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ACOUSTICAL LOCATION OF PREY BY THE MARSH HAWK: ADAPTATION TO CONCEALED PREY

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ABSTRACT.—The ability of Marsh Hawks (*Circus cyaneus*) to locate prey acoustically was measured in both the laboratory and the field. Laboratory experiments indicated that the directional hearing of the Marsh Hawk 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 2° for the Marsh Hawks, 1–2° for the owls, and 8–12° for the sample of typical diurnal raptors. For the Marsh Hawks, angular resolution along the vertical axis was at least 2°. The maximum range at which prey could be detected by sound was estimated to be 3–4 m for the Marsh Hawk and 7 m for the Barn Owl (*Tyto alba*). Field experiments indicated that free-ranging Marsh Hawks 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 Marsh Hawk integrates auditory and visual cues while capturing concealed prey. These experiments show that the Marsh Hawk does not require motion cues or auditory depth perception to determine the elevation of a sound source. Received 23 December 1980, accepted 5 October 1981.

THE Marsh Hawk and other members of the genus *Circus* are distinguished from other diurnal raptors by a pronounced convergence with nocturnal owls. Comparative anatomical work by a number of authors (Pycraft 1898, Chandler 1914, Kelso 1940, Clark and Stanley 1976) indicates a strong convergence of the facial anatomy of the Marsh Hawk with that of owls capable of locating prey through sonic cues while in total darkness. Like most owls, the Marsh Hawk possesses a curved, sound-reflecting facial ruff composed of both a ridge of skin and several rows of densely packed feathers. In an intact specimen, the facial ruff is shielded by a layer of highly specialized, sound transparent feathers that obscure most of this pinna-like structure from view. The auditory meatus is relatively large, and its for-

ward margin is directed outward. This arrangement forces high frequency sound, originating in front of the bird, to reflect off of the facial ruff before entering the ear opening.

The foraging behavior of the Marsh Hawk and other members of the genus *Circus* is also unusual for a falconiform. The Marsh Hawk typically forages by continually quartering over an area at relatively low elevation. This is in marked contrast to most other open-land falconiforms, which typically forage from a relatively high flight or perch position. Schipper et al. (1975) found the average foraging height of the Marsh Hawk to be less than 2 m when it foraged over short (≤ 1 m) vegetation. Although the low quartering behavior of the Marsh Hawk is atypical of falconiforms, it is commonly found in both nocturnal and facultatively diurnal strigiforms, e.g. *Tyto alba*, *Asio otus*, and *Asio flammeus*.

The facial ruff and low foraging posture of owls are important adaptations that permit prey to be located in total darkness. The facial

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ruff and associated structures (e.g. preaural ear flaps) have been shown by a number of researchers to be necessary for the accurate locating of prey when only sonic cues are available (Payne 1962, 1971; Konishi 1973; Knudsen and Konishi 1979a, b). A low foraging position is also a prerequisite to locating prey by sound. Empirical and theoretical work by Norberg (1968), Manley (1971), Payne (1971), Schwartzkopff (1973), and Knudsen and Konishi (1979a, b) indicates that, in birds, locating prey by sound is extremely restricted in range, requiring a foraging position that is relatively close to the prey. These observations suggest that the convergence of the facial anatomy and foraging behavior of the Marsh Hawk with those of owls may be due to a reliance by both on the auditory detection of prey.

The behavioral and anatomical similarities between the Marsh Hawk and owls prompted the following hypothesis: the Marsh Hawk (order Falconiformes) has converged with certain nocturnal owls (order Strigiformes) in the ability to locate concealed prey by use of acoustical cues. This reliance on auditory cues in part explains the Marsh Hawk's low foraging position.

EXPERIMENTAL METHODS

GENERAL DESIGN AND RATIONALE

The study included both laboratory and field experiments. In the laboratory experiments, I measured the directional hearing ability of the Marsh Hawk by determining its position along a spectrum of capabilities. All birds were expected to have some directional hearing ability, so the Marsh Hawk was compared with an owl species with an experimentally established high capacity for directional hearing (Barn Owl), a second owl species with a behavioral repertoire similar to that of the Marsh Hawk [Short-eared Owl (*Asio flammeus*)], and two typical diurnal raptors lacking apparent anatomical specializations for directional hearing [Red-tailed Hawk (*Buteo jamaicensis*) and American Kestrel (*Falco sparverius*)]. The sample of diurnal raptors was chosen to bracket the head size of the Marsh Hawk, so that any difference between the auditory resolution of the Marsh Hawk 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 at which prey could be detected

