound field. The experiment was performed in the following way. A narrow strip cut from a Japanese 'mist net' (fine silk with 1 in mesh) was tightly stretched on a frame that held it in the horizontal plane. Legs attached to the frame allowed adjustment of the suspended net to any altitude up to 4 ft above the floor. This apparatus was set-up in total darkness, and a dead mouse with a leaf glued to its body and a long thread tied to its tail was placed on the net. By retiring and tugging on the thread I could cause the leaf to make rustling sounds. I watched the owl with an infra-red viewer.

In 12 trials, made on three consecutive nights, with the position of the net changed for each trial and the average distance between the owl and the mouse about 13 ft, the owl overshot the net and struck the floor beyond it six times. A straight line when projected from the owl's head (while it sat on its perch) through the mouse on the net intersected the floor at a point within 6 in of all six unsuccessful impact points. Of the six remaining strikes, five were alightings (see below) in which the owl fluttered to the floor short of the net. In the remaining trial, the owl landed on the net and caught the mouse. However, I am not sure that it was truly striking at the mouse; it may have simply collided with the net and been lucky enough to land on its feet.

Had the owl successfully struck the mouse on the net, one could immediately conclude that it was determining not only direction but also distance to a sound, and that this owl was capable of locating the position of a point source of sound in space. Failure to strike the mouse on the net does not prove anything, however, since the owl might simply have been ignoring distance information available to it. This is a serious objection since the owl had been living in the same room and striking from a perch at the same height for over a year before I tried these experiments, and had probably developed an accurate appreciation of where the floor was at any particular angle from the perch. I am presently trying to improve these observations.

Although in darkness a barn owl calculates the position of a sound source with its

ears, it must strike the source with its feet. There exists, then, a problem of parallax requiring a rather complex solution, since the size of the angle feet-to-mouse-to-eyes is inversely proportional to the distance of the mouse from the owl. At least a rough distance perception would be mandatory for the owl to correct adequately, becoming more critical the closer the owl is to the mouse and or the closer the owl is to the ground when locating the mouse. The barn owl circumvents this problem altogether, however, by flying straight at a sound source along a line from its ears to the mouse and replacing the path of its ears at the last moment with its widely spread talons. In order to initiate a flight along a straight path between its ears and the mouse, a barn owl lowers its head to a point well below its feet and then slowly falls forward until airborne. (The straightness of the path needs to be measured better than I have done to date, however.) Another aspect of a barn owl's behaviour when it misses a mouse or alights near it in total darkness is interesting in this regard. For, even if the owl has landed where it could easily reach the mouse without moving, it will leap into the air when the mouse makes a sound and drop again from above. This is apparently done so as to be able to move its talons along the line from ears to mouse.

Great freedom of movement of the talons is a character peculiar to owls and ospreys (genus *Pandion*). When grasping a perch an owl keeps two toes in front and two behind. When walking, the hallux is behind with the remaining toes directed forward; when striking, the toes are pointed roughly at right angles to each other (Ridgeway, 1914). In addition, I have observed that when a barn owl strikes in darkness not only are the talons on each foot evenly spaced, but the distance between the halluces and inside toes of the two feet is the same as the distance between any two talons. Further, the feet are aligned so that the total pattern created by the talons on both feet is roughly an oval with the talons spaced equidistant along its periphery. I first discovered this by placing a sheet of thin paper over a loud speaker through which I played the sounds of a mouse rustling in leaves. When the owl struck it in total darkness the pattern appeared from punctures left in the paper. Six repeats yielded identical results except for slight variations in individual talon placement. The most unevenly spaced punctures obtained in this series are reproduced in Pl. 4C. Later, infra-red photography clearly showed the position of talons before striking (for two examples from different strike sequences see Pl. 4A, B). The position and spacing of talons just before a strike thus results in uniform coverage and enclosure of the maximum possible area (conforming roughly in its shape and dimensions to a mouse's body), creating the greatest chance that the owl will get at least one talon into a mouse.

How an owl adjusts its body position in accordance with its prey's movements

The question immediately arises, however, whether it is of greater advantage to an owl to hit a mouse with a single talon or to miss it altogether, for a mouse or larger rodent so held should be capable of biting the owl's foot. (The owl's method of stopping a mouse's attempts to bite by tightening its grip would of course be impossible when pinning it with only one claw.) A way for the owl to ensure the final success of a strike, assuming that it is in the right area, would be to orient the strike itself so that the long axis of the talons' oval strike pattern was parallel to the long axis of the

mouse. This is just what a barn owl does and it does it not only in light, but in darkness also—by rotating at the last moment of flight so that long axes of strike pattern and mouse are parallel (see Pl. 4D-G; H-O); both photographed in total darkness).

That a barn owl can make such an orientation when striking at prey which it has located acoustically implies that it knows in which direction the prey is facing. The following experiment provides evidence that an owl's appreciation of the heading of its prey is based on hearing.

A leaf was glued to a dead mouse. Two threads were also attached to the mouse and were so arranged that the mouse could be remotely manipulated by an observer in the blind. The two threads made it possible to tow the mouse along either of two paths at right angles to each other. The paths were oriented so that one was normal to the owl's expected flight path (a straight line from perch to mouse) and the other parallel with it. Using this apparatus I filmed a total of 12 trials in darkness. The procedure in each case was to drag the mouse along one path for 4 in or less, about 2 min after the lights had been turned off. If the owl did not then leave its perch, the mouse was again moved (this time back along the same path) with a pause for a few seconds at the end, and so on until during some quiet period between tows the owl would leave the perch and strike. In this series of 12 trials six were tows along the path at right angles to the owl's flight path and six along the path parallel to it. The owl struck always with the long axis of its talon pattern held parallel to the path just taken by the mouse. This meant that in all trials with the mouse moving on a path parallel to the owl's strike path (approach path) the owl had to rotate (and did) about the axis of its approach path at the last moment, whereas all strikes at mice moved along a path perpendicular to the approach path required no such manoeuvre (and I could never detect any).

In all 12 trials the position of the dead mouse's body bore no fixed relation to the direction along which it was dragged—it was sometimes pulled sideways and sometimes tumbled over in an unpredictable way. Thus the final orientation of the long axis of the owl's oval strike pattern (talon pattern) though random with respect to the mouse, was always approximately parallel to the direction in which the mouse was moved. (No effort was made to determine the angle between talon pattern and mouse long axes other than by quick visual approximations as this would have required many refinements in technique). The conclusions to be drawn from these experiments are obvious. The owl could not have been directing the orientation of its strikes by vision or by echolocation as its orientation was based not on the position of the mouse's body but only on the direction in which it had been moving. I feel, therefore, that the only possible explanation of how a barn owl in total darkness can determine the direction in which a live mouse is facing is by hearing it move from one position to another (the assumption being that mice face in the direction they move). As a parenthetical observation I have noticed since these experiments that mice running on the floor will stop and immediately turn sideways when a noise is made. This behaviour might have the adaptive advantage of presenting the mouse in an unperceived orientation to an owl which has located it acoustically, thereby increasing the chances that the owl will miss. This is merely speculation, however, since one could immediately mention a variety of alternative advantages for such behaviour and I have made no effort to study it in any detail.

Knowing that a barn owl can determine the direction in which its prey faces, one might next ask: what is the minimum angle that a mouse's change in position must subtend for an owl to detect it and appreciate the mouse's heading? I have some scant information on this from the experiments described above. As I have said, the owl turned in flight in all trials which required such a turn for effective orientation of the talons. Since the mouse was translated 2 in in some of these trials and the distance of the owl's flight path was 140 in, the minimum angle subtended by any of these translations was 0.6° (for the vertical plane) and 1° (in the horizontal plane).

I have not yet tried smaller translations of a mouse, requiring finer acoustical localization by the owl. Such experiments would lead to a more reliable estimate of an owl's angular accuracy since the owl will turn in flight whether or not it misses the mouse, and one can thus separate the ability of the owl to fly a straight line without visual cues from its accuracy in locating a sound source acoustically. Such experiments, however, would require that the exact position of the talons and the mouse's body at the instant of impact be recorded. For the accuracy with which the owl places the long axis of its strike pattern parallel to the mouse's body is also an indication of the owl's ability to determine the location of a sound source (if it is able to do this within 20° , it is astonishingly good).

Accuracy of location; frequency dependence

To investigate which frequencies are necessary for accurate acoustic orientation, I tested an owl flying at a hidden loudspeaker. The speaker was mounted beneath a perforated metal screen to prevent damage from the owl's talons, and was hidden under a layer of leaves which covered the flight-room floor. Using leaves enabled me to test the owl in light and thus eliminate from the calculation of the owl's acoustic accuracy any error in its ability to fly a straight path in darkness, without visual clues. The placement of the speaker in the leaves before each experiment was made in darkness; a dead mouse was hidden with the loud speaker only about every six strikes. This increased the owl's incentive to strike. (Hiding of the mouse was done in darkness, with great care to disturb a wide area of leaves so visual inspection would not disclose its position. The owl occasionally provided a check of how well this was done by striking in the leaves before I had turned out the lights or had played any sounds over the loudspeaker. The closest the owl came to the loudspeaker in such cases was 4 ft and though I allowed the owl to search among the leaves for a few minutes it never found either speaker or mouse.) I judged the accuracy of each strike by measuring the distance between the centre of the loudspeaker and the centre of the owl's strike pattern as it was imprinted on Plasticine surrounding the loudspeaker. Ambiguity from extra footprints was avoided by the owl's tendency to remain motionless after striking. My measurements were probably correct to within ± 1.5 in. To minimize the effect of this measurement error I tried to induce the owl to strike at the greatest possible distances.

The information obtainable from these experiments was limited by the poor high-frequency response of the loud speaker. It was a Philmore no. 707 voice coil speaker, $1\frac{1}{2}$ in in diameter, chosen for its small size and price. In a rough test using an Altex microphone with uniform frequency response up to 15,000 Hz, the speaker showed a reasonably uniform output from 1000 to 8000 Hz but was 35 db down by 15,000 Hz.

The owl could locate the speaker playing recorded sounds of rustling leaves in darkness and in light but with less willingness, i.e. after longer waits, than it exhibited when locating rustling leaves directly.

Using a loudspeaker playing recorded leaf rustlings the mean of 23 misses out of 44 trials in darkness was $2.9 \pm 2.0^\circ$ in the horizontal plane and $2.5 \pm 1.6^\circ$ in the vertical plane. When I used a recording from which all frequencies above 8500 Hz had been removed, the owl missed 10 times in 10 trials with a mean miss of $5.8 \pm 4.4^\circ$ in the horizontal plane and $7.2 \pm 3.7^\circ$ in the vertical plane. (It is interesting to note, from the directional sensitivity plots discussed below, that near the region of its line of sight the barn owl's sensitivity to a frequency of 8000 Hz changes in the vertical plane by about 1 db in 7° . If we assume that an owl can detect sound intensity differences of 1 db, it should on the average miss a sound source containing no frequencies above 8000 Hz by 7° in the vertical plane—which is what I observed.) When I used a recording from which all frequencies above 5000 Hz had been removed, the owl refused to strike.

The owl's acoustic orientation appears from these crude data to depend upon frequencies above 8.5 kHz. Any theory involving the effect of the owl's asymmetrical head on the sounds which arrive at its ears must take account of this observation.

Measurements of angular accuracy in acoustic orientation

I tested an owl flying in darkness at a dead mouse with a leaf tied to its body and dragged over bare sand. By pulling on a thread tied to the mouse's tail, I caused the mouse to move every 10 sec for a period of about 1 sec. As the owl left its perch, a switch clicked and I instantly relaxed the thread, so as to provide no additional clues to the owl while in flight (owls can make mid-flight corrections if provided with mid-flight sounds).

This method had several limitations: (1) an error of ± 1.5 in was possible in taking my measurements of the owl's accuracy from imprints in the sand. (2) Any error in the owl's flight path due to lack of visual clues is incorporated into my final calculation of acoustic orientation accuracy. However, such an error is probably small since the owl's accuracy when striking at a hidden loudspeaker in the light was the same as its accuracy when striking at the same target in the dark. (3) It was never possible to be completely sure that the owl had received no additional information from a chance rustle during flight. (When I purposely caused a target to rustle during flight, the owl seldom failed to strike it, even up to 40 ft away from the perch.)

