AN ABSTRACT OF THE THESIS OF

William Richard Rice for the degree of Doctor of Philosophy

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Title: Acoustic Localization of Concealed Prey by the Diurnal Harrier

(Circus cyaneus). _ *Redacted for Privacy*

Abstract approved: _____

John A. Wiens

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_____

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I experimentally examined the adaptive significance of the

anatomical and behavioral convergence between the harrier (Circus

cyaneus, also refered to as the marsh hawk) and certain owls that are

capable of capturing prey in total darkness. Anatomically, both the

harrier and owls have evolved a sound collecting facial ruff (a curved

wall of skin and feathers surrounding the ears) analogous to the

mammalian pinna. Behaviorally, both the harrier and the owls forage

very close to the substrate. This position substantially reduces the

field of view but concomitantly increases the intensity and directional

resolution of the acoustical cues emitted by concealed prey.

There are at least two mutually exclusive evolutionary alternatives

for localizing highly concealed prey. A predator relying on high

resolution vision can circumvent the reduced visibility of individual

prey by foraging from a high perch or flight position. Increased

foraging height can increase the field of view and hence the number of

prey simultaneously scanned. The likelihood of detecting a vulnerable prey item can thus increase with increasing field of view. A second alternative is to employ sonic cues that can penetrate the vegetational barrier to visual prey detection. This alternative constrains a raptor to forage from a low position due to the restricted range of sonic prey localization compared to visual prey localization. Thus, a raptor detecting concealed prey through sonic cues must forfeit the larger field of view available to raptors relying exclusively on visual cues. In this research I test the hypothesis that the diurnal harrier (Order Falconiformes) has converged with certain nocturnal owls (Order Strigiformes) in the ability to sonically locate concealed prey. I also test the idea that a reliance on auditory cues in part explains the harrier's low foraging position.

My thesis research was divided into two parts, a laboratory and a field study. In the laboratory, the auditory localization capacity of the harrier was compared to that of an owl species (barn owl, Tyto alba) with an experimentally established ability to acoustically locate prey in total darkness, to a second owl species (short-eared owl, Asio flammeus) with a behavioral repertoire similar to that of the harrier, and two typical diurnal raptor species (red-tailed hawk, Buteo jamaicensis and the American kestrel, Falco sparverius) lacking apparent anatomical specializations for directional hearing. Two individuals from each species were tested. The directional hearing of the harrier was found to be superior to that of the sample of typical diurnal raptors and similar to that of the sample of owls. Specifically, the horizontal resolution was two degrees for the harriers, eight to twelve degrees for the sample of typical diurnal raptors, and one to two degrees

for the sample of nocturnal owls. The range of effective sonic prey detection was estimated to be three to four meters for the harrier compared to seven meters for the barn owl.

In the field experiments a subterranean wiring network (test grid) was used to broadcast synthetic vole vocalizations (squeaks) from concealed miniature loudspeakers. The speakers were covered with replaceable plastic membranes. When a wild free-ranging raptor flew over the test grid, the vole vocalization was broadcast at a normal volume. The sound stimulus was terminated when the bird approached to within three to four meters of the speaker. Five harriers were tested for a total of ten trials. In all but one case the harriers responded to the sound stimulus by striking through the overlying vegetation and piercing the speaker membrane with their talons. Neither of two American kestrels that were tested responded to the auditory stimulus even when actual recordings of the resident voles were used. Because no visual or olfactory cues were available, the harriers determined the simulated vole position exclusively through auditory cues. The field experiments also demonstrated that the sonic localization capacity determined under highly idealized conditions in the laboratory is sufficiently elaborate to compensate for the distortions produced by heterogeneities in the more complex natural environment.

Thus the harrier, like many nocturnal owls, is capable of capturing concealed prey by locating them through sonic cues. Because the sonic localization capacity of the harrier only has an effective range of three to four meters, this species is constrained to forage relatively close to the substrate while employing sonic prey detection.

Acoustical Localization of Concealed Prey

by the Diurnal Harrier (<u>Circus</u> <u>cyaneus</u>)

by

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ACOUSTICAL LOCALIZATION OF CONCEALED PREY
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INTRODUCTION

This thesis is divided into two parts, corresponding to two manuscripts to be published separately. The first manuscript demonstrates that the diurnal harrier can utilize acoustical cues under field conditions to localize concealed prey. This paper is aimed at a general audience in an attempt to reach a diversity of disciplines (e.g., acoustics, behavioral biology, ornithology, psychophysics, and sensory physiology).

The second manuscript considers the sonic localization capacity of the harrier in a more detailed format and also from an evolutionary and an ecological perspective. Results from laboratory tests are used to argue that the directional hearing of the harrier has diverged from the norm of typical diurnal birds of prey and converged with that of nocturnal owls capable of locating prey in total darkness. The laboratory tests also indicate that the range of sonic prey detection is very limited compared to that of visual prey detection. The field experiments confirm the laboratory prediction, deduced from experimentation under highly idealized conditions, that the harrier can and does sonically locate prey that cannot be detected visually or through olfaction. The field experiments also indicate how visual and auditory cues are integrated in the detection of concealed prey.

CHAPTER II.

CAPTURING INVISIBLE PREY:

AUDITORY PREY LOCALIZATION IN A DIURNAL RAPTOR

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Abstract: Field tests with a subterranean network of loud-speakers indicate that a diurnal raptor can localize concealed prey through the use of highly refined directional hearing. Five free-ranging harriers were tested. These birds were able to use sonic cues to locate 2.5 centimeter targets from a distance of three to four meters.

Several laboratory studies have demonstrated that certain nocturnal owls possess a passive sonar capability that permits sound-emitting prey to be captured in complete darkness (1) Passive sonar is a form of highly refined directional hearing that differs from active sonar (e.g. the echolocation of bats) by a reliance on an external sound source. Passive sonar has ostensibly evolved in owls as an adaptation for hunting when light levels are insufficient for visual prey detection (2) Here I present experimental evidence from the field that the diurnal harrier (Circus cyaneus, also commonly called the marsh hawk) has converged with many owl species by using auditory localization to capture functionally invisible prey.

Microtine voles are the principal prey of the harrier over much of its range (3) These voles are active during the day but spend most of the time in an extensive system of grass-covered runways that they construct (4) The roof of the runway system conceals the voles from visually hunting predators except when the voles move between runway systems or when they pass through channels lacking a complete canopy. The vole runway system presents a problem to diurnal raptors comparable to the low illumination experienced by nocturnal owls, i.e., an individual vole cannot be seen most of the time. A diurnal raptor could compensate for the reduced visibility of its prey in two ways. First, it could increase its separation from the substrate by hunting from a high perch or flight position. This alternative increases the field of view and thereby increases the likelihood of detecting voles as they move between concealed runway segments. However, the visual acuity of the raptor and the duration of vole vulnerability will place constraints

on the extent to which increased foraging height will improve hunting success. The second alternative is to use nonvisual sensory cues that can penetrate the roof of the runway system. If auditory cues are used to localize prey, the foraging position must be close to the ground due to the restricted range of passive sonar (5).

Unlike most other diurnal birds of prey, the harrier forages close to the ground, usually at a height of 0.5-3 meters. This foraging position substantially reduces the bird's field of view but concomitantly increases both the amplitude and directional resolution of auditory cues. Anatomical features suggest that the harrier is highly adapted for processing auditory information (6). The feathers surrounding the ear are highly modified forming a sound-reflecting facial ruff analogous to the mammalian pinna. The auditory meatus is large, and the orientation of both the facial ruff and the auditory meatus appear to be under muscular control. All of these features produce an owl-like appearance. Thus, both the behavior and the anatomy of the harrier suggest that it utilizes auditory information in detecting prey.

To test the hypothesis that the harrier uses passive sonar to detect concealed prey, I used a subterranean wiring network (a 50 x 16 meter grid) connecting ten miniature speakers to an elevated observation blind 50 meters away (7). All experiments were conducted in a natural grassland area (on the William S. Finley Wildlife Refuge) in west-central Oregon. Each speaker communicated with the surface through a short membrane-covered conduit. The top of the conduit was flush with the surface and covered by the natural grass vegetation. When a wild

harrier flew over the test grid, I manually activated one of the speakers that emitted a synthetic vole squeak (8). The position of the active speaker was randomly determined, the nine silent speaker assemblies serving as controls. The sound stimulus was terminated when the bird approached to within about three meters of the speaker assembly (9). If the harrier could capture prey through auditory cues alone, I expected it to strike through the overlying vegetation and puncture the speaker-conduit membrane with its talons as it attempted to capture the simulated vole.

Five different harriers were tested for a total of ten trials. In each case the harriers reacted to the artificial vole vocalization by striking through the overlying vegetation and, with one exception, piercing the speaker-conduit membrane with their talons (10). The harriers sometimes remained on the ground in the vicinity of the speaker assembly for several minutes. During this time they would investigate the surrounding area and sometimes beat the vegetation with their wings, apparently trying to flush the simulated vole.