by sound for each species. The laboratory experiments permitted me to address two questions: (1) is the directional hearing ability of the Marsh Hawk sufficient to be functionally useful in locating concealed prey? and (2) is the accuracy of directional hearing in the Marsh Hawk 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. Findley National Wildlife Refuge). Squeaking vocalizations were broadcast from the loudspeakers to test the reaction of wild, free-ranging Marsh Hawks to auditory stimuli under natural conditions. With these experiments I attempted to answer two broad questions: (1) to what extent are sonic cues actually used by Marsh Hawks? and (2) how are visual and auditory stimuli integrated in the detection of concealed prey?

LABORATORY EXPERIMENTS

Horizontal resolution.—MAA values were measured along the horizontal axis through forced-choice experiments conducted in an echo-dampening test chamber (Fig. 1). 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. The dimensions of the test chamber were 2.5 m high by 2.75 m wide by 5.25 m long. 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 single 300-watt incandescent light.

All birds used in these experiments were raised from eggs or hatchlings, which were collected from local raptor nests. The birds were trained to alight on an elevated perch located 1 m from the far wall of the test chamber (Fig. 1). Two solid wooden 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 100–16,000 Hz, with 200 ms of sound alternating with 200 ms of silence), 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 food (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

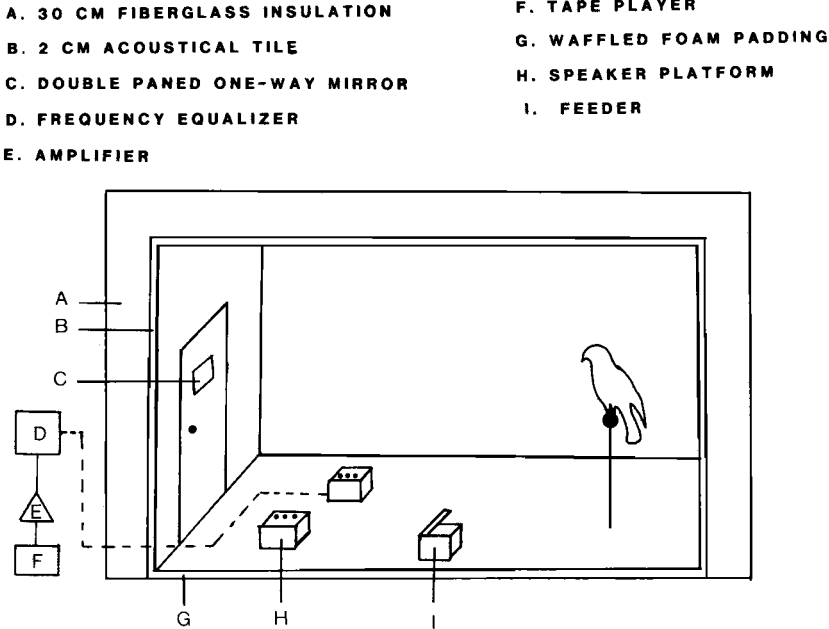


Fig. 1. Diagram of the test chamber. Speaker platforms are positioned for measuring MAA values along the horizontal axis.

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 error rate exceeded 25%. The number of trials at a particular spacing depended upon 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 speaker platforms. At the end of each day, I analyzed the cumulative set of data to determine whether or not I could be 99% confident that the bird could make the correct choice at least 75% 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 assay of sensory

capabilities involving conditioning 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, such as the possibly different frequency or amplitude characteristics of the speaker platforms. 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 was that a bird never heard the same sound twice during a single day's 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) was $0.88^\circ \pm 0.75^\circ$ SD] were close to the norms reported by Mills (1973).

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 × 50 m) connected 10 miniature loudspeakers to an elevated observation blind 50 m away. All wiring was "sewn" under the sod (with a 1-m-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 test stations were constructed in nearby areas (i.e. within 1 km). Each of these contained two speaker assemblies (one experimental, one control) located 3 m from a 2-m-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 10 m 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 occurring squeaks.