In order to exclude any trials in which the owl may have gained additional information during flight, I base my final calculation of the owl's angular accuracy only upon strikes in which the owl missed. Thus, while I believe I have avoided crediting the owl with too great an accuracy, I have probably biased my calculations by excluding all successes. However, the data is probably not worthy of more precise treatment. In summary, I feel that my figures on angular accuracy are crude and can give only a general indication of the accuracy of the barn owl's remarkable acoustic system.

For experiments in which I moved a dead mouse on bare sand, five misses were chosen out of a series of more than 200 successful strikes. The results to the nearest 0.1° give a mean miss of $0.8 \pm 0.5^\circ$ in the horizontal plane and $0.5 \pm 0.3^\circ$ in the vertical plane.

It is interesting to note that, except with frequencies above 8.5 kHz removed, the owl's angular accuracy appears to be finer in the vertical plane than it is in the horizontal plane. I expect that further experiments will indicate the same trend. For unless an owl is looking down from directly above its prey its orientation will always be more critical in the vertical than in the horizontal plane for location of an area the size of its spread talons which would include a fair portion of the mouse. (This of course becomes more critical in strikes from lower perches.)

Alightings

Frequently the owl did not strike at all, but simply flew down and 'alighted' on the floor. On the basis of more than 200 observed 'alightings' and analysis of the infra-red motion pictures several significant differences arise between flights culminating in a 'strike' and flights culminating in 'alighting'. Plate 5 shows frames from an alighting sequence. In alighting the owl flaps its wings continuously after leaving the perch, much as it does during a strike flight in darkness. Towards the end of the flight, however, rather than facing the direction of its motion, the owl slowly drops to the ground with its line of sight held horizontally and while flapping its wings. The feet are not brought forward beneath the tip of the bill and the owl does not bring its talons into the trajectory of its ears at the end of the flight. The talons do not appear to be extended in the rigid, constant-distance attitude seen in a strike and at the moment of impact the eyes are open. The owl lands softly, and in every case its final position is short of the sound source. After landing the owl does not search in the leaves but stands facing straight ahead. If a new sound is made the owl tries to fly or leap forward and strike, but if there is no sound the owl will eventually walk forward and search in the leaves at a point several feet removed from its alighting point. All of these differences from strikes seem to me to indicate that the owl does not 'expect' to find the mouse in the position in which it has landed, and is, therefore, not striking but merely approaching to await the next sound from the mouse.

In alightings, unlike strikes, a barn owl shows greater accuracy in the horizontal than in the vertical plane. For example, in nine consecutive flights toward a loud-speaker 35.5 ft away the owl alighted every time, and its mean position in relation to the speaker was off by $3.8 \pm 1.9^\circ$ in the horizontal plane and $12.8 \pm 4.1^\circ$ in the vertical plane.

The conditions under which alightings were seen were the following: (1) when a loud noise occurred during the owl's flight in total darkness, (2) when something unusual was done either to the owl's hearing, e.g. when its ears were plugged; or to the sound, e.g. when frequencies above 5000 Hz were removed, and (3) when the target was more than about 23 ft away (except when the rustling sound continued as the owl flew). From this it appears that 'alightings' are simply the owl's best means of getting close enough to a sound for a final orientation and strike; for, in general, a barn owl appears to alight either when alarmed, or while flying at a distant sound source, or when the acoustic information received is insufficient for a successful strike.

It is noteworthy that the owl does not attempt a flight at a sound source unless it is close enough to have a fair chance of hitting it, and that when the distance is too great or the information in the sound is inadequate or distorted the owl improves its position by approaching closer before making the final orientation for the strike. (In more

natural surroundings and with faint illumination its silent flight should be a valuable asset in this regard.)

It should be possible at this point to calculate the maximum distance at which we can expect a barn owl to make a successful strike and to compare this distance with the distance beyond which we know it will not strike. The barn owl I used in the angular accuracy tests had a talon spread measuring 6 in horizontally and 3 in vertically. If we assume an average talon spread of 4·5 in and an average dimension of 2·25 in for a mouse 3·5 in long and 1 in wide, then, if the owl hits inside a circle with a diameter of 6·75 in (the sum of the average dimensions of strike pattern and mouse) it should catch the mouse. A circle of 6·75 in on the horizontal plane (the floor) when viewed from a vantage point of 84 in (the height, in my experiments, of the owl's head when sitting on its perch) subtends a maximum angle of about 0·9° in the horizontal plane and a maximum angle of 0·5° in the vertical plane at a distance of 20 ft. From this rough calculation we see that a barn owl should be able to hit a mouse at distances up to 20 ft under the conditions I used. This distance is extremely close to the distance beyond which my owls would not strike (23 ft). It also lends support to the figure for angular accuracy which I attained by the means described.

I feel there may be more luck than truth in this close agreement of figures, and I feel therefore, that other means of defining the angular accuracy of a barn owl in locating a point source of sound should be tried.

Acoustic location of prey in nature

One of the larger gaps in this work is the almost complete lack of observations indicating that owls do indeed use their remarkable acoustic ability to locate prey in the wild. But I can only cite one instance which indicates that owls in the wild were using their ears for prey location. A. Oeming (personal communication) observed great grey owls (*Strix nebulosa*) diving into deep snow and bringing up lemmings. According to his account, the lemmings were invisible from the surface, nor were there any traces of runway systems from above to give away the lemmings' position below the snow. What sounds would an owl hear from lemmings beneath the snow? Chewing seems likely in this case. I know, from spectrographic analysis, that the sounds of a mouse chewing seeds are rich in high frequencies. Because so many other motions of mice are executed quietly, it seems likely to me that the owl's auditory clues, in the wild, would be quite different from the sound of rustling leaves which I chose as a stimulus in the laboratory. I can well imagine cases in which confusion of a mouse's footfalls with sounds made by small motions of lesser parts of larger animals would be an error that an owl could ill afford to make. Chewing or squeaking, on the other hand, should identify their author more reliably, and it is likely that these sounds, whenever available, are most useful to owls in locating their prey.

Other species with asymmetrical ears

It is interesting to note that the great grey owls observed by Oeming have asymmetrical ears and can therefore be expected to place special reliance upon their ears for some purpose. It has been my experience that owls with symmetrical ears cannot be trained to locate prey in total darkness, whereas those with asymmetrical ears can.

I tried to train two screech owls (*Otus asio*) and three great horned owls (*Bubo virginianus*) to capture prey in total darkness with no success. I spent many hours at this and tried numerous variations of technique (such as turning out lights only after the owl had seen, and in some cases actually started to fly toward, prey) but none was ever successful. On the other hand I was easily able to train two saw whet owls (*Aegolius acadica*) to capture prey in total darkness, and I am convinced that Dice (1947) demonstrated that long-eared owls (*Asio otus*) locate prey acoustically even though he did not stop his main line of inquiry to prove this rigorously. Saw whet, long-eared and barn owls all have asymmetrical ears, but the asymmetry is achieved by very different means in the three species. In saw whets, the skull is asymmetrical, in the others it is symmetrical, but the skin structures lying near the ear form asymmetrical entrances to the ear canals (achieved by horizontal membrane in the long-eared owl, and by skewed opercula in the barn owl). Thus asymmetrical ears seem to have evolved on three independent occasions among owls, and the barred owl (*Strix varia*) may represent still a fourth variation, though I have not tested their ability to capture prey in darkness.

*The effect of the barn owl's head on the intensities of sounds
arriving at the ear from various angles*

Physical analysis; three-dimensional directional sensitivity plots

In the discussion of behaviour during a strike we have seen some aspects of the barn owl's capacity to locate a sound source using hearing alone. It now seems pertinent to ask how the owl does it, i.e. how might a barn owl use the information available in a complex sound like rustling leaves or chewing to direct a strike acoustically?

Presumably an owl can extract four kinds of information from incoming sound waves: frequency, intensity, phase and time-of-arrival. Leaving aside monaural localization since the time delays necessary for 0.5° accuracy seem unreasonably short and since an owl with only one ear available does not strike prey, let us concentrate on systems involving two ears. Using both ears together directional information can be gathered by comparing differences in time-of-arrival or phase of sounds. As pointed out by Mills (1958) and by Schwartzkopff (1962) and later by Payne, Roeder & Wallman (1966) the most favourable conditions for time-of-arrival comparisons occur when sounds come from straight ahead, so that the animal need not attend to the magnitude of the time delay but only to the presence or absence of a delay. Schwartzkopff (1962), Grinnell & Grinnell (1965) and Payne *et al.* (1966) have also pointed out that any difference in time-of-arrival of sounds at the two ears will be enhanced by the fact that the latency of acoustic neurone activity is inversely proportional to sound intensity. Thus we should seek to study an owl's acoustic system from the point of view of interaural time differences as well as taking a detailed look at directional sensitivity of each ear in three dimensions (since an owl locates direction to its prey in both vertical and horizontal planes). We must also concentrate our attention on frequencies above 5000 Hz since we have seen that such wavelengths are essential to a barn owl for accurate location of a sound source.

I was unaware at the outset of this work of Mills's (1958) paper and Batteau (1967) had not yet published on his work with the human pinna as a delay line for monaural

localization (the pinna has obvious similarities in form with the barn owl's external ear). The hypothesis upon which I based my work therefore was that if the intensity of sounds reaching the owl's eardrum varied markedly with the angle from which the sounds came, the owl might be able to estimate the direction of a complex sound by observing intensity changes as it turned its head to face the sound. Accordingly, I made detailed analyses at several frequencies of a barn owl's directional sensitivity patterns in three dimensions. Since a barn owl's angular accuracy in locating a sound source is at least as good in the vertical as in the horizontal plane, I plotted the sensitivity patterns in three dimensions. Although I favoured in these early days the view that directional sensitivity was of greatest significance to an owl for finding the direction of a sound source (and presented this view in an earlier report; Payne, 1961) I now feel that it is more likely that the owl uses two cues: (1) variations in sound intensity with direction and (2) interaural time differences enhanced by intensity dependent latencies.

To obtain directional sensitivity plots I played a series of pure tones at constant intensity from various angles to a dead owl suspended in space, while monitoring the intensity of sounds received at the site of the eardrum with a microphone probe tube penetrating the skull. The apparatus I used for this is shown in Text-fig. 2.

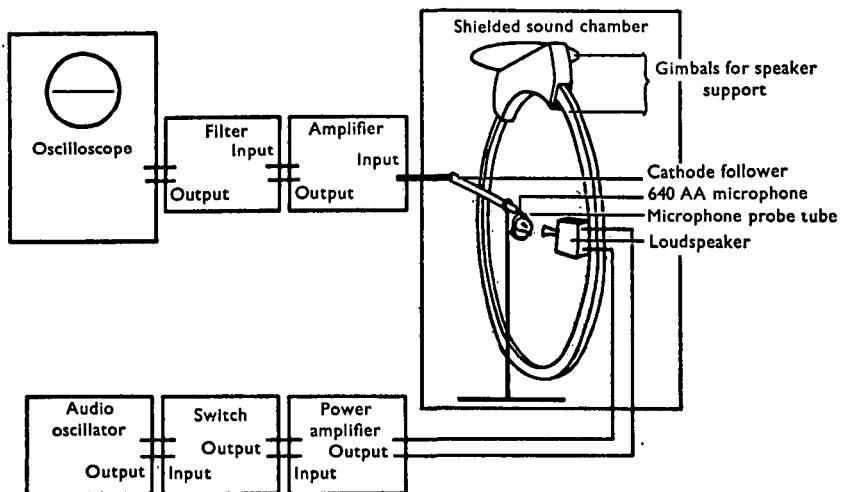
Method of measuring directional sensitivity

It was important that the apparatus holding the owl should be of minimum dimensions so that the owl could be suspended in as close an approximation to a free sound field as possible. In initial experiments I strapped an owl into a curved frame which supported the body from behind. A series of clamps allowed me to fix the owl rigidly in any posture. Pl. 1 I shows the support. The object going down towards the head is the cathode follower for a Weston 640 AA calibrated microphone. A probe tube attached to a microphone penetrated the skull and came out with its tip in the position formerly occupied by the eardrum, which had been destroyed. Thus, the only sound getting to the microphone arrived via the probe-tube tip, which sampled intensity changes at the former site of the eardrum (the probe tube was normal to the eardrum). Later, after discovering that the owl's body had little or no effect on directional sensitivity plots, I was able to do away with the structure which supported the owl by testing the head alone as is shown in Pl. 1 H. The probe tube supported the head, so that only the clamp which held the microphone was necessary. The external structures of the ear being tested were in all cases unobstructed because the probe tube penetrated the skull from the contralateral side of the head. The external opening of the ear being tested was fixed at the centre of an imaginary sphere. A loudspeaker was mounted on a set of gimbals which allowed it to rotate to any position on the surface of that sphere (see Pl. 1 H-J). Thus, sounds of constant intensity and frequency, at a constant distance from the ear, could be directed at the ear from any angle. I tried to make sure that sounds would be broadcast only towards the centre of the sphere by mounting the speaker in a box filled with fibreglass insulation. Since the maximum signal output was necessary to override the extreme attenuation of the microphone probe tube, I fitted the speaker with an exponential horn moulded from acrylic plastic. The speaker was attached to the periphery of a wooden ring. Revolving the ring about its centre allowed positioning of the speaker in the vertical plane.