Two wild American kestrels (Falco sparverius) were also tested by placing short perches three meters from an inactive (control) and active (experimental) speaker assembly. This species was chosen to represent a typical diurnal raptor lacking both the behavioral and anatomical specializations of the harrier. Tests were conducted in winter (January) when the kestrels in this area subsist primarily on voles that they capture from perchs or from flight. Neither of the kestrels reacted to the auditory stimuli, even when recordings of the resident vole species rather than the synthetic squeak were used.

These experiments indicate that the harrier is capable of capturing concealed prey through a form of highly refined directional hearing. This is the first study to examine passive sonar under field conditions. Recent work (12) has shown that the sonic cues available in nature are highly distorted by the sharp gradients in temperature, humidity, and vegetational density that occur in the area immediately above the surface. Thus the accuracy of sonic localization obtained under highly simplified laboratory conditions may be misleading. By showing that the harrier can accurately use sonic cues to localize prey in the field, I have shown that the sensory system is able to cope with the distortions encountered under natural conditions.

References and Notes

1. M. Konishi, Am. Sci. 61, 414 (1973); E.I. Knudsen and M. Konishi, J. Comp. Physiol. 133, 13 (1979). G.A. Norgberg, Arkiv. Zool. 20, 181 (1968), R.S. Payne. J. Exp. Biol. 54, 535 (1971).

2. L.R. Dice, Am. Nat. 79, 384 (1945); R.S. Payne, J. Exp. Biol. 54, 535 (1971).

3. A.C. Bent, Life Histories of North American Birds of Prey, (Dover Publications, New York 1961) vol. 1, pp. 85-87.

4. W.H. Burt and R.P. Grossenheider. A Field Guide to the Mammals (Houghton Mifflin, Boston 1964); O.P. Pearson, J. Mammal. 40, 169 (1959).

5. R.S. Payne (1) found that the barn owl, a species highly adapted for passive sonar, would not strike at prey more than seven meters distant when only auditory cues were available. Additional laboratory and field experiments (Rice, in prep.) indicate that the harrier can use passive sonar to localize voles accurately only when they are within a range of three to four meters.

6. A.C. Chandler, Univ. Calif. Publ. Zool. 11, 329 (1914), R.J. Clark, and B.L. Stanley. Proc. Penn. Acad. Sci. 50, 86 (1976).

7. All wiring was "sewn" under the sod with a long wire needle. Speaker assemblies were sufficiently hidden that I could not determine their position even as I stood over them. Speaker positions were determined from the elevated observation blind by reference to a grid of small (0.2 meter) slats that surrounded (at no point closer than four meters) the subterranean wiring grid.

8. The frequency characteristics of the synthetic vole vocalization were substantially different from those of an actual vole squeak. However, the synthetic sound stimulus was sufficiently similar to an actual vole squeak to cause the birds to attack it as if it were prey. Spectral analyses of both natural vole squeaks and the synthesized squeak demonstrated that both have a wide frequency range with harmonics extending to 8000 Hz. The artificial sound stimulus was used to accommodate other experiments that will be reported elsewhere. The volume of the sound stimulus was adjusted to match the normal volume produced in the field. I expected the squeak stimulus to attract the harriers because I frequently observed these vocalizations to occur during the agonistic

encounters that I observed in the field while recording the activity pattern of the voles on my test grid.

9. In four instances I made certain that the bird-to-speaker distance was exactly three meters. I accomplished this by waiting for the bird to land on an artificial perch that I placed exactly three meters from both an active (experimental) and an inactive (control) speaker assembly. When a bird landed on the perch the sound stimulus was activated. Using a spotting scope, I terminated the sound source as the bird started to leave the perch.

10. In one of the ten trials the speaker membrane was not broken, although the overlying vegetation was removed as the raptor struck at the concealed speaker membrane. Because the birds sometimes remained on the ground for an extended period of time, it was possible that the speaker-membrane target was hit as a result of repeated strikes, and that the simulated vole was not accurately localized via sound. However, in at least two cases I can be certain that this did not happen. In the first case the bird never landed. It hit the speaker membrane from a single swoop, yanking the entire speaker assembly from the ground. In the second case the bird landed but immediately flew off before repeated trials were possible.

11. See A. Michelsen, In Sensory Ecology Review and Perspectives, M.A. Ali (Ed.) (Plenum Press, New York 1978) pp. 345-373 for references.

12. I thank J.A. Wiens for advice in the design and B.A. Menge for advice in the implementation of these experiments. I also thank P. Dawson, G. Fink, J. Lubchenco, B.A. Menge, F. Ramsey, and J.A. Wiens for critically reviewing an earlier draft of this manuscript. I thank

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CHAPTER III

SONIC PREY DETECTION BY THE DIURNAL HARRIER:

ADAPTATION TO CONCEALED PREY

Abstract: The acoustic location capacity of the harrier (<u>Circus</u> <u>cyaneus</u>) was measured in both the laboratory and the field. Laboratory experiments indicated that the directional hearing of the harrier was substantially better than that of a sample of typical diurnal raptors and similar to that of owls capable of capturing prey in total darkness. Angular resolution along the horizontal axis was two degrees for the harriers, one to two degrees for the owls and eight to 12 degrees for the sample of typical diurnal raptors. For the harriers, angular resolution along the vertical axis was at least two degrees. The maximum range of sonic prey detection was estimated to be three to four meters for the harrier and seven meters for the barn owl (<u>Tyto</u> <u>alba</u>). Field experiments indicated that free-ranging harriers could locate vole vocalizations (squeaks) accurately and attack prey successfully without the aid of visual or olfactory cues. Additional field experiments were conducted to determine how the harrier integrates auditory and visual cues while capturing concealed prey. These experiments show that the harries does not rely on motion cues or auditory depth perception to determine the elevation of a sound source.

INTRODUCTION

The process of adaptation is an important link between ecological and evolutionary theory. Evolutionary theory is directed at explaining how adaptations are produced through differential fitness and natural selection while certain ecological theory attempts to explain why different phenotypes have varying fitness. Unfortunately, many studies of adaptation have relied on intuition or correlation analyses and resulted in little more than scientific story-telling (see Williams 1965 for examples). Here I present an experimental analysis of the adaptive significance of the convergence in anatomy and behavior between the diurnal harrier and certain nocturnal owls. The purpose of the study was to determine what ecological factors presently promote this convergence.

Runway-inhabiting voles are a major prey item for a variety of raptorial birds that hunt in large open areas (Bent 1937). These rodents are diurnally active and construct an extensive network of tubular runways beneath the grass canopy (Burt and Grossenheider 1964; Pearson 1959). Because the runway system is roofed, voles can only be seen by aerial predators when they move between noncontiguous runway systems or when they pass through channels with an incomplete roof. Aerial predators have two evolutionary alternatives for coping with the reduced visibility of their prey: (1) Increase visual resolution to permit foraging from a high elevation where a large field of view can be scanned effectively, or (2) increase the resolution of other sensory modes that are capable of penetrating the roof of the runway system.

Alternative (1) circumvents the reduced visibility of individual voles by simultaneously surveying many individuals and thereby increasing the likelihood of detecting a vulnerable individual. A major constraint on alternative (1) is the duration of vole vulnerability. If voles are visible for a relatively short period of time, then the optimal foraging height will be determined by a trade-off between vole detection rate and the likelihood of capturing a vole once detected.

Both olfactory and auditory cues can be used for alternative (2). Although Grubb (1972) and Stager (1967) have shown that certain birds can accurately orient to olfactory cues, there is no anatomical evidence to suggest that olfactory cues are used by raptorial birds. Konishi (1973) and Payne (1962, 1971) have shown that barn owls (Tyto alba) can localize prey through auditory cues in complete darkness and that olfactory cues could not be used, even at very close range. An important aspect of the sonic prey location of the barn owl is its restricted range. Payne (1971) empirically demonstrated that the barn owl would not strike at prey more than seven meters away when only auditory cues were available. Additional work by Manley (1971), Norberg (1968) and Schwartzkopff (1973) suggests that auditory localization will be short-ranged for most bird species due to the general inability of birds to perceive high frequency sound and the relatively small distance separating the two ears.

A growing body of laboratory evidence suggests that owls are divided into two functional groups: those capable of sonic prey detection (e.g., Aegoleus, Asio, Strix, Tyto) and those with poorly developed auditory localization capacity (e.g., Bubo, Nyctea, Otus; Payne 1971,

Norberg 1968, Schwartzkopff 1973, Van Dijk 1973). Sonic prey

localization by owls is accomplished through a form of highly refined

directional hearing (passive sonar) and differs from the echo-location

of bats and pinnipeds (active sonar) by a dependence on an external

sound source. For example, an echo-locating bat can infer the position

of silent or sound-emitting prey by interpreting reflectional

distortions of its own vocalizations. Owls can only locate sound-

emitting prey by determining the direction, and possibly the distance,

of the sound source.