The purpose of the synthetic vole squeak was to produce a sound stimulus that attracted the Marsh Hawk but that also had special characteristics that were needed for my field experiments. To construct the synthetic vole squeak, I made sonograms of actual *Microtus montanus* 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 Marsh Hawks, but its spectral composition was substantially different from actual vole squeaks. I recorded my imitation squeak with an erratic 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 3–4 m of a speaker assembly, I manually terminated the sound. The position of the Marsh Hawk was determined by interpolation from a grid of slats (0.25 m 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 Marsh Hawk and the American Kestrel. The kestrel was used as an example of a diurnal raptor lacking the behavioral and anatomical specializations of the Marsh Hawk.

RESULTS

Horizontal MAA.—The ability of the Marsh Hawk to discriminate the horizontal direction of sound was 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% certain that the bird could properly determine the direction of the sound at least 75% 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 Marsh Hawks were the most difficult to train, and this may be reflected in their performance. During the 1° trials, the speaker platforms were separated only by 3 cm. As a result the Marsh Hawks frequently landed on both platforms simultaneously, which interfered with my measurements (I did not count these trials). Even after four series of experiments in which I gradually reduced the angle of separation to 1°, however, I was unable to demonstrate statistically that the Marsh Hawks could resolve 1°. One Short-eared Owl and one Barn Owl were able to resolve only 2°. Both of these birds were difficult to train, and this may partially explain their higher MAA. Because of spatial constraints, tests at 0.5° could not be made. It seems unlikely, however, that either of the owls successfully resolving 1° could re-

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

Species	Individual	Horizontal tests			Coarse vertical resolution ^c
		Minimum horizontal resolution ^a	Number of trials ^b	Number correct	
Red-tailed Hawk ^d	1 (F)	8°	56	51	No
	2 (M)	10°	46	42	No
American Kestrel	1 (M)	10°	107	96	No
	2 (F)	12°	33	31	No
Barn Owl ^d	1 (M)	1°	23	22	Yes
	2 (F)	2°	34	32	Yes
Short-eared Owl ^d	1 (F)	1°	37	35	Yes
	2 (F)	2°	52	47	Yes
Marsh Hawk	1 (F)	2°	40	37	Yes
	2 (M)	2°	106	96	Yes

^a Values reported are minimum audible angles (MAA).

^b Number required to be 99% confident that the correct choice could be made at least 75% of the time.

^c Ability to resolve a 40° vertical displacement; see text for details.

^d Sex based on size.

solve 0.5°. Both of these owls frequently refused to fly at the speaker platforms when they were separated by 1° but would readily respond if I increased the separation to 2°. 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° along the horizontal axis. While these values do not represent MAA values (resolution must be sufficient 75% of the time for a MAA value and approximately 50% 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 1°. My best estimate for the Marsh Hawk's and owl's MAA's are 2° and 1°, respectively. Thus, the horizontal resolution of the Marsh Hawk appears to have diverged from that of typical diurnal birds of prey and converged with that of owls capable of locating prey by sound 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°. Similarly, all of 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 Marsh Hawks, however, could successful-

ly 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 Marsh Hawks 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 increased 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, I measured the vertical resolution of the Marsh Hawk indirectly during the field experiments. The only conclusion from these tests was that both the owls and the Marsh Hawk 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 its head in response to the vertical stimuli. This eliminated the need for head restraints. I did observe a "head rotation" response in both of the Marsh Hawks, but in none of the other birds, when the Marsh

TABLE 2. Field tests of the ability of two raptor species to locate concealed loudspeakers that emitted a synthetic vole squeak. The sound stimulus was present at a normal volume and terminated when the bird approached to within 3 m.

Species	Individual	Position	Number of trials	Target hits	Target misses
American Kestrel	1	Perch ^a	2	— ^b	—
	2	Perch	1	—	—
Marsh Hawk	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 3 m; the sound stimulus was terminated when the bird left the perch.

^b Neither of the kestrels made any response 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 when the raptor struck at the speaker assembly.

Hawks were exposed to a novel sound. The Marsh Hawks looked directly at the speaker and rotated their heads ($\frac{1}{2}$ 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, I no longer observed this response.

Field experiments.—In the field experiments, five different Marsh Hawks were tested for a total of 10 trials (Table 2). The Marsh Hawks were able to locate 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 either to the synthetic vole squeak or to the squeaks I recorded from the resident voles occurring naturally in the area. I was certain that the kestrels were naturally capturing voles during the time of my field experiments (December–February), because I observed them capturing voles in my study 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 vole squeak.