Placements in the horizontal plane were achieved by revolving the ring about any diameter.

The position of the speaker in the horizontal plane was recorded in degrees, according to the standard method (see Wever & Lawrence, 1954). In the horizontal plane at 0° sound was aimed at the owl along its line of sight; at 90° at the right side of the head; at 180° , directly at the rear of the head; at 270° , at the left side of the head. In the vertical plane, 0° coincided with a plane normal to the owl's body axis that included the line of sight.

I used a pulsed, pure tone; rise time 1 msec; duration 45–450 msec. The electronic switch which pulsed the sound divided 'on' and 'off' time equally at any repetition rate and repetition rates were chosen so that the 'anechoic' chamber in which I worked could quiet down completely between pulses. The output of the calibrated microphone passed through a decade amplifier and a variable band-pass filter. It was then displayed on the face of an oscilloscope and photographed. I measured peak-to-peak



Text-fig. 2. Black-box diagram showing apparatus used in mapping directional sensitivity patterns.

voltage from the resulting film with a set of calipers which were calibrated in decibels relative to 0.0002 dynes/cm² for all oscilloscope voltage ranges. By this means I was able, after adding the appropriate frequency correction values, to calculate the intensity of sound as received at the owl's eardrum at any frequency for any position of the sound source. By measuring the intensity before the end of the third millisecond of any pulse I avoided any effects of echoes or standing waves. (The nearest surface, other than the owl's support and the microphone, was 3 ft away.)

The main equipment problem encountered in this approach was transmission of sound through the walls of the probe tube. Eventually sound penetration through the walls was reduced 50 db by using a heavier-walled probe tube (the walls were of stainless steel: 3/32 in thick) covered with four insulating layers: cotton innermost, then 'Play-doh' (a children's modelling compound with good sound attenuation characteristics), then a second layer of cotton, and on the outside, aluminum foil.

Because of the difficulty of aligning the owl's head at the centre of the sphere and

properly positioning the probe tube, I tried as much as possible to work continuously through a series of frequencies or through a series of tests at one frequency before dismantling the apparatus. In three cases, measuring sessions went on 16 h a day for over 2 weeks, during which time more than 5000 intensity readings were taken. From such sessions comparisons of directional sensitivity patterns at different frequencies may be made. Frequent stability checks throughout all sessions assured me that the equipment was stable within 2 db.

In order to gain a fairly complete picture of the directional sensitivity plots at any one frequency, data were usually taken at 5° intervals in both vertical and horizontal planes. The procedure was to photograph one oscilloscope sweep for each 5° increment in the horizontal plane, while holding the vertical position of the speaker constant. After each horizontal run I searched for sudden changes in intensity, by increasing the pulse rate and sweeping the speaker rapidly from side to side in the area between the horizontal line of readings just taken and the horizontal line about to be taken. If a 'low' (a region of very low sensitivity) was discovered, first its deepest point (region of lowest sensitivity) was measured and then the area around it was sampled by two lines of measurements whose intersection at right angles overlay the deepest point. I usually took 20 measurements 1° apart, starting and ending 5° to each side, in both vertical and horizontal planes. By such procedures I tried to avoid missing regions of sudden change.

Once all measurements for one frequency were taken and their values computed to the nearest decibel, they were placed on a grid (in the same co-ordinate positions as those in which they had been taken during an experiment), with horizontal degrees as abscissa and vertical degrees as ordinate. This resulted in a Mercator projection of speaker positions at which data had been collected. In order to give some form to the resulting array of numbers, iso-intensity lines were drawn at 1 db intervals enclosing areas of equal intensity. The resulting graph of any one frequency resembles a weather map, where 'highs' are areas in which the owl would hear the frequency being tested well and 'lows' are areas in which it would hear poorly. The rate of change of intensity is computed by counting iso-intensity lines/latitude or longitude degree.

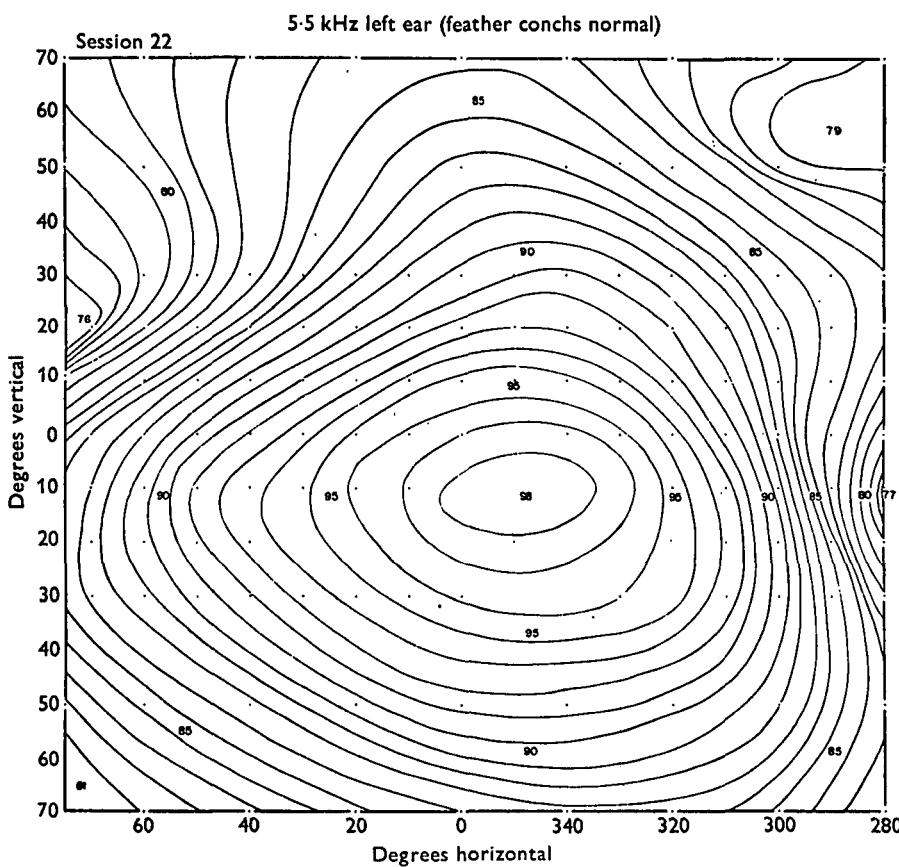
I used six different barn owls in 22 measuring sessions. The figures shown here for the right ear are from five different sessions (four different owl heads).

I made six complete directional sensitivity plots at 13 kHz which have convinced me that although my results did not repeat in detail, they are basically similar, differences being for the most part superficial or insignificant. I have not averaged my results at corresponding frequencies for two reasons: (1) the position of the ear flaps and feather conchs was found to be highly critical and could not be easily enough controlled to make sure that any two sensitivity plots merited consideration as being point-for-point comparable. (2) the position of some lows was so critical and their cut-off rates so sharp that a slight tap of the ring supporting the speaker sometimes made a difference of 6 db or more. Because the lows are, in fact, very real—and, probably, important—features of the owl's directional sensitivity pattern—being always present and pronounced (only their position varies)—and because any form of averaging would only have obscured their existence, I decided to draw each sensitivity pattern by itself. The opposite decision was made by Schwartzkopff (1962) with the consequence that one is left with the impression that intensity changes in an owl's

directional hearing are gradual and of only a few db; whereas perhaps their most prominent feature is that they are abrupt and may reach attenuations of 50 db, or more, within a few degrees.

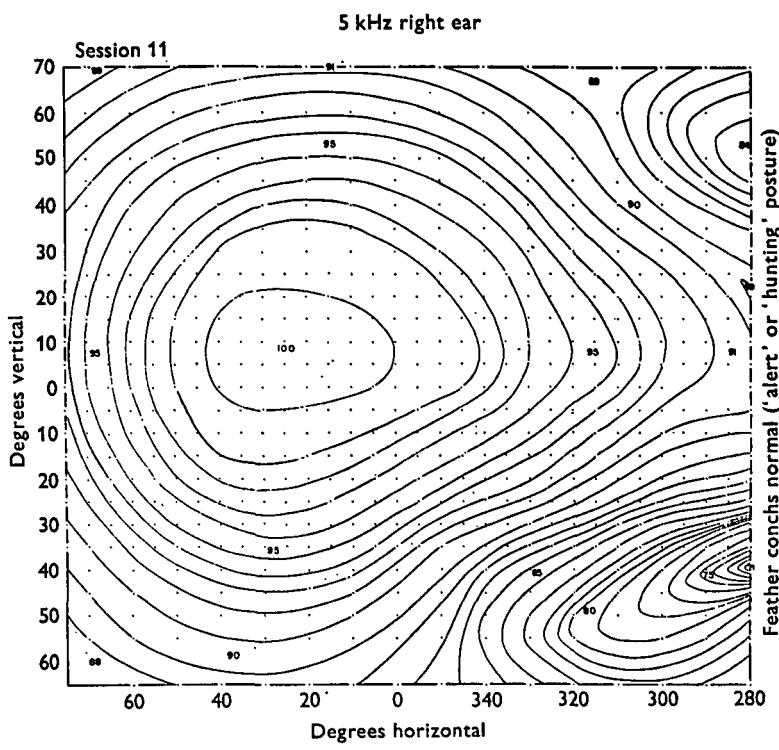
I used a calibrated microphone because I hoped that by making calculations of absolute sound pressure I could observe the effect of the owl's head in attenuating or enhancing various frequencies. Unfortunately, I did not discover until later in my measuring sessions that the position of the probe-tube tip relative to the eardrum was critical. Although the positions of all features of any one sensitivity plot were independent of the position of the probe-tube tip, the absolute values of all features changed with any change in position of the tip.