A dependence on range restricted auditory cues has important

consequences on foraging behavior. Because of the short range of

auditory localization, owls relying on auditory cues will be forced to

forage close to the substrate whereas owls relying primarily on visual

cues can hunt from a higher foraging position. For example, consider a

raptor hunting on a flat surface and relying entirely on auditory cues

(Figure 1). If the vegetation is sufficiently transparent to sound,

then the surface area effectively scanned will be related to foraging

height as follows:

Field of Auditory Detection = $A_s = \pi(R_s^2 - h^2)$

where R_s is the maximum range of sonic prey detection and h is the

foraging height (see Figure 1 for the geometric rationale). The first

partial derivative of A_s with respect to h is always negative, and thus

lower elevations produce the largest field of auditory prey detection.

Of course this simplistic model does not account for many important

variables such as distortions from echos and a variety of physical

gradients that are more pronounced near the surface and interfere with

sound localization. However, it does point out why the auditory
perceptual field can be expected to decline with increasing elevation.
If instead the raptor is strictly visual, a high foraging height can be
favored. When prey are detected visually, vegetation such as grass can
be expected only to permit visual penetration when viewed from an angle
less than some critical maximum (θmax, see Figure 1). Thus the
vegetation permits observation from above but not from the side. With
this constraint:

Field of Visual Detection = A_v = π $[h(\tan(\theta_{max}))]^2$,

where h< R_v [Cos (θmax)] and R_v is the maximum range of visual prey
detection. The first partial derivative of A_v with respect to h is
always positive and a higher foraging height produces a larger field of
view. Other constraints such as the duration of vole vulnerability will
favor a lower foraging height, but, at least in this simplistic
analysis, it can be seen that a reliance on sonic and visual cues have
opposing effects on foraging height.

Passive sonar has ostensibly evolved in owls as an adaptation to the
low light levels encountered on moonless nights, when cloud cover is
extensive, or in areas which are shaded by canopy vegetation. The
ultimate factor selecting for sonic prey detection, however, is reduced
prey visibility. As a result, it seems feasible that auditory
localization may have evolved also in diurnal raptors that hunt highly
concealed prey.

To assess this idea I observed the voles inhabiting an open field
area in western Oregon. The vole species observed was _Microtus montanus_
and the density of this species was high at the time of my

observations. Observations were made from a five meter high blind.

Three generalizations can be made: (1) vole sightings were fairly

common (two to three per minute), (2) the duration of a vole sighting

was very short, rarely of sufficient duration for a raptor to fly to the

vole's position, and (3) the rodents were surprisingly noisy. From my

elevated blind I was only able to hear squeaking vocalizations, which I

observed to occur during agonistic encounters. However, from a standing

position on the ground, I could also hear the voles when they were

chewing the vegetation and when they ran through the runway system.

Of the five raptors that compose the openland guild of diurnal

raptors in western Oregon, [red-tailed hawk (Buteo jamaicensis), rough-

legged hawk (Buteo lagopus), white-tailed kite (Elanus leucurus),

American kestrel (Falco sparvereus), and harrier; also called the marsh

hawk] only the harrier seemed likely to utilize option (2); use of non-

visual cues. This species forages remarkably close to the ground (0.5 -

3 meters), a position that reduces the field of view but potentially

provides auditory or olfactory cues that would be unavailable from a

higher flight position. Examination of study skins at the Oregon State

Natural History Museum and other published studies (Chandler 1914, Clark

and Stanley 1976, Kelso 1940, Pycraft 1898) indicate strong convergence

between the facial anatomy of the harrier and that of owls capable of

sonic prey detection. The harrier possesses a curved, sound-reflecting

facial ruff composed of both a ridge of skin and a row of densely packed

feathers. This structure is analogous to the mammalian pinna. The

auditory meatus is relatively large and its orientation appears to be

under muscular control (personal observation). In addition, the forward

margin of the auditory meatus is enlarged and directed outward, forcing

high frequency sound originating in front of the bird to reflect off the

curved wall of the facial ruff before entering the ear opening. Thus,

both the behavior and anatomy of the harrier suggest the use of auditory

information.

The behavioral and anatomical similarities between the harrier and

owls prompted the following hypothesis: The harrier (order

Falconiformes) has converged with certain nocturnal owls (order

Strigiformes) in the ability to locate concealed prey using acoustical

cues, and this reliance on auditory cues may in part explain the

harrier's low foraging position.

EXPERIMENTAL METHODS

General Design and Rationale

The study was divided into two parts, a set of laboratory and a set

of field experiments. In the laboratory experiments, I measured the

directional hearing ability of the harrier by determining its position

along a spectrum of capabilities. All birds are expected to have some

capacity for auditory localization. The harrier, was therefore compared

to an owl species with experimentally established high acoustic location

capacity (barn owl), a second owl species that has a behavioral

repertoire similar to that of the harrier [short-eared owl (Asio

flammeus)], and two typical diurnal raptors lacking apparent anatomical

specializations for directional hearing (red-tailed hawk and American

kestrel). The sample of diurnal raptors was chosen to bracket the head size of the harrier so that any difference between the auditory resolution of the harrier and this group could not be attributed to differences in the separation of the ears. Two individuals of each species were tested. The minimum audible angle (MAA- the angular margin of error in determining the direction of a sound) for each species was measured along both the horizontal and vertical axes. These angles were used to determine the functional range of sonic prey detection for each species. The laboratory experiments permitted me to address two questions: (1) Is the auditory localization capacity of the harrier sufficient to be functionally useful in localizing concealed prey , and (2) Is the accuracy of auditory localization in the harrier extraordinary or is it similar to that of typical diurnal raptors

In the field experiments a subterranean network of miniature loudspeakers was constructed in an old field area in west-central Oregon (William L. Finley National Wildlife Refuge). Squeaking vocalizations were broadcast from the loudspeakers to test the reaction of wild, free ranging harriers to auditory stimuli under natural conditions. With these experiments I attempted to answer two broad questions: (1) to what extent are sonic cues actually utilized by wild harriers? , and (2) how are visual and auditory stimuli integrated in the detection of concealed voles?

Laboratory Experiments

Horizontal resolution: MAA values were measured along the

horizontal axis through forced choice experiments conducted in an echo-dampening test chamber (Fig. 2). The test chamber was a converted controlled temperature room. The walls and ceiling were covered with acoustical tile (noise reduction coefficient = 0.89) and the floor was covered with 4 cm of waffled foam rubber padding. All instrumentation and controls were located outside the test chamber which was viewed through a double-paned one-way mirror. The test chamber was illuminated with a single 300-watt incandescent light.

All birds used in these experiments were raised from eggs or hatchlings that were collected from local raptor nests. The birds were trained to alight on an elevated perch located one meter from the far wall of the test chamber (Figure 2). Two solid wood cubes (10 cm on a side, hereafter called speaker platforms) were positioned in front of the bird, separated along the bird's horizontal axis. Each speaker platform was fastened securely to the floor and housed three 2.5 cm diameter loudspeakers along its interior edge. The speakers were recessed on the surface of each speaker platform so that the birds could not see any part of the loudspeakers from the perch. When one of the loudspeakers broadcast a pulsed noise (range was 100-16,000 Hz with 200 msec of sound alternating with 200 msec of silence; Figure 3) the bird was trained to fly toward the speaker platforms. The sound was terminated when the bird left the perch. If the bird landed on the platform that emitted the sound, a feeder delivered a piece of meat (cut up, day old poultry chicks). The birds were trained initially by placing the feeder, perch, and speaker platforms all within a 30 cm radius and using standard operant conditioning techniques. Once the

testing routine was learned, the scale of the testing apparatus was gradually increased. All experiments were conducted in full illumination because visual cues were of no help in choosing the sound emitting platform and because the diurnal raptors would not fly in total darkness. The birds initiated a new trial by flying back to the elevated perch.

During initial training the speaker platforms were widely spaced. On successive days the platforms were moved closer together until the proper choice could not be made at least 75 percent of the time. The number of trials at a particular spacing depended on performance and ranged from 20 to 150. When the separation between the speaker platforms was decreased, the bird was allowed to "practice" at the more difficult task for one to several days. I then tested the ability of the bird to discriminate between the silent and the sound emitting sound platforms. At the end of each day I analyzed the cumulative set of data to determine if I could be 99 percent confident that the bird could make the correct choice at least 75 percent of the time. When a lower limit was found, the speaker platforms were repositioned at a wider separation and the tests repeated (i.e., the platforms again moved closer) until iterative trials did not improve performance. For the duration of a testing session (2-4 months), incentive was maintained by having a bird earn the majority of its diet in this manner.

An important problem with any conditioning assay of sensory capabilities is the potential for the organism to cheat, i.e., to use inadvertently produced concomitant cues instead of the experimental treatment. To guard against this problem, I initially tested four

humans and asked them purposely to try to use cues other than sound

direction, e.g., did one speaker platform have slightly different

frequency or amplitude characteristics, etc. These tests led to the

following design: (1) three speakers were used in each speaker

platform, (2) the six speakers were carefully screened to ensure that

they had similar frequency and amplitude characteristics, (3) the same

speaker was never used to broadcast consecutive sound stimuli, (4) the

speakers were frequently shuffled between speaker platforms, and (5) the

frequency response characteristics and the volume of each speaker were

electronically altered between each sound presentation. The result is

that a bird never heard the same sound twice during a single days'

testing (15-30 trials). These precautionary measures were sufficient to

prevent my human subjects from consciously cheating and MAA values

obtained for these individuals (MAA (horizontal); x = 0.875 degrees, SD

= .75 degrees) are close to the norms reported by Mills (1972).