DISCUSSION

The utility of directional hearing.—The purpose of the laboratory studies was to determine whether or not the directional hearing capacity of the Marsh Hawk is sufficiently accurate to be useful in detecting concealed voles and whether or not this ability is extraordinary

compared to that of other diurnal raptors. My laboratory measurements indicate that a Marsh Hawk can resolve the horizontal displacement of a sound to an accuracy of at least 2° . Although the laboratory measurements of vertical resolution were unsuccessful, I was able to infer the upper limit of the Marsh Hawk'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 3 m of the speaker assembly (exactly 3 m in the four trials where the bird struck from a perch). This required the bird to locate 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" might be the result of repeated attempts. In two instances, I can be certain that this did not occur. In one case the Marsh Hawk pulled the entire speaker assembly out of the ground during a single stoop. This bird never landed. In a second instance the bird flew off immediately after landing and repeated strikes could not have occurred. In one instance, however, I saw a bird strike repeatedly at the vegetation and also beat the vegetation with its wings, apparently attempting to flush the simulated vole. If one infers from these data that a Marsh Hawk with a 10-cm talon spread can repeatedly hit a 2.5-cm target from 3 m away, then the vertical resolution must be at least 2° , i.e. the vertical resolution is equal to or better than the 2° horizontal resolution determined in the laboratory (see Rice 1980 for computational details). A similar result was reported for Barn Owls by

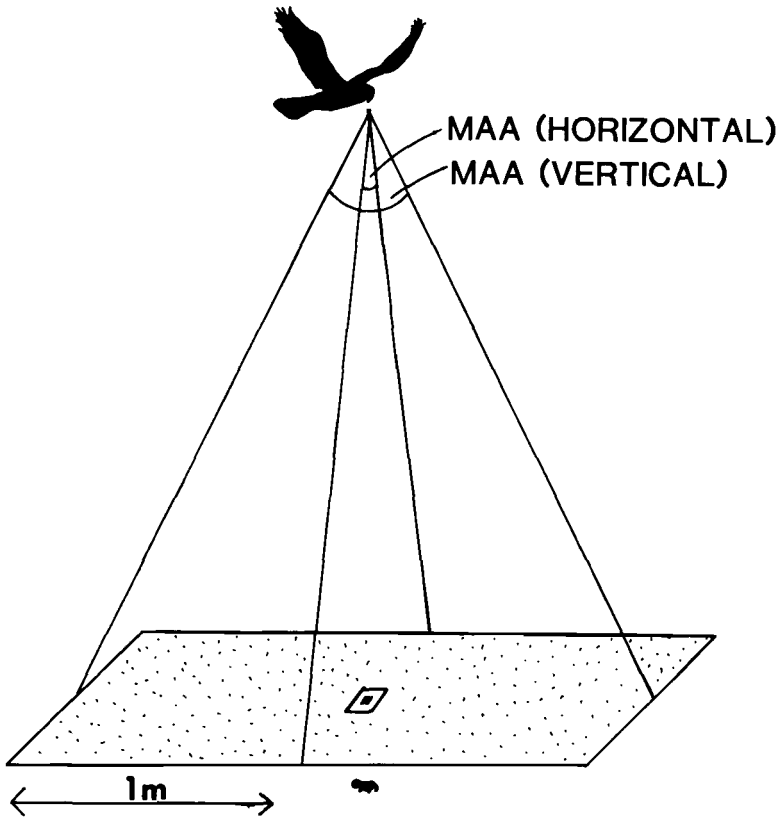


Fig. 2. The "rectangle of uncertainty" for location of concealed prey by sound. Distance between raptor and prey is 3 m. The outer rectangle (stippled) is for the Red-tailed Hawk or American Kestrel, the mid rectangle (clear) is for the Marsh Hawk, and the inner rectangle (solid) is for the Barn Owl. The height and width of each rectangle is determined by the vertical MAA and the horizontal MAA, respectively. A typical sized vole (8 cm) is shown for scale.

Payne (1971), Konishi (1973), and Knudsen and Konishi (1979a, b). 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 (1°) and the Marsh Hawks (2°) and an upper limit for the vertical resolution of the two diurnal raptors of 40° , the utility of directional hearing in these species can be compared (Fig. 2). The effective range at which prey could be detected by sound 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. For a Marsh Hawk with a

talon spread of 10.0 cm and resolution of 2° along both axes, maximal striking range is estimated at 3–4 m. For an owl with a similar talon spread and a resolution of 1° , the range is about 7 m. The 7-m 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 7 m away. Instead, the owls would fly to a closer position and wait for additional acoustical cues. The angular resolution achieved by the sample of typical diurnal raptors would be insufficient for any useful location of prey, even at very close range (Fig. 2). Thus, the capacity of the Marsh Hawk for locating prey by sound 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 detection demonstrated by free-ranging Marsh Hawks in the field experiments.