Without the owl's head in place, the intensity as measured at the centre of the sphere was 100 db relative to $0.0002 \text{ dynes/cm}^2$ for all frequencies; with the head present

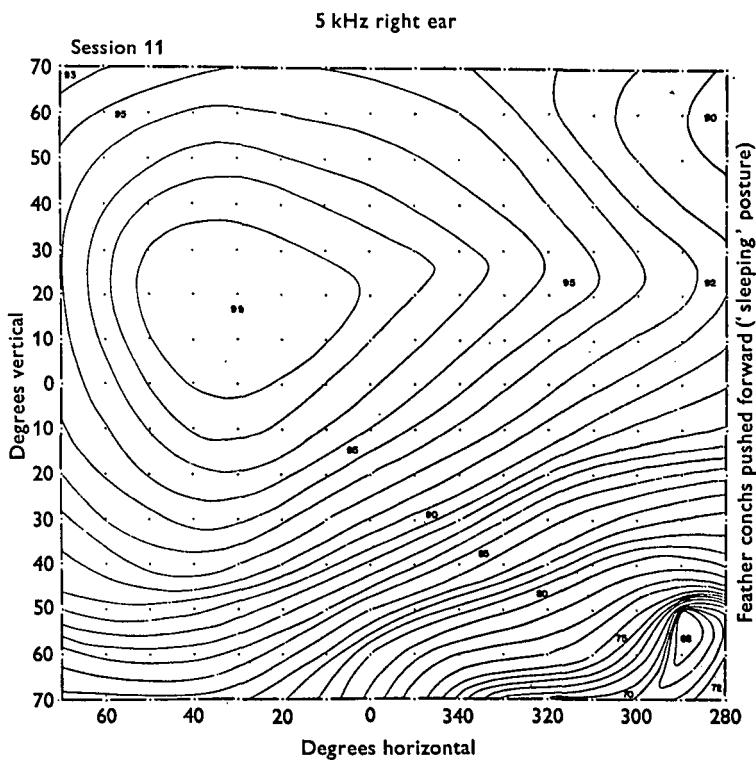


Text-fig. 3a (continued on next page)

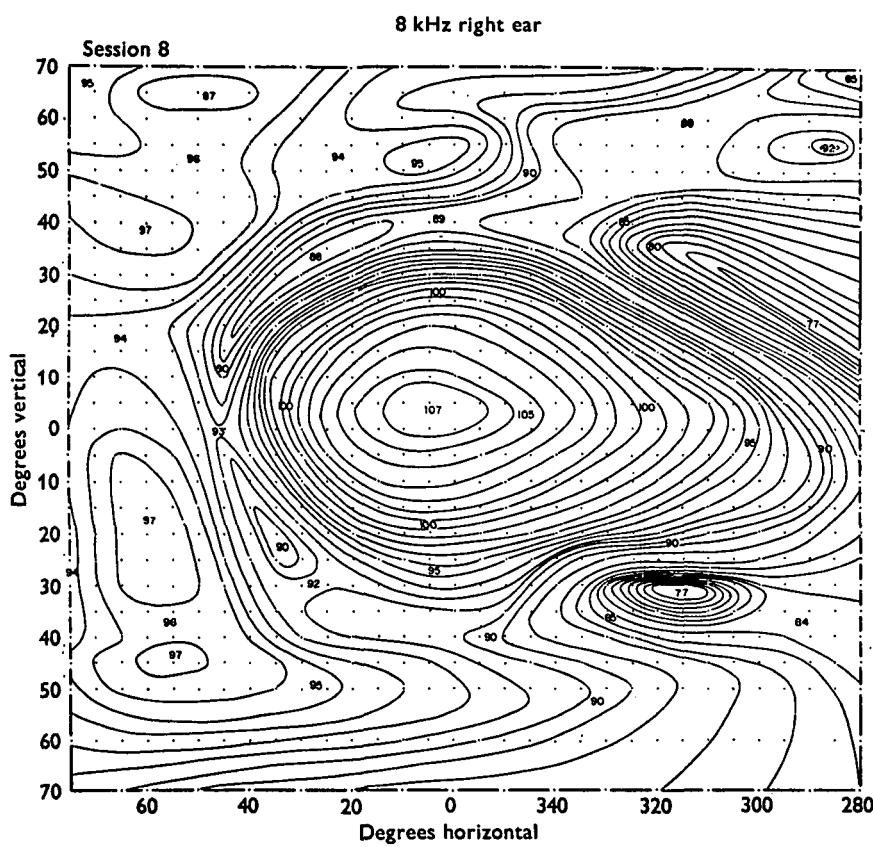
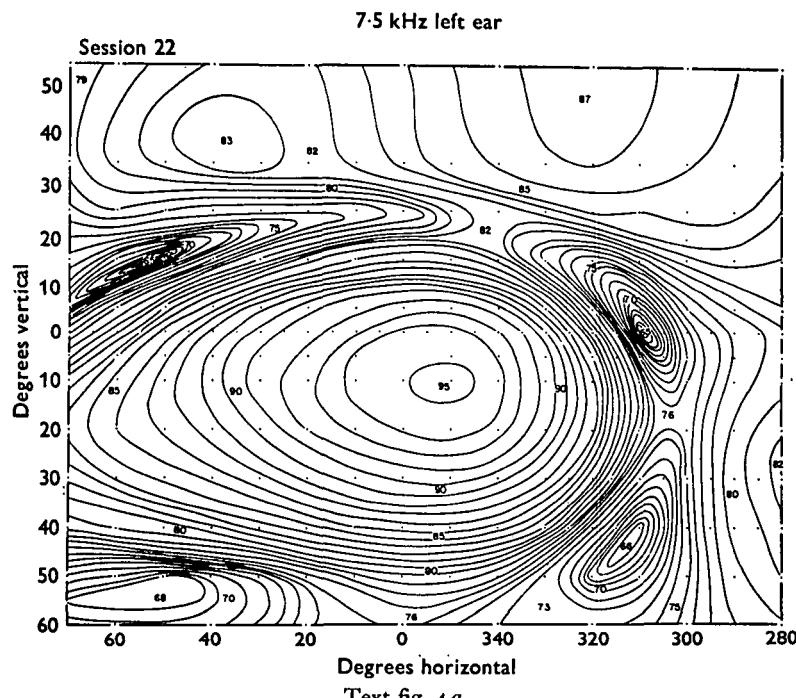
Text-figs. 3-5. Mercator projections of barn owl directional sensitivity patterns when tones of constant intensity are directed at an ear from different angles. On each plot, one ear and one frequency is examined. Sensitivity is recorded in decibels; iso-intensity lines being drawn every decibel. The sound intensity at the site of the owl's ear without the head in place is 100 db in all cases. Points on the plots are points at which data were taken. Charts are drawn from an observer's point of view, i.e. the owl, if it were drawn on the plot, would face the observer from 0° vertical and 0° horizontal. Text-figs. 3 and 5 also illustrate the effects on directional sensitivity of disturbing feather conchs and ear flaps (respectively).



Text-fig. 3 b.



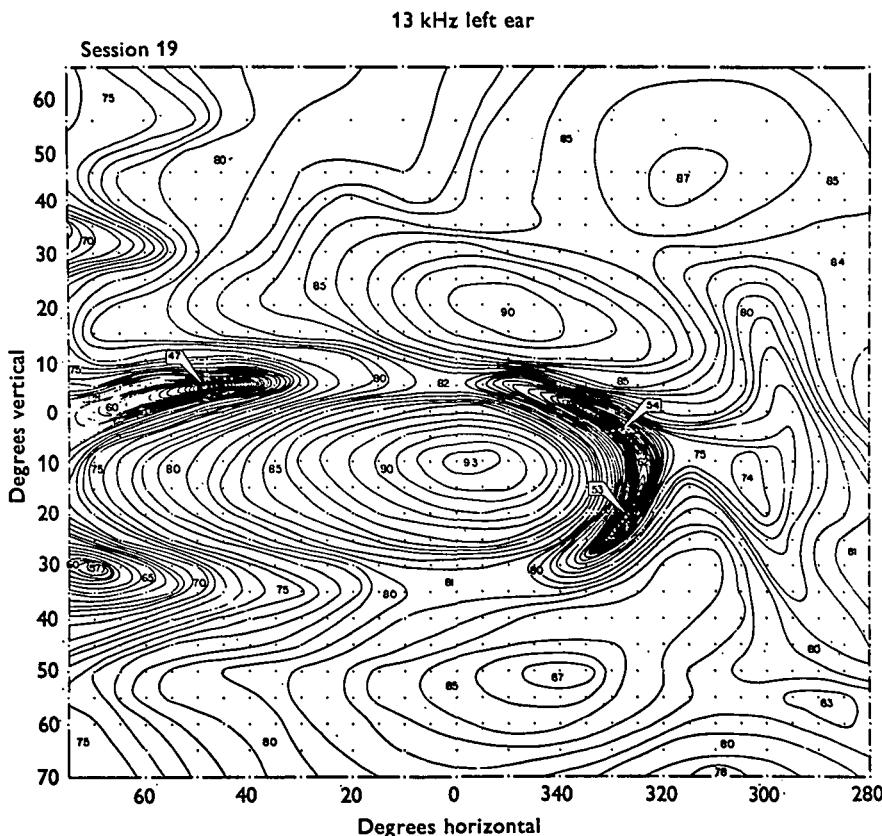
Text-fig. 3 c (cont.). For legend see p. 557.



Text-fig. 4b. For legend see p. 557.

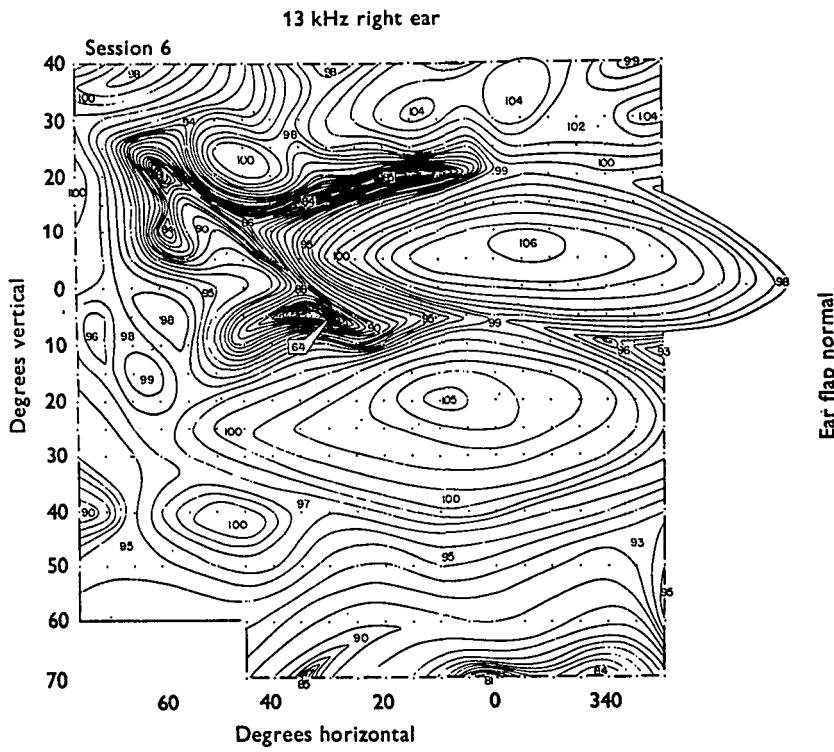
the maximum values at different frequencies varied: for example, in session 22 (a continuous experiment without any change in the set-up) from 93 to 112 db. Thus, although my results seem to indicate that there is some increase in capture area—and thus in focussing of sounds—as frequency is increased from 8 to 13 kHz, the magnitude of increase of intensity is still unresolved. (In my experiments, absolute sound-pressure measurements are only accurate to ± 3 db.)

I feel that the technique which I have described above may be criticized in two respects. (1) Slight displacements of opercula and feathers caused radical changes in sound intensity. I took great pains to get feather placement on an experimental owl head as natural as possible by trying to adjust feather postures to resemble feather postures in a photograph of a live owl facing the camera directly, but these efforts could be improved. (2) The positioning of the head was somewhat imprecise relative to the axes of the sphere. Once the ear being tested was located at the centre of the sphere, positioning was achieved by sighting along a radius through 0° vertical and 0° horizontal, and rotating the head vertically and horizontally until it compared as perfectly as possible (from visual inspection) with the same head-on photograph of a barn owl mentioned above. A series of more than 500 photographs taken later, however, when I replaced the loudspeaker with a camera and photographed the owl's head by 5° increments, convinced me that my method of orienting the head by visual inspec-

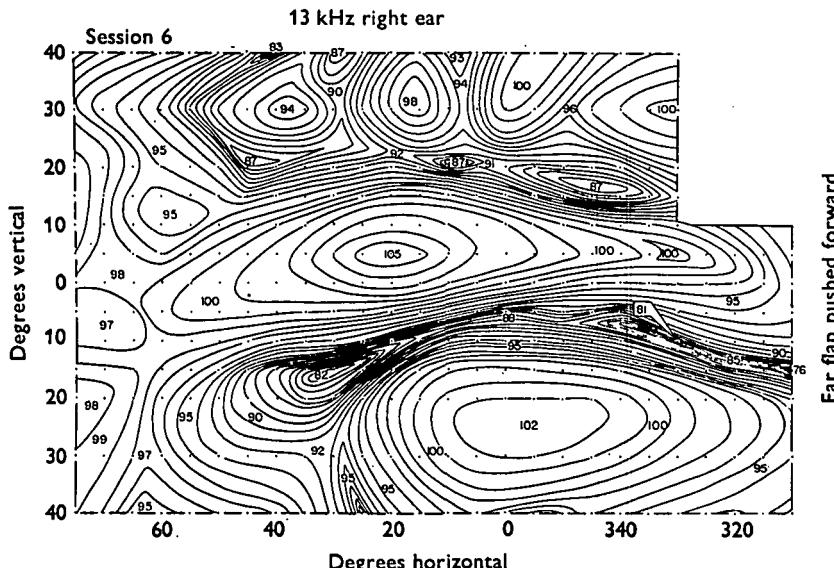


Text-fig. 5a (continued on next page). For legend see p. 557.

tion during initial placement may have been no better than $\pm 2.5^\circ$ in the vertical and horizontal planes. This, coupled with the fact that relative intensity measurements from filmed oscilloscope sweeps were only accurate to ± 2 db means that the detail



Text-fig. 5 b.