Vertical resolution: The procedure for determining vertical

resolution was identical to that described for the horizontal tests,

with the following exceptions. Because the upper speaker platform

interfered with a bird landing on the lower platform, a design was used

that did not require the bird to fly to the sound emitting platform.

The upper sound platform was painted black and the lower white. Two

feeders (one white, one black) were positioned on either side of the

elevated perch. The bird obtained a reward if it flew to the feeder

that matched the color of the sound-emitting platform. Each platform

was equipped with an indicator light. The birds were initially trained

visually by obtaining a reward when they flew to the feeder that matched

the color of the platform with its indicator light flashing. Next the sound source was simultaneously presented with the flashing indicator light. Finally, the lights were eliminated and the choice was made totally by auditory cues.

Field Experiments

A subterranean wiring network (16 x 50 meters) connected ten miniature loudspeakers to an elevated observation blind 50 meters away (Figure 4). All wiring was "sewn" under the sod (with a one meter long "needle" fashioned from heavy gauge wire) to avoid a conspicuous trench leading to the speaker assemblies. Each speaker assembly included a loudspeaker that was housed in a short plastic conduit (2.75-cm diameter) placed beneath the ground surface. The upper end of the conduit was flush with the surface and covered with a replaceable plastic membrane. All portions of each speaker assembly were painted brown to match the soil color. All speaker assemblies were covered with the existing vegetation and were sufficiently hidden that I had to relocate them through trial and error. In addition to the main test grid three other tests stations were constructed in nearby areas(i.e. within 1 kilometer). Each of these contained two speaker assemblies (one experimental, one control) located three meters from a two meter high perch. These additional test stations were placed in areas lacking natural perches and were readily used by the local raptors. When a free ranging raptor flew within ten meters of the test grid (or landed on one of the artificial perches) a randomly selected speaker assembly

broadcast a synthetic vole vocalization (squeak). The volume of the synthetic vole squeak was adjusted by ear in the field to match that of naturally occuring squeaks.

The purpose of the synthetic vole squeak was to produce a sound stimulus that attracated the harriers but also had special characteristics which were needed for my field experiments. To construct the synthetic vole squeak I made sonographs of actual <u>Microtus monatus</u> vocalizations. I then trained myself to imitate the vole squeak with my lips. I gradually perfected my imitation squeak until it was sufficient to attract wild harriers but its spectral composition was not identical to an actual vole squeak. I recorded my imitation squeak with an erradic volume; slightly higher volume squeaks alternating with slightly lower volume squeaks. The resulting synthetic squeak had novel spectral characteristics and an irregular volume. These characteristics were needed to prevent my wild test birds from using volume or spectral cues for auditory depth perception.

When a raptor approached to within three to four meters of a speaker assembly, I manually terminated the sound. The position of the harrier was determined by interpolation from a grid of slats (0.25 meters tall) surrounding the test grid. The nine silent speaker assemblies acted as controls. If the raptor could determine the simulated vole's position accurately from sonic cues alone, I expected it to strike through the overlying vegetation and puncture the conduit membrane with its talons. Two species were tested in the field, the harrier and the American kestrel. The kestrel was used as an example of a diurnal raptor lacking the behavioral and anatomical specializations of the harrier.

RESULTS

Horizontal MAA

The ability of the harrier to discriminate the horizontal direction
of sound is significantly greater than that of the sample of typical
diurnal raptors but statistically indistinguishable from that of the owl
species tested (one-way anova, N = 10 birds, P <0.01; Table 1). For
each MAA value in Table 1 I can be 99 percent certain that the bird
could properly determine the direction of the sound at least 75 percent
of the time (based on the binomial distribution and an equal probability
of choosing each speaker platform). It should be pointed out that these
MAA values may be conservative. During all of the experiments the two
harriers were the most difficult to train, and this may be reflected in
their performance. During the one degree trails the speaker platforms
were only separated by 3 centimeters. As a result the harriers
frequently landed on both platforms simultaneously which interfered with
my measurements. However, even after four series of experiments where I
gradually reduced the angle of separation to one degree, I was unable to
statistically demonstrate that the harriers could resolve one degree.
One short-eared owl and one barn owl were only able to resolve two
degrees. Both of these birds were difficult to train and this may
explain their higher MAA. Because of spatial constraints, tests at 0.5
degrees could not be made. However, it seems unlikely that either of
the owls successfully resolving one degree could resolve 0.5 degrees.
Both of these owls frequently refused to fly at the speaker platforms

when they were separated by one degree but would readily respond if I increased the separation to two degrees. A similar response was produced in the typical diurnal raptors at the minimum audible angle. Knudsen and Konishi (1979a, b) found the average angular error of a sample of two barn owls to be 1.5 degrees along the horizontal axis. While these values do not represent MAA values (resolution must be sufficient 75 percent of the time for a MAA value and approximately 50 percent of the time for an average angular error estimate) they support my contention that the MAA values for the barn owl are not likely to be less than one degree. My best estimate for the harrier and owl MAA's are two and one degrees respectively. Thus, the horizontal resolution of the harrier appears to have diverged from that of typical diurnal birds of prey and converged with that of owls capable of sonic location in the absence of visual cues.

Vertical MAA

MAA values for the vertical axis were not determined quantitatively. All of the birds were able to discriminate visually between the two speaker platforms when they were vertically separated by 40 degrees. Similarly all the birds were capable of choosing the proper speaker platform when visual (indicator lights) and auditory (pulsed noise) stimuli were presented simultaneously. Only the owls and harriers, however, could successfully choose the sound emitting platform when the visual stimuli were gradually removed and only the auditory cues remained. I was unable to train either the American kestrel or the

red-tailed hawk to make even this coarse elevation determination despite intensive efforts and several different training methods. Further attempts to determine the vertical MAA values for the owls and harriers were eventually terminated because of erratic fluctuations in the birds' performance. These occurred when a bird was not run on consecutive days and when the birds apparently became "frustrated" after making several errors. The complexity of the behavioral conditioning used to assess the vertical MAA values made these tests less tractable than the horizontal discrimination procedure. To eliminate this problem the vertical resolution of the harriers was measured indirectly during the field experiments. The only conclusion from these tests was that both the owls and the harrier have some degree of vertical resolution, while the two typical diurnal raptors were apparently unable to make even crude elevational determinations.

During preliminary experiments I found that none of the birds rotated their heads in response to the vertical stimuli. This eliminated the need for head restraints. I did observe a "head rotation" response in both of the harriers but in none of the other birds when the birds were exposed to a novel sound. The harriers looked directly at the speaker and rotated their head (1/2 turn in each direction) in the plane perpendicular to the direction of the sound. The head movement was discontinuous so that periods of movement were alternated with short pauses. After a bird heard a sound several times this response was no longer observed.

Field Experiments

In the field experiments five different harriers were tested for a total of ten trials (Table 2.). The harriers were able to localize the synthetic vole squeak both when they were stationary and when they were moving relative to the sound source. Neither of the two kestrels responded to either the synthetic vole squeak or to recordings of squeaks I recorded from the resident voles occurring naturally in the area. To ensure that the kestrels could hear the sound stimulus, I gradually increased the volume to very high levels. The kestrels did not even turn to face in the direction of the mouse squeak.

DISCUSSION

The Utility of Sonic Prey Detection

The purpose of the laboratory studies was to determine if the sonic location capacity of the harrier is sufficiently accurate to be useful in detecting concealed voles and if this ability is extraordinary compared to that of other diurnal raptors. My laboratory measurements indicate that a harrier can resolve the horizontal displacement of a sound to an accuracy of at least two degrees. Although the laboratory measurements of vertical resolution were unsuccessful, I was able to infer the upper limit of the harrier's vertical resolution from my field experiments. During all of my field experiments the sound source was

terminated when the bird approached to within roughly three meters of the speaker assembly (exactly three meters in the four trials where the bird struck from a perch). This would require the bird to localize the sound source both vertically and horizontally. A problem with this analysis is that a bird might search for the speaker assembly while on the ground and the "hit" may be the result of repeated attempts. In two instances, I can be certain that this did not occur. In one case the harrier pulled the entire speaker assembly out of the ground during a single stoop. In this case the bird never landed. In a second instance the bird flew off immediately after landing, and repeated strikes could not have occurred. On one instance, however, I observed a bird to strike repeatedly at the vegetation and also to beat the vegetation with its wings, apparently attempting to flush the simulated vole. If one infers from these data that a harrier with a 10 cm talon spread can repeatedly hit a 2.5 cm target from three meters away, then the vertical resolution must be at least two degrees, i.e., the vertical resolution is equal to or better than the two degree horizontal resolution determined in the laboratory (Figure 5). A similar result was reported for barn owls by Knudsen and Konishi (1979a, b), Konishi (1973) and Payne (1971). Their data indicate that the vertical resolution of the barn owl equals or exceeds its horizontal resolution.

