

## How robins find worms

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**Abstract.** An understanding of diet selection in animals requires knowledge of not only what animals eat in relation to what is available, but also how they perceive the foods available to them. Birds use auditory, visual, olfactory and possibly vibrotactile cues to find prey, but vision is the predominant mode of prey detection. In a series of controlled experiments in an aviary, four American robins, *Turdus migratorius*, found buried mealworms in the absence of visual, olfactory and vibrotactile cues, suggesting that they could use auditory cues to locate the prey. They also had significantly reduced foraging success when auditory cues were obscured by white noise. These results conflict with the only other experimental study of foraging in American robins, which concluded that they foraged using visual clues alone.

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In studies of foraging behaviour, researchers must often make assumptions regarding the relationship between the food present in an animal's environment and the food that the animal can actually perceive. Measuring prey choice, for example, requires knowledge not only of what an animal eats, but also what potential prey items might be detected but not eaten. Assumptions about food availability, in turn, require some knowledge about the sensory modalities used in prey detection, because prey that an animal cannot detect is functionally unavailable to it.

With notable exceptions (e.g. Konishi 1973), the sensory modalities used by foraging birds have not been well studied. In part because of their remarkable auditory apparatus and their uncanny ability to localize prey, owls, and particularly barn owls, *Tyto alba*, have been extensively studied (e.g. Knudsen 1980). Studies of colour perception, like those conducted with black-chinned hummingbirds, *Archilocus alexandri* (Goldsmith & Goldsmith 1979), also have potential relevance to foraging behaviour, but this has not been the subject of much research. In the present study, we used an experimental approach to determine how American robins, *Turdus migratorius*, use

auditory, visual, olfactory and vibrotactile cues when hunting for worms.

Most diurnally active birds appear to be visually oriented foragers. Birds seem poorly adapted for localizing prey by hearing because their relatively small heads produce little sound shadow and their closely set, inconspicuous ears generate small interaural time differences (Knudsen 1980). None the less, songbirds have reasonably good auditory abilities as evidenced by numerous studies of song detection and discrimination (e.g. McGregor 1991). Further evidence of the sound-localizing abilities of songbirds comes from an experimental study of Australian black-backed magpies, *Gymnorhina tibicen*, foraging on buried scarab beetle, *Rhopaea verreauxi*, larvae with auditory, vibrotactile and visual cues masked in a variety of combinations (Floyd & Woodland 1981). Magpies were able to find the buried larvae exclusively by localizing the low-amplitude, low frequency sounds made when the larvae were burrowing or feeding.

American robins are common garden birds over much of North America and their distinctive foraging behaviour is well known, although little studied (Heppner 1965; Eiserer 1980; Paszkowski 1982; Swihart & Johnson 1986). Earthworms may comprise up to 20% of their diet (Kalmbach 1914; Howell 1941), particularly during the breeding season, and these are typically captured on mown

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lawns. Foraging robins run several steps at a time, cock their heads to one side for up to a few seconds, then lunge at the ground, often driving their bill well into the soil where they grab an earthworm, pull it to the surface and consume it or take it to feed their nestlings. Some lunges are unsuccessful, but capture rates as high as 20 earthworms per hour have been recorded (Heppner 1965; R. Montgomerie, unpublished data). In an experimental study of robin foraging behaviour, Heppner (1965) concluded that American robins locate earthworms exclusively by visual cues. He based this conclusion on a series of experiments in which robins were able to find earthworms placed in holes in a lawn (but still visible) even in the presence of loud white noise (which would have obscured any auditory cues).

Our own field observations of robins foraging suggested to us that they might also use other sensory modes while searching for earthworms. When they cock their head they appear to be listening (see also Tyler 1949), and we have watched robins successfully foraging on lawns where the grass was long enough to make earthworms difficult to see. We also watched a captive robin catch earthworms buried in soil where we could detect no visual cues that would reveal an earthworm's location. Thus it seemed to us that auditory, olfactory or vibrotactile cues might be used in addition to visual cues when localizing prey. Our objective in this study was to test experimentally the ability of captive robins to use each of these sensory modalities when hunting for worms.