Text-fig. 5 c (cont.). For legend see p. 557.

shown in any set of charts from one measuring session exceeds what can be reliably stated when comparing different measuring sessions.

RESULTS

In spite of the limitations outlined above, I feel that several trends in the directional sensitivity plots are apparent and real. (1) Directional sensitivity patterns become more complex as one goes from lower to higher frequencies. (2) At frequencies above 8 kHz sharply defined lows appear on the same side of the head as the ear being tested. (3) As frequency is increased additional lows appear, and lows which were present at lower frequencies move closer to the line of sight, thus more sharply confining the central, line-of-sight region of maximum sensitivity. (4) Comparison of positions at which regions of maximum and minimum sensitivity occur in the vertical plane reveals that in the right ear such regions are roughly 10–15° higher than in the left ear. This is presumably due to the asymmetry of external ears. (5) As frequency is increased, the slopes of lows become steeper.

So far in discussing the sensitivity patterns we have assumed that the structures of the external ear are held in one position. This seems to be a reasonable assumption since birds do not have mobile pinnae as do mammals. However, it is quite possible that barn owls move their ear flaps and feather conchs, and thus change the sensitivity pattern for any frequency. Several authors (e.g. Stellbogen, 1930; Heinroth & Heinroth, 1958) have assumed that owls can and do move their ear flaps, basing these claims on the presence of especially well-developed muscles attached to the ear flap. However, I know of no direct observations of owls moving their ear flaps while attempting to locate sounds. (Schwartzkopff (1963) has seen opercular motions in a lightly anaesthetized *Asio otus*). The feather conchs, however, can be and are moved, at least to the extent of erecting and depressing the feathers in the course of a few seconds. This can be observed readily by comparing feather-conch postures in a 'sleeping' and in an alert or hunting owl. When hunting or alert, the feather conchs are fully expanded, the heart-shaped face appears broad, and the two central rows of feathers running down the edge of the bill are compressed together into a sharp ridge (see Pl. 1B). When the owl is 'asleep' lateral edges of the feather conchs are brought forward and together medially, which makes the face appear much narrower, and the central rows of feathers are tilted laterally and fluffed out, almost obscuring the eyes from in front and giving the formerly sharp ridge a broad flat top. When one watches the face of a barn owl that has just been abruptly awakened it looks somewhat like a time-lapse motion picture of an opening flower as it expands and opens its feather conchs.

What effect might changing the position of ear flaps and feather conchs have on directional sensitivity patterns? Text-fig. 5 shows two directional sensitivity plots at 13 kHz taken during one experiment on the same owl head. The only thing changed in this experiment was the position of the ear flap. In one set of measurements the flap in front of the ears was in the normal relaxed posture, while in the other the flap was held forward with a fine wire during collection of data. The following differences are apparent: with the flap held forward, the slope of the horizontal low around –10° is increased; and the crescent-shaped low has practically disappeared. Text-fig. 3 shows that when the feather conchs are compressed into the 'sleeping' posture, the region of maximum

sensitivity shifts laterally and upwards from its position when feather conchs are in the normal hunting posture. A series of detailed tests in lows showed that the slightest adjustment of the feathers in the feather conchs also shifted the position of the lows.

On several occasions I tried to see whether a barn owl moved its ear flaps and/or feather conchs when orienting to prey acoustically. My attempts were all frustrated by not being able to get close enough to the owl to detect such motion with the Sniper-scope without so disturbing it that it spent all its time watching me. This should be tried with better equipment.

Intracranial sound transmission

There is one final question upon which I have only touched before, but which must be discussed more fully. Does the connexion between the two middle ears (see section on anatomy) allow for acoustic coupling between the two ears; and, if so, does the right ear hear sounds which have entered via the left ear and vice versa? In the penultimate measuring session I was suddenly faced with results which were completely different from anything I had obtained before; instead of two or three lows at 13 kHz, I found 16, and when I plotted this data, I found that the lows ran together with maxima and minima going across the head in a parallel series of diagonal bands. After a number of experiments I concluded that these patterns resulted from acoustic interaction between the two ears via the canal connecting the two middle ear cavities. I later found by dissection of the owl head used in this session that the connecting canal was completely free and unblocked; whereas inspection of owl heads used in previous experiments (and stored since their use in a freezer) showed that their connecting canals were blocked in three out of four cases by brain tissue which had apparently leaked in from the hole broken through the wall of the brain case to allow passage of the microphone probe tube. Whether the leakage had occurred during or after the previous experiments I could not tell. (All other auditory cavities were completely unobstructed). To test the possibility that brain-tissue leakage had invalidated the previous experiments, I removed all brain tissue from a fresh barn owl's head, dried the cavity thoroughly and stuffed it with 'Play-doh' before implanting the microphone probe tube. Again, I found the familiar three lows. The aberrant experiment showing the many lows had also rendered a normal polar pattern of sensitivity at 13 kHz (such as Text-fig. 5, left ear) which fits well with previous results, but this was only obtained when the right ear (the ear not being tested) was plugged with cotton. Since all values composing the abnormal directional sensitivity plots were c. 14 db lower than values obtained in all other measuring sessions I conclude that there was some blockage between the entrance of the ear being tested and the implanted probe-tube tip. This would make for an abnormal ratio of intensities between sounds arriving at the probe-tube tip from left and right ears.

Interaural transmission of sound has been studied by Schwartzkopff (1952) and Schwartzkopff & Bremond (1963). These workers find an average interaural attenuation of 20–40 db in birds. In the more recent paper they report that a click was attenuated by 35 db in passing through the intracranial interaural passages of a tawny owl (*Strix aluco*). Such measurements suggest that a blockage of the ear being tested, reducing direct entrance of sound by 16 db could be expected to produce the sort of results I obtained with the aberrant owl.

It is worth noting that cross communication between the two ears would be of consequence when a sound source was located in the region of a low for one of the ears. In such a case even sounds attenuated by 35 db in passing through the canal connecting the two ears would override sounds arriving directly at the ear aimed in the direction of a low. It seems, from inspection of the directional sensitivity plots, that such conditions are rare, and if they do occur only a narrow frequency band would be affected.

Analysis from cochlear microphonics

In efforts to check the results which I obtained using a microphone, I also tried to measure intensities received at the eardrum by recording the microphonic activity of the cochlea of a live anaesthetized owl. It has long been known that by placing an active electrode on the round window of the cochlea one can obtain an electrical replica of acoustical waves being received at the inner ear. (For a review, see Stevens & Davis, 1938; also, Wever & Lawrence, 1954.) Such 'cochlear microphonics', since they reproduce frequency faithfully up to the limit of hearing, do not show what nerve impulses are reaching the brain, but they do represent a fair assay of sounds reaching the oval window of the cochlea. If the intensity of a sound played to an animal is plotted against the intensity of cochlear-microphonic response (both co-ordinates being in decibels), there is a linear relationship with a slope of one for the portion of the curve near threshold and from c. 15 to 35 db above threshold (depending on frequency). Since I was interested in knowing the effect of an owl's head on the intensities of sound arriving at its eardrum from various angles, I measured the relative intensities of cochlear microphonics at various sound-source angles so as to have a check on the more detailed analysis I had made using a microphone probe tube in the head of a dead owl.

To record cochlear microphonics I used the same equipment and procedure that I used in experiments with an implanted microphone, except that the microphone was, of course, not in place, and there were electrodes on the round windows of each cochlea. The electrodes were connected to small matched amplifiers on a shelf behind the owl (see Pl. 1 J), and the output of the amplifiers was then displayed, one ear to each trace, on a dual-beam oscilloscope.

Since the operations necessary to attach electrodes were terminal and barn owls extremely difficult to obtain, I used pigeons as much as possible for developing techniques. The main problem I encountered was in getting an anaesthetic which would keep a bird anaesthetized for several hours with a minimum number of booster doses. I tried ether, nembutal, dial urethane, chloralose and Equithesin (available from the Jensen-Salsbury Laboratories, 32 George Street, Boston, Massachusetts). Of all these Equithesin proved to be much the best. The dosage I used, recommended by W. C. Dilger (personal communication) was 0.023 ml/10 g body weight, injected into the pectoral muscle. Booster injections were about one-tenth the initial dose. The longest time I kept an owl anaesthetized was 23 h, after which it was sacrificed. At this time it was still breathing regularly and showing no symptoms which it had not shown after the initial dose of anaesthetic.

In implanting the electrodes I approached the middle ear from the back of the skull, just at the border between the termination of the neck musculature and the bare

skull above. My active electrode was a fine platinum wire with the tip beaten until thin and flexible and then bent into a U. A micromanipulator held the curve of the U in place against the round window of the cochlea, while the free end of the wire was glued with dental cement to the border of the hole I had made in the skull to expose the round window. Once the wire was firmly cemented, I removed the micromanipulator and capped over the rest of the hole with thick dental cement. The wire emerging from the skull was then cemented liberally to the surrounding skin with Duco cement so that any strains on the wire would be largely relieved in deforming the skin. After the electrodes had been implanted on each round window and a ground wire put in the neck muscles (I used a safety pin), I glued a small tin tripod to the scalp (two legs over the parietal bones; one over the rostral end of the frontal bones). To the peak of this tripod a nut had already been soldered so that by screwing in a bolt I had an attachment point for clamping the head in any position. With the owl centred in the apparatus described for tests with the microphone probe tube (see above), experimentation began.

The results I obtained using this technique were discouraging since in order to override the amplifier noise level I had to increase sound intensities until I was working in the non-linear portion of the microphonic response *v.* intensity curve. The consequence was that when approaching a low in the owl's directional sensitivity patterns, moving the speaker slowly in order to collect data, the sensitivity of the ear kept changing to give an almost uniform response; unless I swept the speaker rapidly past a low, the ear simply became more sensitive, presumably by relaxation of intra-aural muscles. When moving into a region of good sensitivity the reverse happensd, the intra-aural muscles presumably contracting. To knock out the intra-aural muscles would have required a drug such as curare, which would also have affected the respiratory centre, thereby requiring some means of administering artificial respiration throughout the experiment. Thus, the only way that I could collect data, short of major equipment modifications, was to move the speaker quickly and note the regions in which sudden attenuations took place. By this means I observed disappearances of the microphonic record in the same places that I had found lows when using a probe-tube microphone at the site of the eardrum. Here also I found none of the many lows which had appeared in the single experiment in which the canal of the ear being tested was presumably plugged (see above), which supported my feeling that it had been an aberrant experiment.

In spite of the limited amount of data which I was able to collect in these experiments, I did test for the presence of microphonics at all frequencies up to 40 kHz in the three owls from which I obtained useful microphonic records. In no case was I able to elicit any microphonic response above 20 kHz even though I played frequencies above 20 kHz at an intensity of 112 db relative to 0.0002 dynes/cm² (intensity measured afterwards at the centre of the sphere). Since strong microphonics are usually found in any animal up to but not above the limit of its frequency sensitivity, they are often used as a rough indication of the limits of acoustical sensitivity in the frequency spectrum. However, the upper limit of hearing indicated by microphonics can also be too high (when compared with results from behavioural tests) so I must emphasize that better work than mine is needed before we know the true upper limit of a barn owl's hearing.