Assuming similar resolution along both the vertical and horizontal axes for the barn owl (one degree) and the harriers (two degrees) and an upper limit for the vertical resolution of the two diurnal raptors of 40 degrees, the utility of sonic prey detection in these species can be compared (Figure 6). The effective range of sonic prey detection was

estimated by determining the accuracy needed to capture a prey item of typical size. In this analysis an average vole is assumed to be 8.0 cm long and 2.0 cm wide. To simplify calculations, the vole is modeled as a disk with a diameter equal to the average linear dimensions of a vole, i.e., a disk with a diameter of 5.0 cm (see Figure 5). For a harrier with a talon spread of 10.0 cm and resolution of two degrees along both axes, maximal striking range is estimated at 3-4 meters. For an owl with a similar talon spread and a resolution of one degree, the range is about seven meters. The seven meter range for the barn owl is very close to the value reported by Payne (1971), who found that barn owls tested in total darkness refused to strike at prey when they were more than seven meters away. Instead, the owls would fly to a closer position and wait for additional acoustical cues. The angular resolution achieved by the typical diurnal raptors would be insufficient for any useful localization of prey, even at very close range (Figure 6). Thus, the auditory prey localization capacity of the harrier is substantially better than that of the sample of typical diurnal raptors and the horizontal resolution determined in the laboratory is sufficient to explain the nonvisual localization demonstrated by free ranging harriers in the field experiments.

Field Experiments

The field experiments were directed at four specific questions: (1) Do harriers use sonic cues naturally?,(2) Does a vole need to be seen to be captured?,(3) Are olfactory cues needed for nonvisual prey

localization?,and (4) How are visual and auditory cues integrated in prey localization? Questions one through three were collectively answered by simulating the position of a vole with a concealed loudspeaker. Because no vole was actually present, localization by olfactory or visual cues was impossible. In addition, because only wild harriers were tested in their natural environment, no training or situational artifacts are likely. Thus, the fact that all the birds tested consistently hit a 2.5 cm sound emitting target with no visual or olfactory cues suggests that the harrier can and naturally does employ sonic prey detection.

Sonic prey detection by diurnal raptors and nocturnal owls have different constraints. To locate a prey item acoustically in total darkness, an owl must obtain three pieces of information (1) azimuth (horizontal displacement), (2) elevation (vertical displacement), and (3) distance (Erulker 1972, Mills 1972). Payne (1971) was unable to determine if the distance to the prey could be determined by the barn owl, but he did show that this owl could determine both azimuth and elevation. Payne reasoned that an owl might not be able to determine the distance to a prey item but still capture it in total darkness. The owl could potentially determine the direction of the prey, based on azmuth and elevation, and then fly along this bearing until increased back pressure on the wings sensed by the flight feathers, indicated that the owl was about to intercept the substrate (on which the prey is assumed to be located). Thus, at the very least an owl must be capable of sonically determining azimuth and elevation.

A diurnal raptor might only need to determine the azimuth of a sound source to detect its position, as elevation may be determined visually. This is because a diurnal raptor also has some visual cues available to it, even if the prey item itself cannot be seen. One factor that suggests that elevation may not be sonically determined by the harrier is a lack of asymmetry in the placement of the ears on the head. All owl species known to be capable of capturing prey in total darkness have asymmetrically positioned ears (or associated structures, e.g., operculum; Norberg 1978). All birds are expected to have a capacity to determine the horizontal position of a complex sound because the timing and intensity of the sound will be different at each ear. For example, a complex sound originating from the left will be heard first and loudest by the left ear. Vertical displacement, however, does not produce unambiguous interaural differences in onset or intensity of a sound if the ears are symmetrically placed on the head (and no pinnae are present). If the ears are asymmetrically positioned on the head then elevation potentially can be determined by interaural differences (Payne 1971, Pumphery 1948). If the ear openings are equipped with a pinna, then monaural elevation determination may be possible because sounds originating from different elevations are expected to produce unique echo patterns (in humans the echos are unconsciously perceived) which can be used to infer elevation (Batteau 1967, Freedman and Fisher 1968). Because the harrier does not have asymmetric ears, I wanted to determine if it used visual cues in combination with auditory cues to determine elevation.

Integration of Visual and Auditory Cues

There are at least three ways for a diurnal raptor to integrate
vision and hearing to localize concealed prey. The first method
utilizes a familiar sound, auditory azimuth determination, auditory
depth perception, and visual perception of the surface contours.
Coleman (1962, 1963) used principals from accoustical physics to argue
that there are only two feasible methods for auditory depth perception
of a complex sound which are operative over distances greater than
approximately one meter: sound intensity and frequency spectrum. As a
complex sound travels through the air, its volume is attenuated and its
timbre changes because higher frequencies are damped to a greater extent
than low frequencies. Thus, the distance that a familiar sound has
traveled can be determined by the extent of base-bias. Distance
specific changes in timbre are temperature- and humidity-specific but
nevertheless potentially could be used by the harrier to judge distance
(Michelsen, 1978). Coleman (1962) has shown that humans can use timbre
changes effectively to judge distance . It is important to note that
this method is only effective when a familiar sound is heard because
some expectation of the spectral characteristics of a sound must be
available. A harrier potentially could locate a concealed prey item
producing a familiar sound in the following way. When the concealed
prey is heard its azimuth and distance could be determined auditorily.
Vision could then be used to determine what point along the auditorily
determined azmuth intersects the surface at the auditorily determined
distance (Figure 7a). If the prey is assumed to be located on or just

below the surface and the surface is reasonably flat, the position of
the prey could be uniquely determined without auditory elevation
perception.

A second method involves auditory azimuth determination, motion, and
vision. If the bird is moving relative to the sound-emitting prey item,
then the auditory azimuth will continually be changing (unless the bird
is approaching the prey head on in which case it could simply change its
orientation slightly). The auditory azimuth bearing determined at
subsequent flight positions will represent a series of intersecting
planes. The line determined by the intersection of these planes will
pass through the prey unit. If the prey is assumed to be at or just
below the surface, which can be perceived visually, then multiple
azimuth determinations and visual determination of the surface contours
will uniquely determine the position of the prey without auditory
determination of elevation (Figure 7b).

The third method involves auditory determination of both azimuth and
elevation and also visual determination of surface contours. The
auditorily determined azimuth and elevation bearings will define a line
intersecting the sound-emitting prey item. If the prey is on or just
below the surface its position can be determined visually, at the point
where the azimuth and elevation bearings intersect the surface (Figure
7c).

Method (3) involves both auditory azimuth and elevation
determinations whereas methods (1) and (2) only require auditory azimuth
determination. To determine if the harrier used auditory cues to
determine elevation, I had to show that prey could be localized when

methods (1) and (2) were not operative. I did this by using a synthetic vole squeak that represented an unfamiliar sound which had variable volume and also had timbre characteristics very different from a normal vole squeak. Thus the variable volume and novel spectral characteristics should prevent the bird from employing auditory depth perception (Coleman 1962, 1963). If the harrier could localize the unfamiliar synthesized vole squeak then method (1) could not be used. I also tested some of the birds from a stationary position (perches), where large-scale motion cues were absent and method (2) could not be used. Because the harriers could localize my synthetic vole squeaks from a stationary position, I concluded that the birds could determine acoustically both the azimuth and the elevation of a sound.

The Need for Field Studies

The field experiments conducted in this study are an important component missing in previous studies of sonic localization of prey. Michelsen (1978) and Wiley and Richards (1978) have reviewed the environmental factors affecting sound transmission. They indicated that sound localization in the field requires substantially more sophistica-tion than localization under simplified laboratory conditions. For example, steep gradients in temperature, humidity, and vegetational density typically occur in the area immediately above the ground (and presumably above ground dwelling prey). These gradients can greatly distort both the direction and the spectral characteristics of a sound in a complex fashion. Prey localization under these conditions requires

adjustments for the apparent and actual location of the sound source. Measurements taken under highly simplified laboratory conditions are desirable because of the increased capacity for experimental control. The sensory information available to a free-ranging organism, however, is likely to be highly filtered by environmental heterogeneities and extrapolation from the laboratory to the field must be confirmed via manipulative field experiments under the complex conditions experienced in nature. In the laboratory I have shown that at least the horizontal auditory resolution of the harrier is sufficient (under highly idealized conditions) to localize prey effectively from a distance of three meters. In the field I have shown that prey can be and are localized at this range despite the more complex nature of a sound stimulus altered by micro-climatic gradients. Thus, the sensory system of the harrier appears to be sufficiently elaborate to allow for the distortions encountered under natural conditions.