## GENERAL METHODS

We conducted this study during the summer in outdoor aviaries at the Queen's University Biological Station, 45 km north of Kingston, Ontario, Canada. The aviaries were made of wood and chicken wire ( $4.5 \times 2.6 \times 1.8$  m) and were located in a quiet woodland setting well away from roads and other sources of noise.

All birds studied were wild-caught in Kingston, Ontario, and were held for up to 2 weeks in the aviaries before experiments began. When not engaged in experiments, the birds were fed ad libitum on diced apples, moist dog food, raisins, mealworm, *Tenebrio molitor*, larvae and drinking

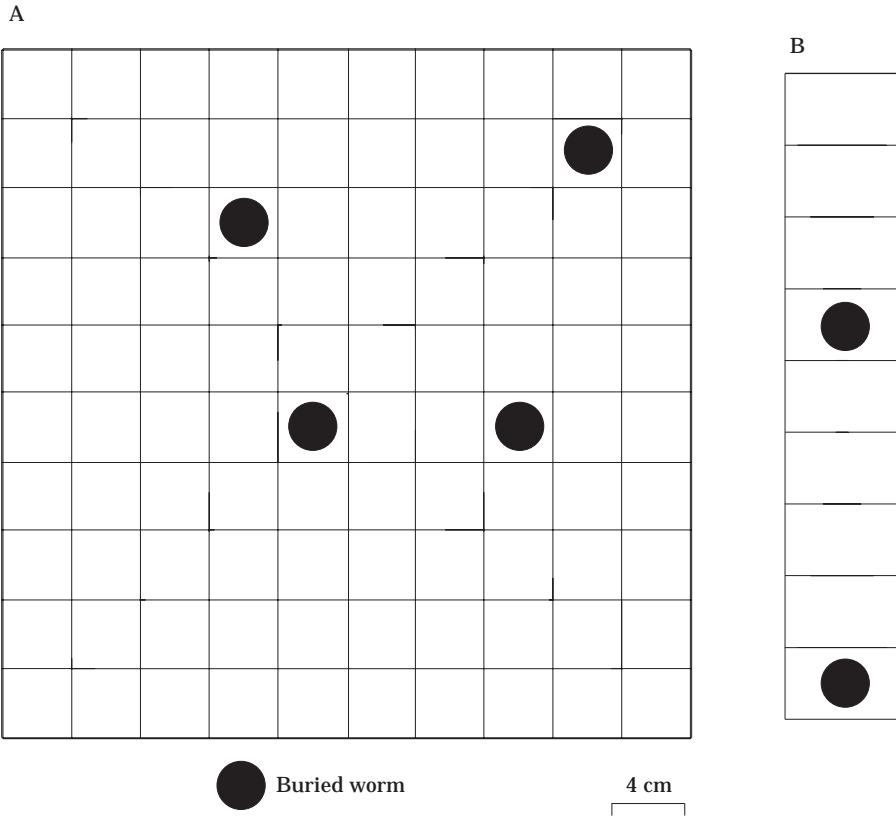
water. Although the floors of the aviaries were soil, it was so compacted that it is unlikely that any natural food was available during the experiments. All birds appeared healthy and active throughout the experimental period. Each bird was housed individually in an aviary during the entire set of experimental trials, then released.

We usually conducted experiments in the mornings, on calm, rainless days to minimize ambient noise. We removed food from the experimental aviary about an hour before experiments began and replaced it immediately following the trials.