DISCUSSION

Theory—How a barn owl can locate a sound source

We have seen that the directional sensitivity diagrams obtained from the probe-tube experiments show certain trends, and that these results are supported by the scant data from the cochlear-microphonic experiments. I feel that although no final conclusions can be drawn, we can speculate fruitfully about how an owl orients to a sound source as accurately as it does.

In 1948 Pumphrey proposed an ingenious theory to explain how an owl could locate a point source of sound in three dimensions. It had not, to my knowledge, been proven at the time that owls could locate prey acoustically—but he assumed they probably could because the anatomy of the ears is so unusual and because it seems probable that they must rely under some hunting conditions upon some non-visual sense. In Pumphrey's theory two conditions must be satisfied: '(1) The sound must be complex and the ears competent to resolve it into at least three bands of frequency in such a way that independent comparison of the signals arriving at the two ears is possible in each band. (2) The two ears must have a direction of maximum sensitivity which is different for each band and is different for the left and right ear for at least two of the bands.'

The explanation of how these conditions, if satisfied, would allow an owl to locate a sound source is as follows (paraphrased from R. J. Pumphrey, personal communication). Between two identical and symmetrical ears there is a plane (the sagittal plane), within which a sound source of frequency F_1 will produce at any point an equal sensory effect in both auditory nerves. There is also a related infinite family of non-intersecting curved surfaces on each side of the sagittal plane, each surface being defined as the locus of all points at which a sound source containing frequency F_1 can be placed to produce a given inequality in the signals in the acoustic nerves. If at some other frequency, F_2 , the ears have dissimilar directional sensitivity patterns they will generate at this frequency a quite distinct family of surfaces; and if at a third frequency, F_3 , their directional sensitivity patterns are again dissimilar, a third distinct family of surfaces will be generated. Any source anywhere in the environment which produces component frequencies F_1 , F_2 and F_3 must lie at a point defined by the intersection of three surfaces, one from each family, and is, therefore, in principle uniquely locatable.

Though it may be found in the future that other species of owls locate sounds in the way that Pumphrey describes, I believe that the barn owl does not, for the following reasons. (1) The barn owl faces a sound source before making a final orientation to it; Pumphrey's theory implies that a sound could be located with equal facility regardless of head orientation. (2) The extraordinary precision of the barn owl in locating a sound source could probably be achieved only if the intersecting surfaces (which uniquely define the point of the sound's origin) were at approximately right angles to each other; but it is hard to imagine how directional sensitivity patterns whose regions of minimum or maximum sensitivity were at right angles to one another could be produced anatomically. (3) The directional sensitivity patterns which I found for the barn owl do not fit with Pumphrey's theory.

Finding that Pumphrey's theory does not apply to the barn owl has led me to

propose an alternative one. Before going on, however, let us note the principal observations on which this theory depends.

(1) Regardless of the owl's position when it hears a mouse rustle it first turns its head to face the mouse. Then, once it is facing the mouse, it must have at least one more sound before it can strike successfully. This being the case, the central region of any directional sensitivity plot—the region near the line of sight—is probably the region of most value to the owl in making a final orientation to a sound source. Therefore, while looking at the main trends and features of the directional sensitivity plots, we must be principally concerned with those which are close to the line of sight. We should expect to find that lows lying to the left and right of the line of sight would be of use in delimiting the regions of maximum sensitivity in the horizontal plane while lows above and below the line of sight would be of use in delimiting the region of maximum sensitivity in the vertical plane. This implies that the chief function of lows is to narrow and thus sharpen that region of maximum sensitivity lying along the line of sight—the important region since it is the area into which the owl brings the source before trying to strike.

(2) In Text-fig. 5 (left ear) we find what I believe to be an important general trend, i.e. a crescent-shaped low to the left of the owl's line of vision. The owl's sensitivity rises sharply to a maximum near the line of sight and falls off *gradually* as the sound is moved towards the opposite ear. The upper and lower borders of this region of maximum sensitivity fall off rather abruptly to two roughly horizontal lines of poor sensitivity. The sensitivity pattern in the right ear at the same frequency is similar except that all major features are about 15° higher than in the left ear. The result of this asymmetry is that one ear is hearing at near maximum sensitivity when sources are above the line of sight, while the other ear hears at minimum sensitivity. For sources below the line of sight, the situation is similar, except that the ears have changed roles—the ear formerly hearing at minimum sensitivity is now hearing at maximum sensitivity and vice versa.

Bearing these facts in mind, I will first consider the problem of orientation in the horizontal plane. Let us assume that a complex sound originates from a point in the horizontal plane about 40° to the left of the owl's line of sight. Frequencies between 8.5 and 13 kHz would be heard very poorly or not at all in the left ear but very well in the right ear. If the owl now turns its head towards the sound source the intensity increases in both ears (faster in the left ear) until when facing the sound directly, intensities are the same in both ears. Should the owl pass the midline and continue to turn its head until the sound comes from the right side at about 40° , the reverse situation will occur—the owl hearing the component frequencies between 8.5 and 13 kHz very poorly if at all in the right ear but very well in the left ear. Thus, it appears that the owl need only monitor one ear with the other, and when it has maximized intensities in both ears it will automatically be facing the sound (at least in the horizontal plane). If it can hear higher frequencies, where its region of maximum sensitivity is cut off closer to the line of sight with steeper cut-off rates—several decibels per degree—it can locate a sound source with a theoretical accuracy of a fraction of a degree (if it appreciates an intensity difference of 1 db). However, higher frequencies have attendant difficulties because they have many and widely scattered lows and the owl presumably cannot tell into which low a sound has disappeared since it can only tell that

the same frequency is louder in one ear than in the other. It seems reasonable that the owl could solve this problem by listening to *all* frequencies in a complex sound either simultaneously or sequentially, and orienting its head so as to maximize the intensity of all frequencies in both ears. The lower frequencies with less complex directional sensitivity patterns would automatically centre the owl on that one region of maximum sensitivity in the complex high-frequency directional sensitivity pattern which is directed along the line of sight and is bounded by lows abrupt enough to make accurate location possible.

Sound location in the vertical plane could be achieved in much the same way. To see this most clearly, first make the wrong assumption, that the ears are symmetrical, so that the line-of-sight regions of maximum sensitivity of each ear are superimposed. Then, as an owl nods its head up and down in the vertical plane, a sound source would alternately become louder and softer in both ears at the same moment and no information would be gained as to direction to the source relative to the head. But, of course, the ears are asymmetrical and therefore the central region of maximum sensitivity in one ear is directed at a different altitude from that in the other ear. Therefore, when a sound containing frequencies between 8.5 and 13 kHz originates from a point, say, 5° above the horizontal line of sight, it will be loud in the right ear and soft in the left ear. If the owl raises its gaze to face the sound it will come to equal loudness in both ears. Should the owl continue tilting its head upwards, the sound would become loud in the left ear and soft in the right ear, i.e. the reverse of the situation when it was looking below the sound source. The complicated directional sensitivity patterns at high frequencies again appear to offer equivocal information, since the owl has no way of knowing into which horizontal low a sound has disappeared. But, again, as in the horizontal plane, if the owl moves its head until it hears *all* frequencies loudest in both ears, the lower frequencies will centre it on the one region of maximum sensitivity which at higher frequencies is along the line of sight and where there is a sufficient slope of cut-off for the necessary accuracy.

Because the owl will hear all frequencies in a complex sound at maximum intensity in both ears only when it directly faces a sound source my theory demands just one thing from the owl, that it try to make *all* the frequencies audible to it in a complex sound as loud as possible in both ears. When this is achieved, the owl will automatically be facing the sound.

One of the principal weaknesses of this theory is the current lack of direct information concerning a barn owl's frequency sensitivity (audiogram, i.e. absolute acoustic threshold plotted against frequency.) My microphonic results suggest that barn owls do hear high frequencies, and a few spectrograms I have made indicate that the scream of a barn owl is energy-rich in frequencies above 8 kHz. I have also demonstrated that owls will not strike at sounds of mice rustling leaves if the sounds lack frequencies above 5 kHz, and that leaf rustles (and chewing sounds, and squeaks) are energy-rich in frequencies above 8 kHz. All of these pieces of evidence suggest that it is not unwarranted to guess that barn owls can hear frequencies at least somewhat higher than 8.5 kHz (particularly since in theory any refined acoustic localization ability requires high frequencies). But, I feel it is desirable to emphasize the need for more accurate information on the frequency sensitivity of owls, particularly at high frequencies.

Advantages of lows in a localization system

A striking feature of the directional sensitivity plots is the pronounced lows. Apparently, the whole external ear is constructed so as to produce these regions. Having structures that make it impossible to hear sounds from certain directions might seem absurd at first were it not for two things: (1) Lows in one ear seem always (at any given frequency) to lie along source directions that are in regions of good hearing for the other ear, and therefore sounds that vanish in one ear are still heard by the other ear, i.e. one ear monitors the other. (2) A low creates a sharp directionality even though it is against a diminishing sound gradient rather than an increasing one (such as a parabolic reflector might provide). This is the principle employed by a radio direction finder or any other null detector. In a radio direction finder, one guesses that the reason one has lost a radio station is because it has been successfully nulled out (one can assume that the station broadcasts continuously). In listening for an evanescent, unpredictable sound like mouse rustlings, however, we cannot assume continuous broadcasting—hence the need to monitor one ear with the other.

The chief advantage of using a null method to sharpen directionality rather than something like a parabola to focus sounds and thus to provide a directionality via amplification is that any structure that focuses must collect energy over a wide area and is therefore large, no matter how you build it. (Usually it must be several wavelengths in principal dimension, six being a useful minimum). On the other hand, directionality can be achieved by the null method with structures that are only about a wavelength in principal dimensions and hence the necessary structures in null-detecting systems can be compact. For an animal that must fly through dense woods the aerodynamic disadvantages of having large parabolas (or other large antennas) to collect sound are obvious.

Since a null-detecting system can only be operated to locate unpredictable sound sources if the lows in each antenna of the system are aimed in different directions, it is interesting to note that asymmetrical external ears in owls are a necessity if null detection is to be of any use. I am, however, only suggesting that the lows in an owl's directional sensitivity are present for the purpose of sharpening the directionality of the frontally directed regions of maximum sensitivity and that it probably is by maximizing intensities of all frequencies that owls locate the direction to a sound source.

In his excellent paper, Norberg (1968) studied directional hearing in a carefully constructed model of the head of Tengmalm's owl (*Aegolius funereus*). He only considered one vertical and one horizontal plane (both through the line of sight) when measuring variations in sound intensity with direction, and therefore may have missed the all-important bordering lows that effectively delimit and define the regions of maximum sensitivity; he also was not able to take into consideration variations in the shape of the ear openings that might be under muscular control (I have seen a close, new-world relative of Tengmalm's owl, our saw whet (*Aegolius acadica*), drastically change the shape of the feather-lined border of its 'parabolas' within a few seconds). In spite of these limitations Norberg's careful measurements of the inter-aural, time-of-arrival differences for differing source angles point out that it is likely that time differences are useful for prey location by owls. Schwartzkopff (1962) has also stressed the importance of time differences accentuated by intensity-determined latency differences. Since intensity and time of arrival are inter-related, the outcome of further

training experiments must be awaited to decide the degree to which each of these cues contributes to acoustic location of prey by owls.

SUMMARY

1. Barn owls (*Tyto alba*) can locate prey in total darkness using only the sense of hearing, with an error of less than 1° in both the vertical and horizontal planes.

2. Differences between the behaviour of barn owls flying at prey in complete darkness (analysed from films taken under infra-red illumination) and their behaviour in the light are correlated with the problems they must face in acoustic orientation.

3. Experiments with owls trained to strike a concealed loudspeaker show that they depend on frequencies of sound above 5 kHz.