The Evolution of Sonic Prey Detection

Given the evidence for sonic prey localization in the harrier, it seems reasonable to speculate on why sonic prey detection is common in nocturnal owls yet rare in diurnal raptors. Of course, most diurnal raptors have not been tested for their ability to locate prey sonically, but no species outside the genus Circus has anatomical features suggesting a reliance on auditory cues. Because auditory cues are very range restricted, an organism must be preadapted to forage close to the substrate where the refinement of directional hearing could gradually

evolve. Van Dijk (1976) used anatomical and phychophysical data to argue that passive sonar independently evolved in owls at least three times. Owls may be preadapted to utilize sonic cues because they frequently hunt under conditions of low illumination, which would make visual prey detection useful only over a short distance (Dice 1945, Suthers 1978). Thus, low illumination may have forced certain owl species to forage close to the ground and hence they would be preadapted to utilize sonic cues. The ancestral forms of the genus <u>Circus</u> may also have been preadapted to use sonic cues if they, like many present species of this genus, foraged over tall-grass vegetation. Tall grass only permits visual penetration from directly above, i.e., observation from an angle will not permit detection of a prey item on the ground if the grass is tall relative to the prey. As a result, increased foraging height does not increase the effective field of view. Under these conditions, a low foraging position can be favored, since the duration of prey vulnerability required for a successful strike would be reduced by a low flight position. Other diurnal raptors, hunting in short or sparse vegetation and relying on a large field of view, would tend to forage from a high flight or perch position where auditory cues are of little use. A gradual evolution of sonic prey localization capabilities would thus be unlikely.

To conclude, my experimental results support the idea that the anatomical and bahavioral convergence between the harrier and certain nocturnal owls is the result (at least in part) of adaptation to highly concealed prey. Among diurnal raptors, there are at least two mutually exclusive solutions to reduced prey visibility; a high foraging height

with increased field of view or a low foraging height with a reliance on auditory cues that can penetrate the barrier to visual prey detection. The evolutionary path followed by a particular species will depend on preadaptations. The sonic solution is only likely to evolve in a visual raptor when environmental constraints force it to forage close to the substrate, where useful auditory cues are available.

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REFERENCES

Batteau, D. W. 1967. The role of the pinnae in human localization.
Proc. Roy. Soc., Ser. B. 158:158-180.

Bent, A.C. 1937. Life Histories of North American Birds of Prey. U.S.
National Museum Bulletin 167. Washington, D.C.

Burt, W.H. and R.P. Grossenheider. 1964. A Field Guide to the
Mammals. Houghton Mifflin, Boston.

Chandler, A.C. 1914. Modifications and adaptations to function in the
feathers of Circus Hudsonius. Univ. Calif. Pub. Zool. 11:329-376.

Clark, R.J. and B.L. Standley. 1976. Facial feathers of the harrier
(Circus cyaneus Hudsonius), long-eared owl (Asio otus) and short-
eared owl (Asio flammeus) compared. Proc. Penn. Acad. Sci. 50:86-
88.

Coleman, P.D. 1962. Failure to localize the source distance of an
unfamiliar sound. J. Acoust. Soc. Amer. 34:345-346.

Coleman, P.D. 1963. An analysis of cues to auditory depth perception
in free space. Psychol. Bull. 60:302-315.

Dice, L.R. 1945. Minimum intensities of illumination under which owls
can find dead prey by sight. Amer. Nat. 79:385-416.

Erulker, S.D. 1972. Comparative aspects of spacial localization of
sound. Physiological Review 52:237-359.

Freedman, S.J., and H. G. Fisher. 1968. The role of the pinnae in
auditory localization. Ch. 8. In: Freedman, S. J., ed. The
Neuropsychology of Spatially Oriented Behavior. Dorsey Press.

Grubb, T. C. Jr., 1972. Smell and foraging in shearwaters and
    petrels. Nature 237:404-405.

Kelso, L. 1940. Variation of the external ear opening in the
    Strigidae. Wilson Bull. 52:24-29.

Knudsen, E.I., and M. Konishi. 1979a. Sound localization by the barn
    owl (Tyto alba) measures with the search coil technique. J. Comp.
    Phusiol. 133:1-11.

Knudsen, E.I., and M. Konishi. 1979b. Mechanisms of sound localization
    in the barn owl (Tyto alba). J. Comp. Physiol. 133:13-21.

Konishi, M. 1973. How the owl tracks its prey. Amer. Sci. 61:414-
    424.

Manley, G.A. 1971. Some aspects of the evolution of hearing in
    vertebrates. Nature (London) 230:505-509.

Michelsen, A. 1978. Sound Reception in Different Environments. Pg 345-
    373. In Sensory Ecology Review and Perspectives, M. A. Ali (ed.),
    Plenum Press, New York.

Mills, A. W. 1973. Auditory Localization. Ch. 8. In C. J. Tobias and
    E. D. Schubert (Eds.). Foundations of Modern Auditory Theory.
    Academic Press, New York.

Norberg, G. A. 1968. Physical factors in directional hearing in
    Aegoleus funereus (Linne) (Strigiformes), with special reference to
    the significance of the asymmetry of the external ears. Arkiv
    Zool. 20:181-204.

Norberg, R.A. 1978. Occurrence and independent evolution of bilateral
    ear asymmetry in owls and implications on owl taxonomy. Philos.
    Trans. R. Soc. Land. B. Biol. Sci. 282:325-410.

Payne, R. S. 1962. How the barn owl locates prey by hearing. Living
    Bird, 1:151-159.

Payne, R.S. 1971. Acoustic location of prey by the barn owl *Tyto*
    alba). J. Exper. iol. 56:535-573.

Pearson, O.P. 1959. A traffic survey of *Microtus* - *Reithrodontomys*
    runways. J. Mammal. 40:169-179.

Pumphery, R. J. 1948. The sense organs of birds. Ibis 90:171-199.

Pyecraft, W. P. 1898. A contribution toward our knowledge of the
    morphology of the owl. Trans. Linnean Soc. London, 2nd Ser. Zool.
    7:223-276.

Schwartzkopff, J. 1973. Mechano-reception. pp. 460-460. *In* D. S.
    Farner and J. R. King (eds.) Avian Biology, Vol. III. Academic
    Press. N.Y.

Stager, K. E. 1967. Avian olfaction. Am. Zool. 7:415-419.

Suthers, R. A. 1978. Sensory Ecology of Birds. Pg 217-251. *In* M. A.
    Ali (Ed.), Sensory Ecology Review and Perspectives. Plenum Press,
    New York.

Van Dijk, T. 1973. A comparative study of hearing in owls of the
    family *Strigidae*. Netherlands J. Zool. 23:131-167.

Wiley, R. H., and D. G. Richards. 1978. Physical constraints on
    acoustic communication in the atmosphere: Implications for the
    evolution of animal vocalizations. Behav. Ecol. Sociobiol. 3:69-94

TABLE 1. Measurements of directional hearing capacity for five raptor species.

| SPECIES | INDIVIDUAL | HORIZONTAL TESTS | | | COARSE [c] VERTICAL RESOLUTION |
		MINIMUM [a] HORIZONTAL RESOLUTION	NUMBER [b] OF TRIALS	NUMBER CORRECT	
Red-tailed hawk [d]	1 (F)	8^0	56	51	No
	2 (M)	10^0	46	42	No
American kestrel	1 (M)	10^0	107	96	No
	2 (F)	12^0	33	31	No
Barn owl [d]	1 (M)	1^0	23	22	Yes
	2 (F)	2^0	34	32	Yes
Short-eared owl [d]	1 (F)	1^0	37	35	Yes
	2 (F)	2^0	52	47	Yes
Harrier	1 (F)	2^0	40	37	Yes
	2 (M)	2^0	106	96	Yes

a- Values reported are Minimum Audible Angles.
b- Number required to be 99% confident that correct choice could be made 75% of the time.
c- Ability to resolve a 40^0 vertical displacement; see text for details.
d- Sex based on size.

TABLE 2. Field tests of the ability of two raptor species to locate concealed loudspeakers emitting a synthetic vole squeak. The sound stimulus was presented at a normal volume and terminated when the bird approached to within approximately three meters.

SPECIES	INDIVIDUAL	POSITION	NUMBER OF TRIALS	TARGET HITS	TARGET MISSES
American kestrel	1	perch [a]	2	- [b]	-
	2	perch	1	-	-
Harrier	1	perch	2	2	0
		flight	1	1	0
	2	flight	4	4	0
	3	flight	1	1 [c]	0
	4	perch	1	1	0
	5	perch	1	1	0

a- Perch to speaker distance was three meters; the sound stimulus was terminated when the bird left the perch.

b- Neither of the kestrels made any responce to the sound stimulus, even when I used recordings of the resident vole species. The volume was sufficient for the kestrels to hear the sound stimulus.

c- In this instance the speaker membrane was not punctured but the grass covering the speaker membrane was removed.