Field experiments.—The field experiments were directed at four specific questions: (1) do Marsh Hawks use sonic cues naturally? (2) does a vole need to be seen to be captured? (3) are olfactory cues needed for nonvisual prey location? and (4) how are visual and auditory cues integrated in prey location? Questions 1 through 3 were collectively answered by simulating the position of a vole with a concealed loudspeaker. Because no vole was actually present, location by olfactory or visual cues was impossible. In addition, because only wild Marsh Hawks were tested in their natural environment, fewer training or situational artifacts are likely. Thus, the fact that all of the birds tested consistently hit a 2.5-cm sound-emitting target with no visual or olfactory cues suggests that the Marsh Hawk can and naturally does employ sound in the detection of prey.

The detection of prey by sound has different constraints in diurnal raptors and nocturnal owls. 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 1973). Payne (1971) was unable to determine whether or not the distance to the prey could be determined by the Barn Owl, but he did show that this owl could use sonic cues to determine both azimuth and elevation. Payne reasoned that an owl might not be able to determine the distance to a prey item sonically but could still capture it in total darkness. The owl potentially could determine the direction of the prey based on azimuth 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 Marsh Hawk is the sym-

metry 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. preaural ear flaps; Norberg 1978). All birds are expected to have a capacity for determining 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 (Pumphery 1948; Payne 1971; Knudsen and Konishi 1979a, b). If the ear openings are equipped with pinnae, then the monaural determination of elevation may be possible, because sounds originating from different elevations are expected to produce unique echo patterns, which can be used to infer elevation (Batteau 1967, Freedman and Fisher 1968). Because the Marsh Hawk does not have asymmetric ears, I wanted to determine whether or not 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 locate concealed prey. The first method requires a familiar sound, auditory determination of azimuth, auditory perception of depth, and visual perception of the surface contours. Coleman (1962, 1963) used principles from acoustical physics to argue that there are only two feasible methods of perceiving the depth of a complex sound that are operative over distances greater than approximately 1 m: 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 lower frequencies. Thus, the distance that a familiar sound has traveled can be determined by the extent of bass-bias. Distance-specific changes in timbre are temperature- and humidity-specific but, nevertheless, potentially could be used by the Marsh Hawk 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 Marsh Hawk potentially could locate a concealed prey item producing a familiar sound in the following way. When the concealed prey was heard, its azimuth and distance could be determined auditorily. Vision could then be used to determine what point along the auditorily determined azimuth intersected the surface at the auditorily determined distance. 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 perceiving elevation by sound.

A second method involves the auditory determination of azimuth, motion, and vision. If the bird is moving relative to the sound-emitting prey item, then the auditorily determined 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 azimuth bearing, determined auditorily 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 item. 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.

The third method involves auditory determination of both azimuth and elevation and 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.

Method 3 involves the auditory determination of both azimuth and elevation, whereas methods 1 and 2 only require auditory determination of azimuth. To determine whether or not the Marsh Hawk used auditory cues to determine elevation, I had to show that prey could be located when methods 1 and 2 were not operative. I did this by using a synthetic vole squeak, which represented an unfamiliar

sound that had variable volume and timbre characteristics very different from a normal vole squeak. Thus, the variable volume and novel spectral characteristics should have prevented the bird from employing auditory perception of depth (Coleman 1962, 1963). If the Marsh Hawk could locate 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. The perched bird could obtain some motion cues by moving its head, but, with a horizontal resolution of only 2° , this scale at motion would not produce an unambiguous second azimuth bearing. Because the Marsh Hawks could locate 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 on the location of prey by sound. Michelsen (1978) and Wiley and Richards (1978) have reviewed the environmental factors affecting sound transmission. They indicate that the location of a sound source in the field requires substantially more sophistication than location 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. The location of prey 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 heterogeneity, and extrapolation from the laboratory to the field must be confirmed by 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 Marsh Hawk is sufficient (under highly idealized conditions) to locate prey effectively from a distance of 3 m. In the field, I have shown that prey can be and

are located at this range despite the more complex nature of a sound stimulus altered by variations in the micro-climate. Thus, the sensory system of the Marsh Hawk appears to be sufficiently elaborate to compensate for the distortions encountered under natural conditions.