4. Measurements of sound pressure in the region of the owl's eardrum, made with a probe-tube microphone while moving a loudspeaker around the owl's head, reveal that for frequencies above 8.5 kHz the ear is highly directional. At such frequencies, regions of high sensitivity (tightly isolated by peripheral regions of low sensitivity) are directed along different paths for the two ears.

5. These regions of good sensitivity are correlated with the asymmetry of the barn owl's external ears. Movements of a flap of skin in front of the ear opening changes the overall directional sensitivity patterns by redirecting the regions of maximum sensitivity.

6. A theory is presented to explain how a barn owl might locate the position of a sound source by moving its head until the intensity of all frequencies comprising a complex sound is brought to a maximum in both ears (aided perhaps by differences in inter-aural time delay that are enhanced by intensity disparities).

The research reported here was carried out by the writer while a graduate student at the Laboratory of Ornithology, Cornell University. It is part of a thesis submitted to the Graduate Faculty of Cornell University in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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EXPLANATION OF PLATES

PLATE 1

- A. Single feather from feather conch of a barn owl. Note thick shaft and narrow, dense web.
- B. Live barn owl, face view. The feather conchs are in the postures assumed during periods of activity.
- C. Auricular feather from region between feather conch and eye. Note lack of secondary branches.
- D. Barn owl's head from which auricular feathers have been removed to reveal ear flaps. The right ear flap is held forward to expose the almost square entrance to the auditory canal.
- E. Frontal view of same head. Note that the owl's left ear flap is above the level of its right ear flap.
- F, G. Left and right lateral views of the same head to show the difference in angle between each ear flap and the line of closure of the bill.
- H. Sound-room apparatus for experiments in which the head alone was tested.
- I. As H but testing ears with whole body present.
- J. Sound room with anaesthetized owl held in frame at centre of loudspeaker ring. Two amplifiers can be seen on shelf behind owl.

PLATE 2

A-P. Frames from a motion picture showing a barn owl striking in the light. After leaving the perch the owl flaps its wings once (frames A-D) then sets its wings and glides towards the mouse. The owl's feet are tucked up under its tail until frame K when it swings its feet forward. It then raises its head (frame N) and strikes with legs extended and eyes closed (frames, O, P). In some hard strikes the owl makes one final stroke of the wings to accelerate itself into the mouse—something I have not observed in strikes in the dark.

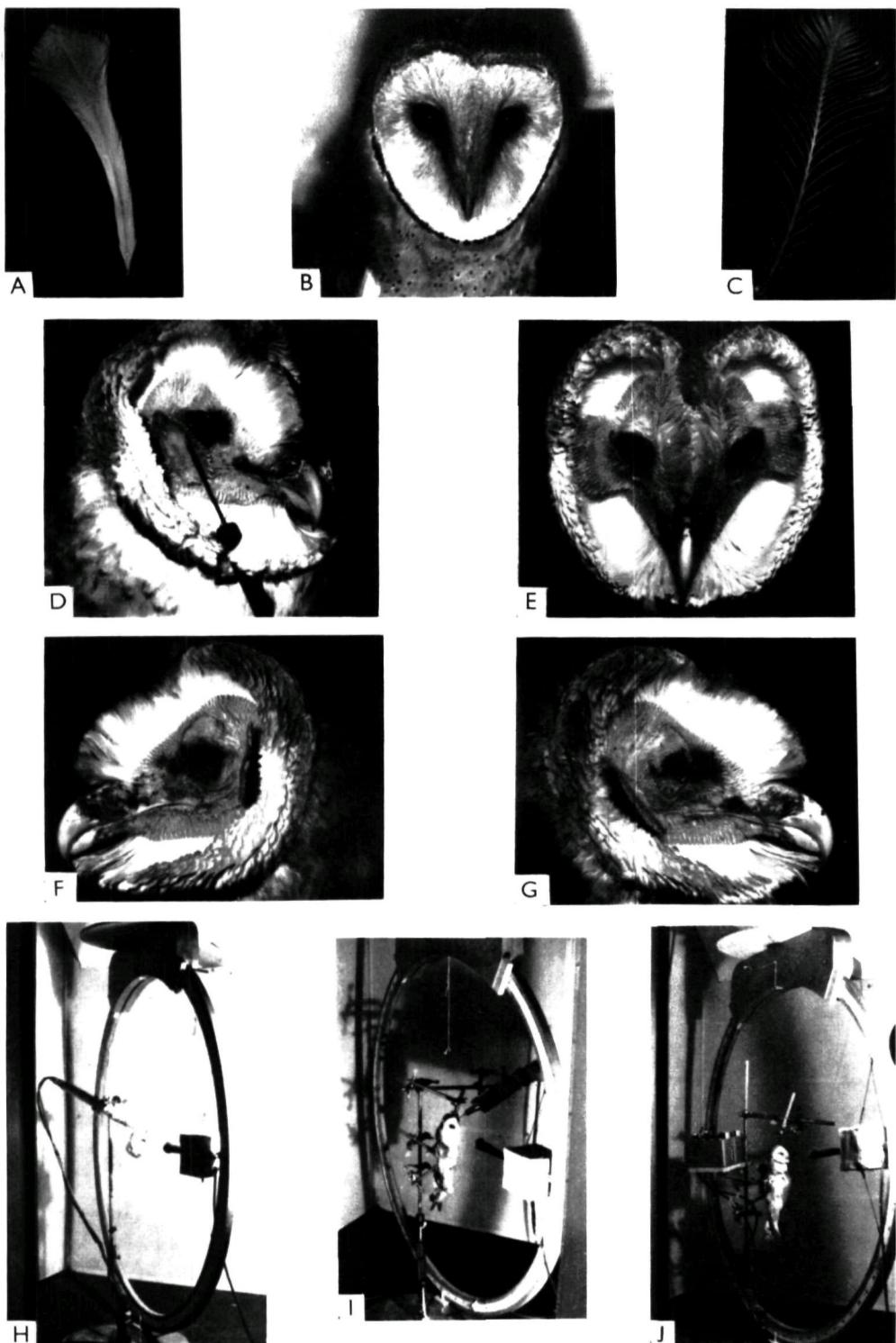
Q-X. Frames from a motion picture filmed in total darkness under infra-red light showing that barn owls cannot see mice under illumination conditions used in making observations and motion-picture sequences. The arrow indicates the mouse. Frames Q-T show the end of a strike in which the owl missed a mouse, landing instead on a leaf tied to the mouse's tail. Since owls do not miss in the light the fact that the owl missed is a fair indication that it could not see the mouse. Frames T to X inclusive are sample frames from the remainder of the sequence. Between frames T and U the mouse moved quietly away over sand on the floor. In doing so it collided with a leaf and at this sound the owl whirled to face it (frame U). The owl now faced the mouse directly from a few inches away but apparently could not see it (even though it reflects infra-red well) as is apparent by the fact that it did not strike. The mouse moved silently on and finally the owl turned away (frame V) searched in the leaves (frame W) and then stopped all searching (frame X). At this point I turned on visible light and the owl struck so rapidly I could not return to the camera in time to film it. (Had the owl seen the mouse in frame U but for some reason refused it it would not have been expected to strike it once there was visible light.)