Figure 1. Schematic diagram depicting the auditory (clear) and the visual (stippled) fields of prey detection. Comparison of the two birds indicates how small changes in foraging height can markedly affect the relative size of the two fields of prey detection. The vegetation is assumed to be transparent to sound but opaque to light except when viewed from an angle less than θ_{max}. θ_{max} declines with increasing height of the vegetation. R_s is the effective range of sonic prey detection, and h is the foraging height.
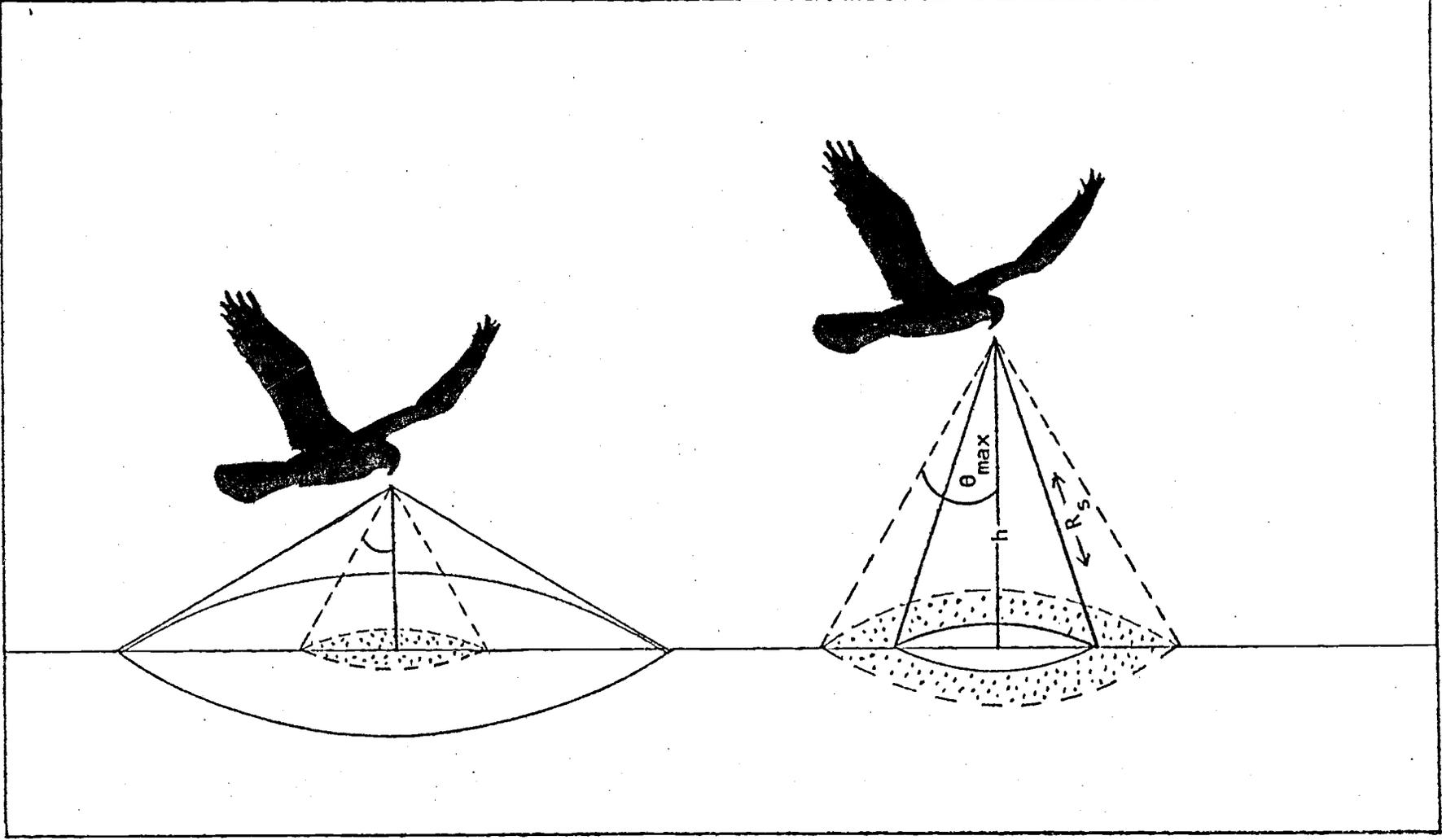
Figure 2. Diagram of the test chamber. Speaker assemblies are positioned for measuring MAA values along the horizontal axis.

A. 30 cm fiberglass insulation
B. 2 cm acoustical tile
C. Double paned one-way mirror
D. Frequency equalizer
E. Amplifier

F. Tape recorder
G. Waffled foam padding
H. Speaker platform
I. Feeder
- Dimensions: 2.5m high
               2.75m wide
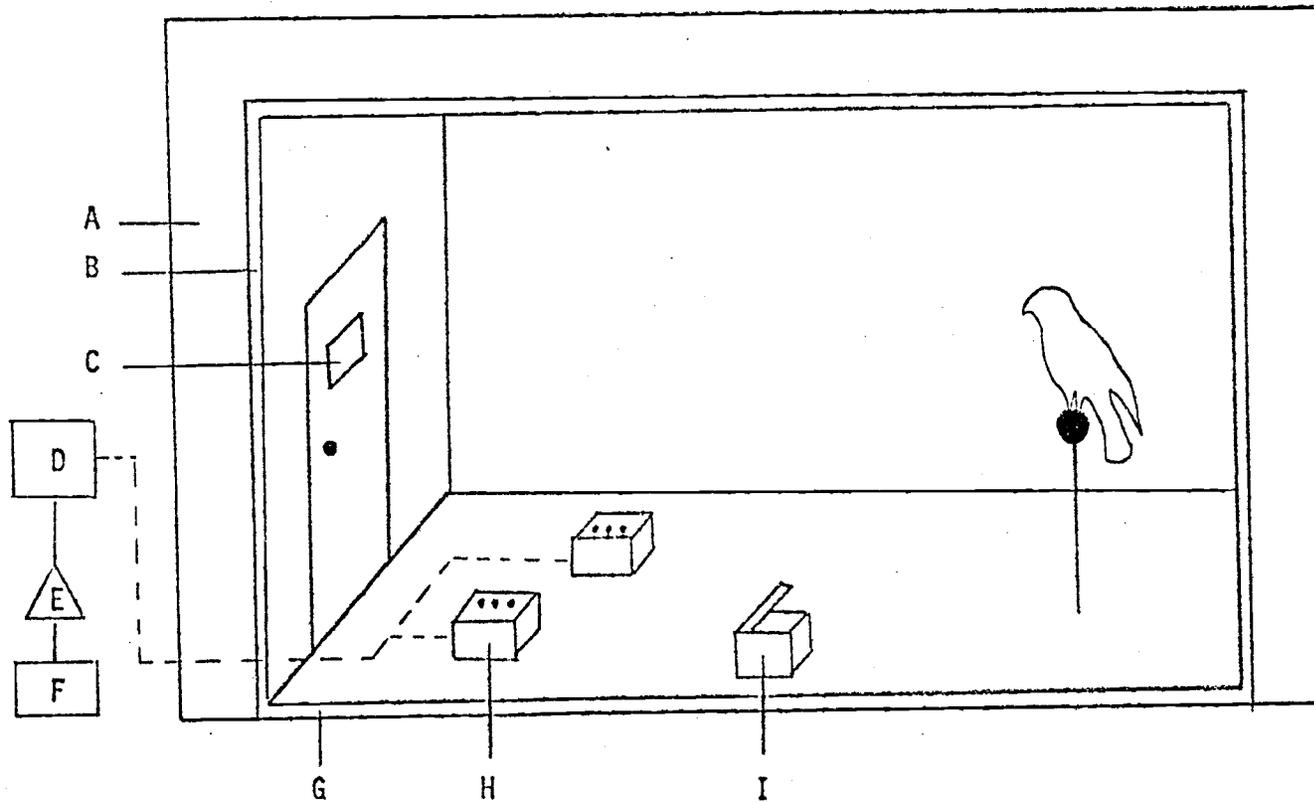   5.25m long