The evolution of directional hearing.—Given the evidence for the ability to detect prey by sound in the Marsh Hawk, it seems reasonable to speculate on why this ability 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 few species outside of the genus *Circus* have anatomical features suggesting a reliance on auditory cues. Because the range at which auditory cues can be used is restricted, an organism must be preadapted to forage close to the substrate, where the refinement of directional hearing could gradually evolve. Van Dijk (1973) used anatomical and psychophysical data to argue that passive sonar independently evolved in owls at least three times. Owls may be preadapted to use 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 *Circus* also may have been preadapted to use sonic cues if they, like many present species of this genus, foraged over tall-grass vegetation. Tall grass permits visual penetration only 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 produces only a small increase in the effective field of view. Under these conditions, a low foraging position can be favored, because 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 the ability to locate prey by sound thus would be unlikely.

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LITERATURE CITED

- BATTEAU, D. W. 1967. The role of the pinnae in human localization. *Proc. Royal Soc. London, Ser. B.* 158: 158-180.
- CHANDLER, A. C. 1914. Modifications and adaptations to function in the feathers of *Circus hudsonius*. *Univ. Calif. Publ. Zool.* 11: 329-376.
- CLARK, R. J., & 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. Pennsylvania 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.
- . 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. Natur.* 79: 385-416.
- ERULKER, S. D. 1972. Comparative aspects of spatial localization of sound. *Physiol. Rev.* 52: 237-359.
- FREEDMAN, S. J., & H. G. FISHER. 1968. The role of the pinnae in auditory localization. Chapt. 8 in *The neuropsychology of spatially oriented behavior* (S. J. Freeman, Ed.). Homewood, Illinois, Dorsey Press.
- KELSO, L. 1940. Variation of the external ear opening in the Strigidae. *Wilson Bull.* 52: 24-29.
- KNUDSEN, E. I., & M. KONISHI. 1979a. Sound localization by the Barn Owl (*Tyto alba*): measures with the search coil technique. *J. Comp. Physiol.* 133:1-11.
- , & ———. 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.
- MICHELSSEN, A. 1978. Sound reception in different environments. Pp. 345-373 in *Sensory ecology review and perspectives* (M. A. Ali, Ed.). New York, Plenum Press.
- MILLS, A. W. 1973. Auditory localization. Chapt. 8 in *Foundations of modern auditory theory* (C. J. Tobias and E. D. Schubert, Eds.). New York, Academic Press.

- NORBERG, R. 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.
- . 1978. Occurrence and independent evolution of bilateral ear asymmetry in owls and implications on owl taxonomy. *Phil. Trans. Royal Soc. London (Biol.)*. 282: 325-410.
- PAYNE, R. S. 1962. How the Barn Owl locates prey by hearing. *Living Bird* 1: 151-159.
- . 1971. Acoustic location of prey by the Barn Owl (*Tyto alba*). *J. Exp. Biol.* 56: 535-573.
- PUMPHERY, R. J. 1948. The sense organs of birds. *Ibis* 90: 171-199.
- PYCRRAFT, W. P. 1898. A contribution toward our knowledge of the morphology of the owl. *Trans. Linnean Soc. London Sec. Ser. (Zool.)* 7: 223-276.
- RICE, W. R. 1980. Acoustic localization of concealed prey by the diurnal Harrier (*Circus cyaneus*). Unpublished Ph.D. dissertation. Corvallis, Oregon, Oregon State Univ.
- SCHIPPER, W. J. A., L. S. BUURMA, & P. H. BOSSENBROEK. 1975. Comparative study of hunting behavior of wintering hen-harriers *Circus cyaneus* and marsh harriers *Circus aeruginosus*. *Ardea* 63: 1-29.
- SCHWARTZKOPFF, J. 1973. Mechano-reception. Pp. 417-477 in *Avian biology*, Vol. 3 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- SUTHERS, R. A. 1978. Sensory ecology of birds. Pp. 217-251 in *Sensory ecology review and perspectives* (M. A. Ali, Ed.). New York, Plenum Press.
- VAN DIJK, T. 1973. A comparative study of hearing in owls of the family Strigidae. *Netherlands J. Zool.* 23: 131-167.
- WILEY, R. H., & 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.