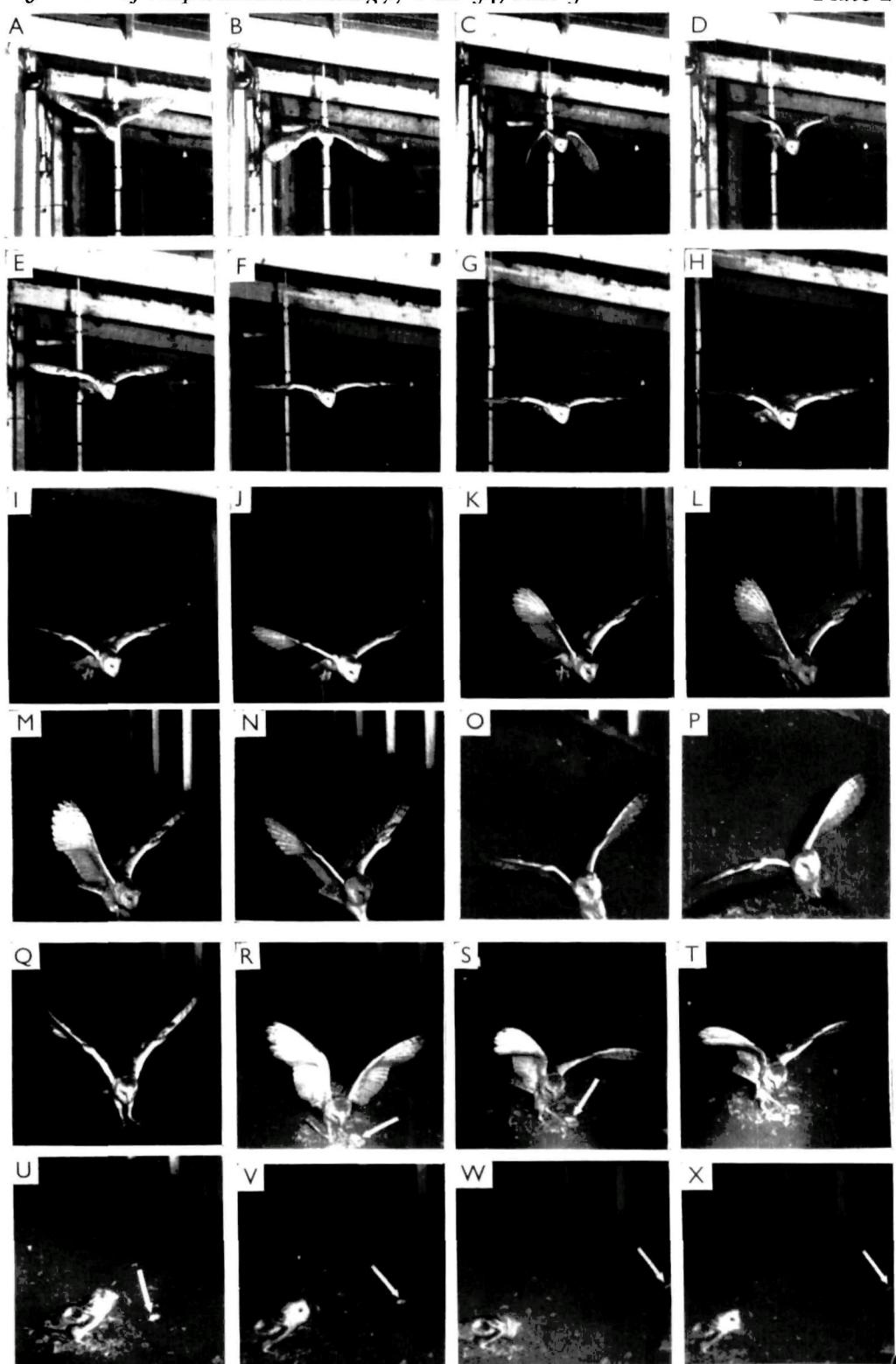
PLATE 3

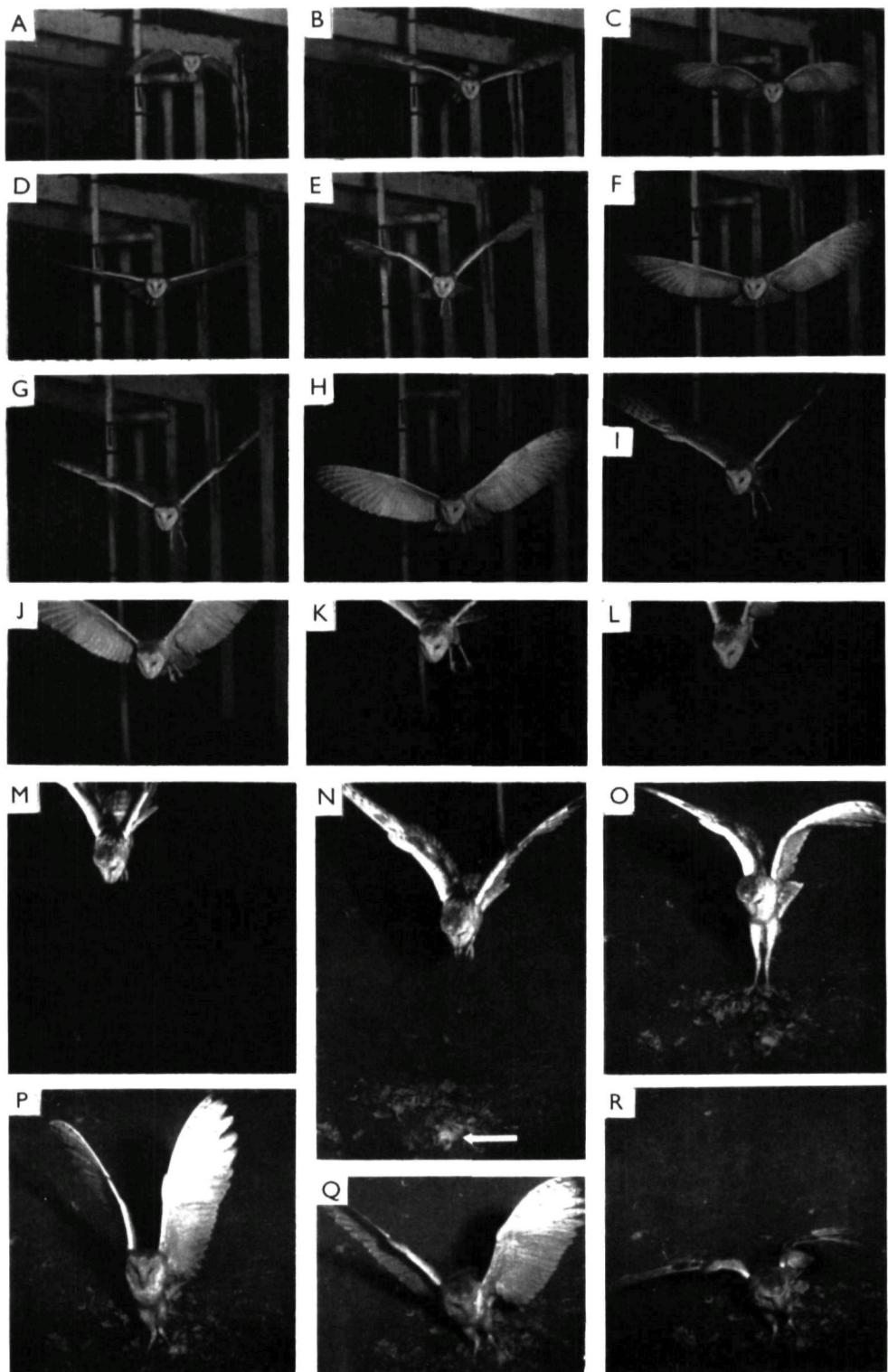
A typical strike in total darkness filmed in infra-red light. After leaving its perch, the owl flaps its wings several times, its feet swinging beneath it like a pendulum. The owl then brings its feet forward until they replace the flight path formerly taken by its ears (frame M-O). In frames P & Q, the owl strikes, grasping the mouse in its left foot. Notice here that even though it cannot see, the owl's eyes are open in flight but closed on impact.

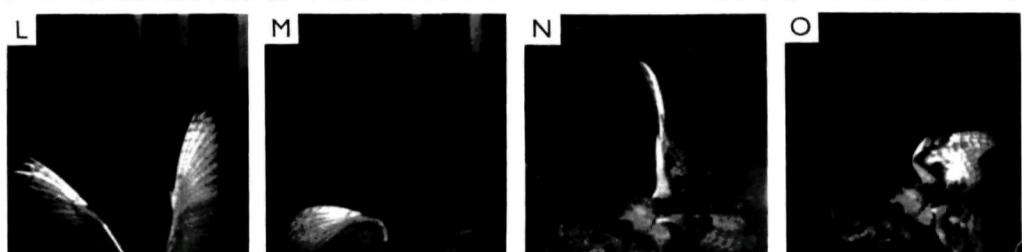
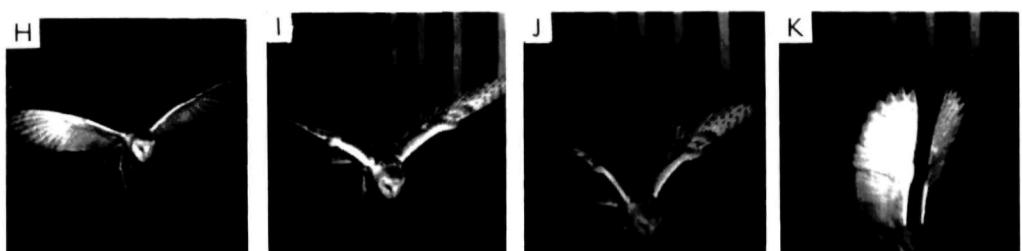
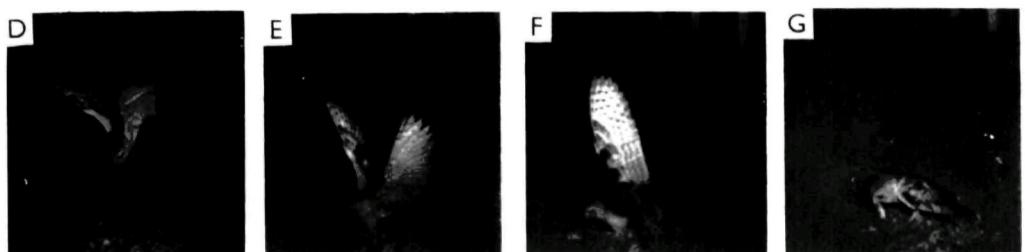
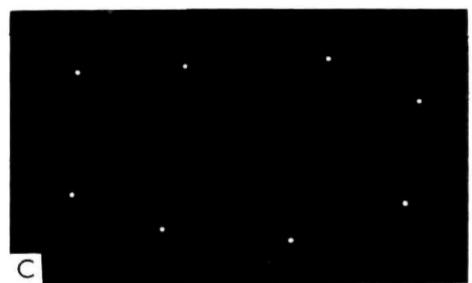
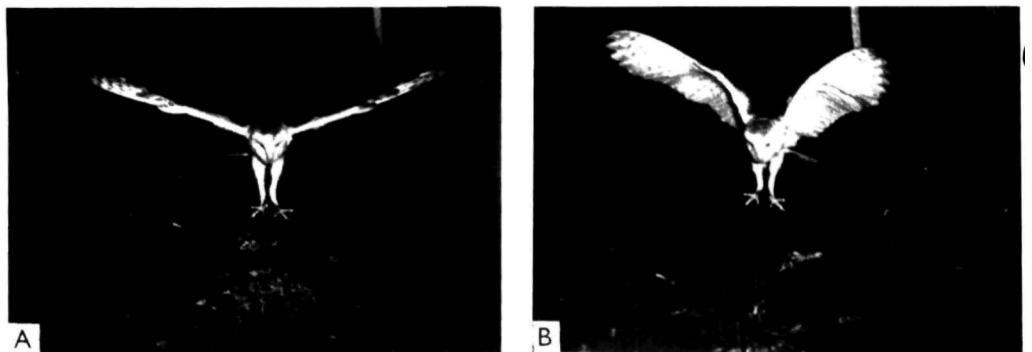
PLATE 4

- A-B. Single frames, taken from two different infra-red motion picture sequences of two different owls striking in total darkness. They show the equidistant spacing of talons before impact.
- C. Reproduction of the holes which an owl's talons pierced in a piece of paper laid over a hidden loudspeaker which was playing the sounds of a mouse rustling leaves. Out of six similar experiments, this was the *least* symmetrical pattern I obtained.
- D-G. The end of an infra-red motion-picture sequence of a strike in darkness to show the owl turning in the last moment of a flight in order to place the long axis of its talon pattern parallel to the long axis of the mouse. Compare the angle of approach (frame D) with the final position after impact (frame G).
- H-O. A second example of the same thing but showing a different owl.









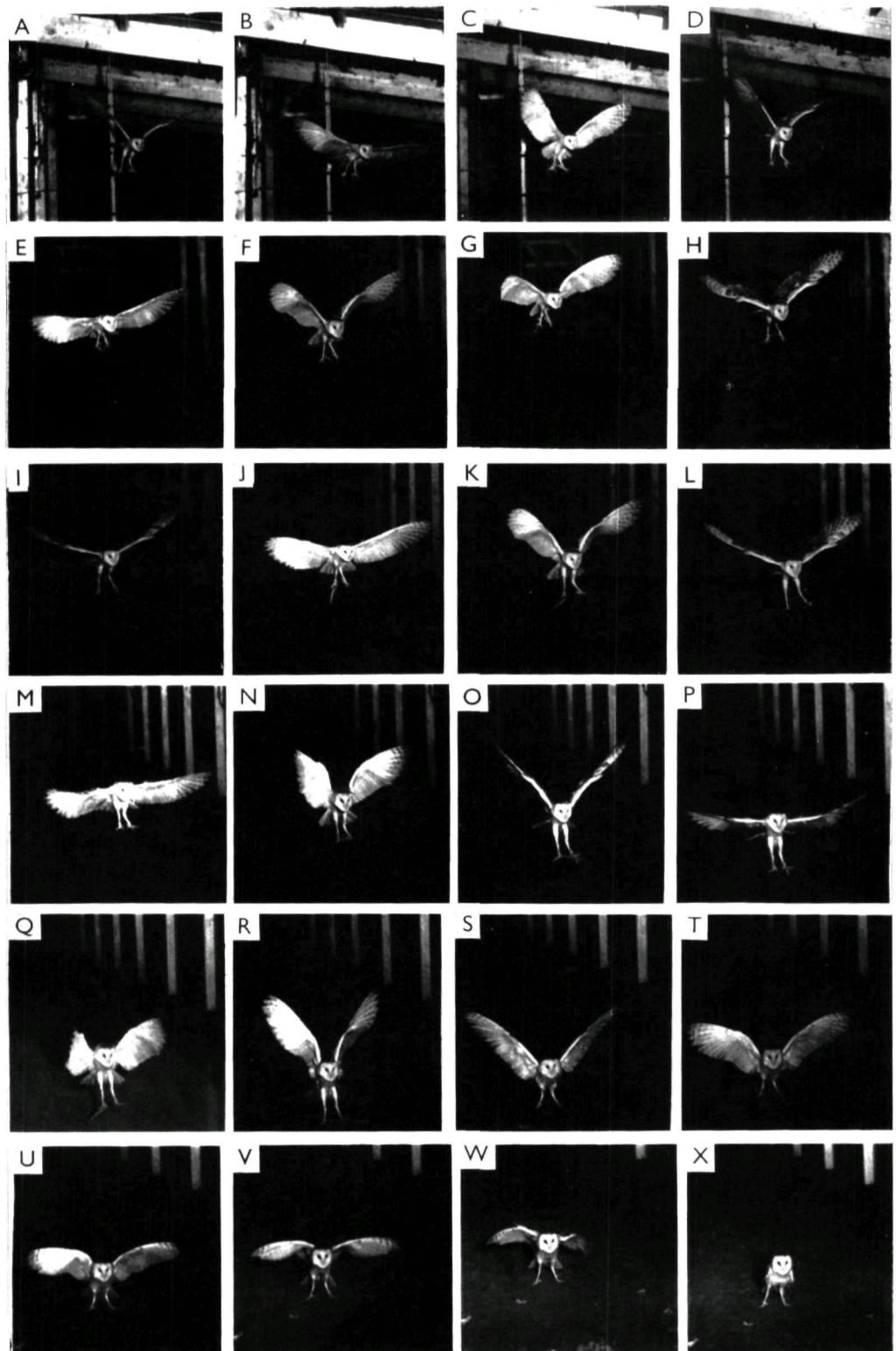


PLATE 5

An alighting sequence in total darkness (filmed in infra-red). After leaving its perch the owl flaps its wings rapidly all the way to the floor. Notice that its feet are not brought forward into the path taken by its head. Notice also that the owl faces straight ahead and not in the direction of flight even after alighting and that it does not close its eyes when landing. (There are about ten frames missing between frames W and X.)