48

Figure 3. The sound spectograph of the pulsed noise used as a sound stimulus in the laboratory experiments. The last pulse of sound (B) is at half speed to show the frequency characteristics between 8,000 and 16,000 Hz.
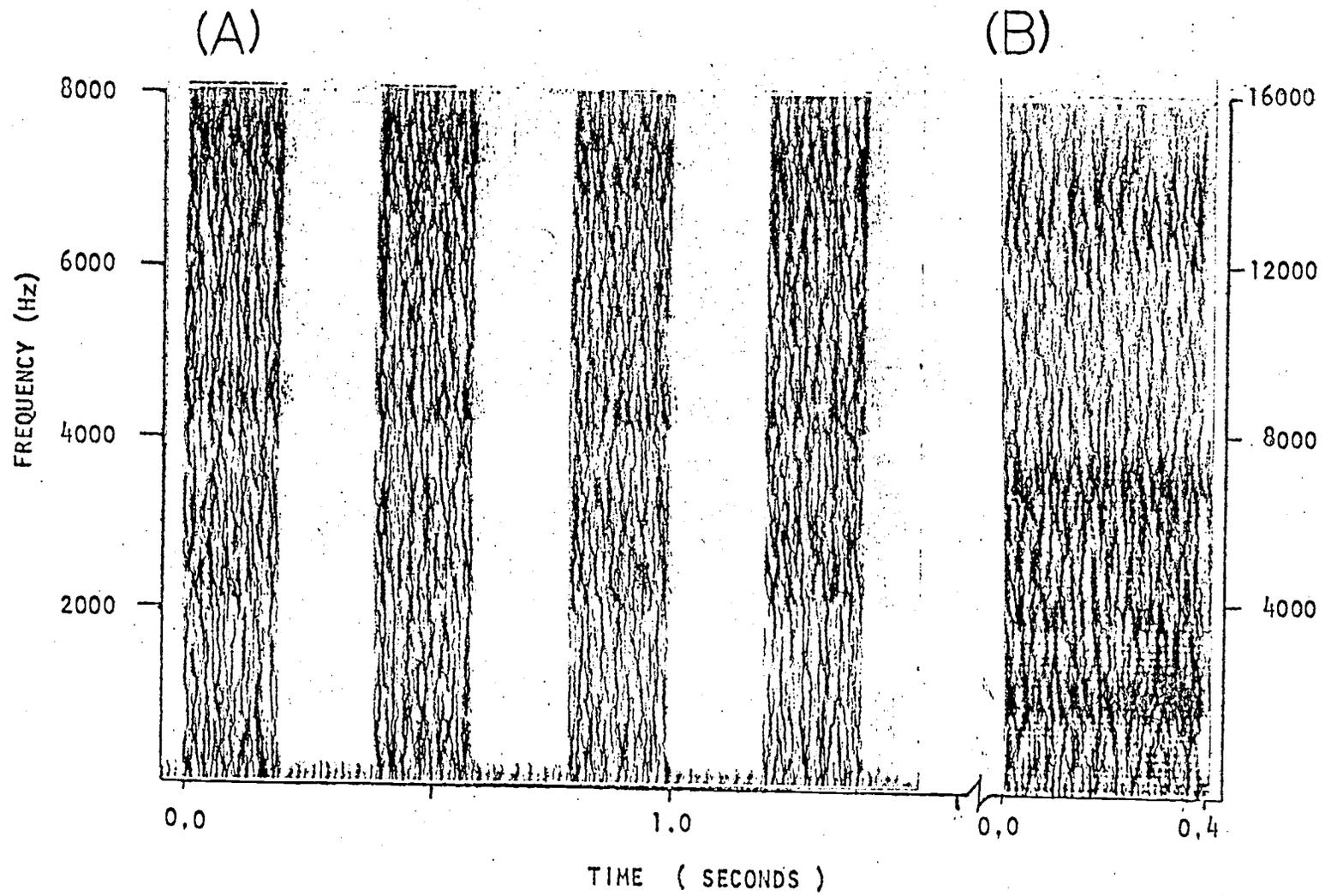
51

Figure 4. Schematic diagram of the test grid used in the field experiments. The elevated blind (left) connected with the ten concealed loudspeakers (circles) via a subterranean wiring network (dashed lines).

10m

Figure 5. Rationale for determining the angular accuracy of the harrier's auditory localization from data generated in the field experiments. The stippled disk represents a target with diameter d separated from the bird by a distance s. If a linear error of size d or less is made, the target will sometimes be missed completely by a bird directing a point source at the target's perceived center.(arrow A). If the bird makes a linear error of size d/2 or less the target will always be hit (arrow B). Because the bird directs an interval (of size TS, representing the talon spread) at the target, the margin of error that can made and still consistantly hit the target is (1/2)d+TS.
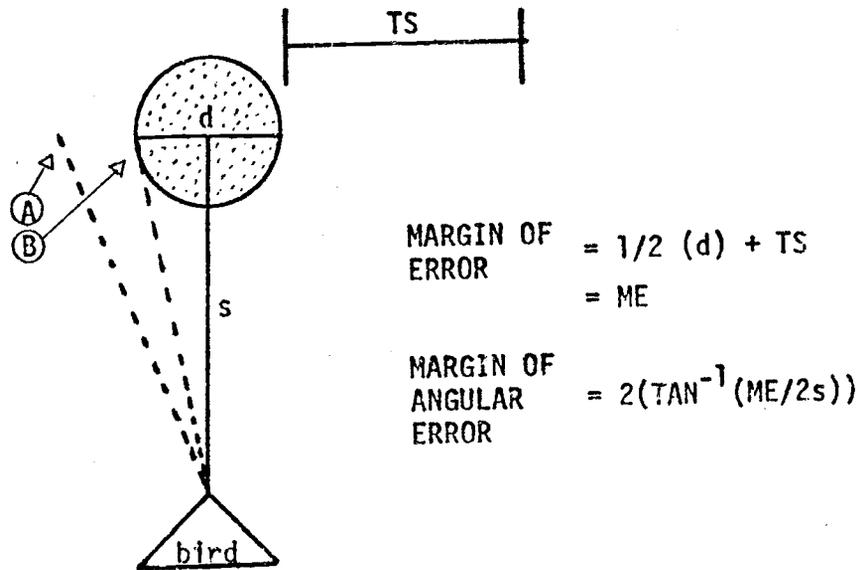
Figure 6. The 'rectangle of uncertainty' for sonic location of concealed prey. Distance between raptor and prey is three meters. The outer rectangle (lightly stippled) is for the red-tailed hawk, the middle rectangle (densely stippled) is for the harrier, and the inner rectangle (clear) is for the barn owl. The height and width of each rectangle is determined by the MAA(vertical) and the MAA(horizontal) respectively. A typical sized vole (eight cm) is shown for scale.
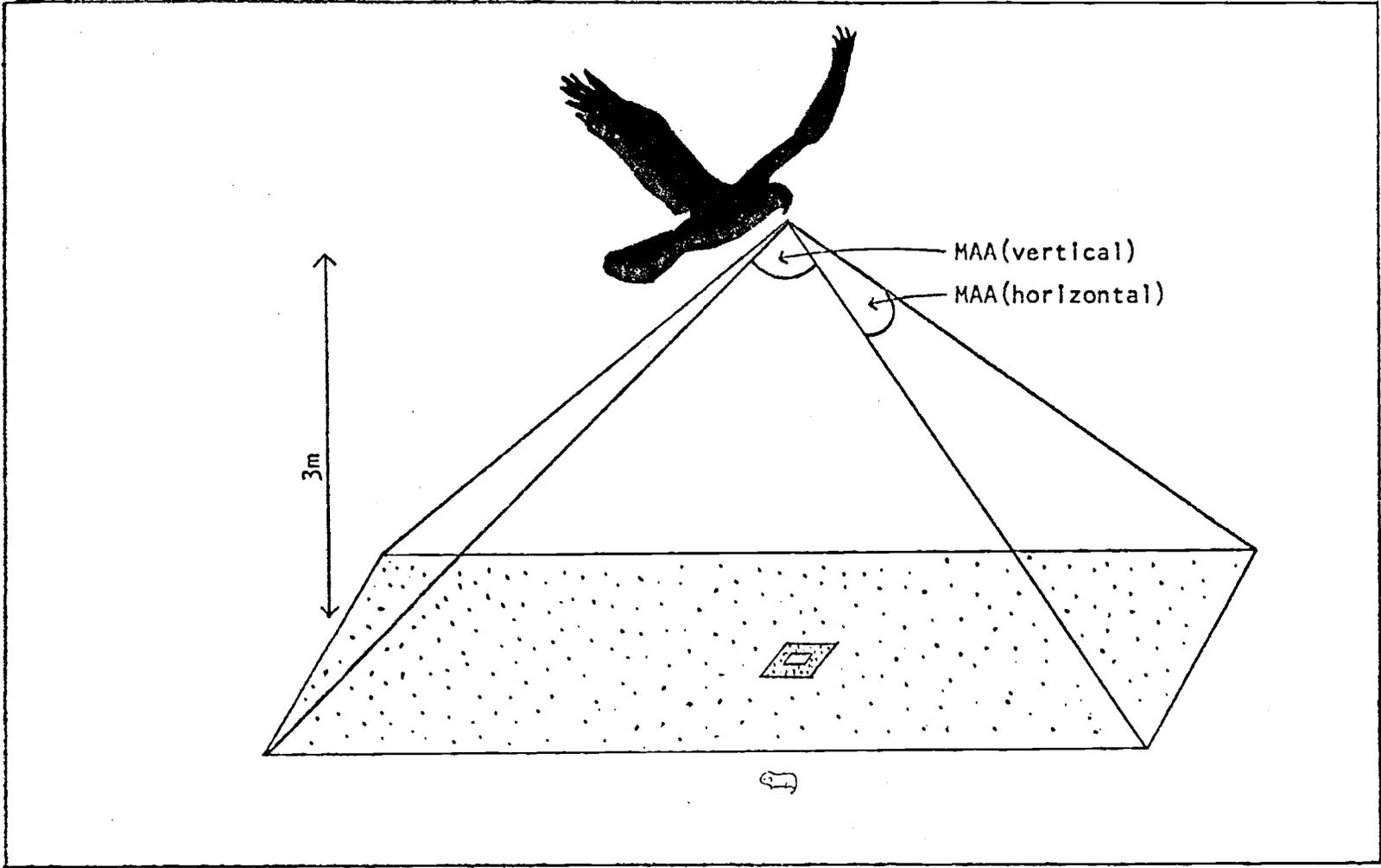
MAA(vertical)

MAA(horizontal)

3m

Figure 7. Three ways that a harrier potentially could locate concealed prey by integrating visual and auditory cues: (A) use of auditory depth perception, (B) use of multiple auditory azimuth determinations, and (C) use of auditory elevation determination. See text for details.

(A)

(B)

(C)