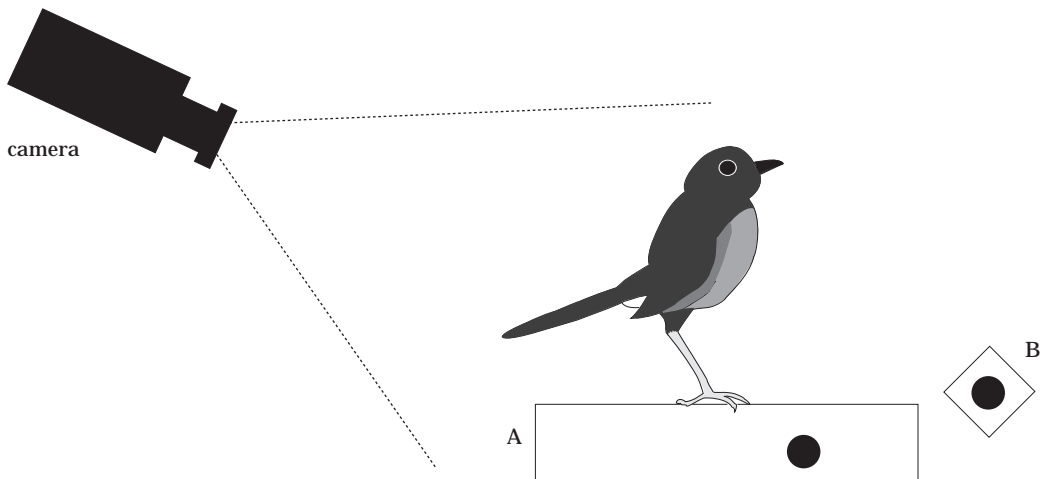
For each experiment, we presented a bird every 20–30 min with a wooden tray (Fig. 1) containing food buried in soil. The trays containing food were either square ( $42 \times 42 \times 10$  cm; experiments 1, 3, 4) or rectangular ( $11 \times 40 \times 9.5$  cm; experiment 2) and were filled to a depth of 5 cm with topsoil that had been baked at  $200^\circ\text{C}$  for 30 min to kill any soil-dwelling invertebrates. The square tray (A in Fig. 1) was divided into 100 grid squares ( $4.25 \times 4.25$  cm); the rectangular tray (B in Fig. 1) was divided into nine grid sections ( $11 \times 4.5$  cm). We marked each tray along the wooden frame to allow accurate determination of the location of grid squares. For experiment 2, tray B was mounted on a wall of the aviary so that the test bird could stand on tray A while searching for mealworms in tray B without picking up any vibrotactile cues from tray B. We buried mealworms by pushing a sharpened pencil into the soil to a depth of 4 cm, inserting the mealworm head first, filling in the soil and tamping it flat to a smooth surface overall. Since mealworms were 2.5–3.0 cm long, they were no closer than 1.0 cm to the soil surface. We then sprayed the soil surface lightly with water to further smooth and dampen it and thus completely obscure the location of the buried food.

For most experiments we used live mealworms, rather than earthworms, because mealworms were more readily available in the large quantities needed both to feed the birds and conduct these experiments. Mealworms, being much smaller (0.12 g, on average) than earthworms, also provided less food, so that we could run more trials during a day without satiating the birds. In addition, mealworms moved much less distance in the soil than earthworms during 30-min experimental trials. Consequently we could be certain that each mealworm remained near the original site of placement. We ran a few trials with

Top view



Side view



**Figure 1.** Test trays (A and B) and camera set-up used in experiments. Tray A was used in all experiments but did not contain food in experiment 2, when the food was placed in tray B. Example random locations of mealworms are shown.

earthworms to ensure that our results were applicable to this prey species as well.

We continuously videotaped each experiment for the entire trial from a position 2 m away from the feeding tray. We placed the camera at an angle of 30° above the tray so that we could easily score the location of each strike made by the bird on the soil surface (Fig. 1). An operator entered the aviary for a few min only at the start and end of each of the 5–10 trials run per day. We analysed videotapes at the end of the day and noted the position of each strike on the soil. For all analyses, we considered only the first strike at the soil surface as indicating the bird's assessment of prey location. Strikes were scored as a hit if the bird struck the same grid square (experiments 1, 3, 4) or section (2) as the mealworm had been placed.

We conducted an intensive study of four birds (three males, one female) because we were interested in assessing the perceptual abilities of individuals rather than examining the distribution of these abilities within a population. Thus, we usually used replicated goodness-of-fit tests for analysis, treating each individual as a replicate and obtaining a total  $G$ -value ( $G_T$ ) to test whether the data as a whole fit expected (random) values (Sokal & Rohlf 1995).

For each of the following experiments, we generally followed the procedures taken by Floyd & Woodland (1981) to test the use of different sensory modes (olfaction, audition, vision, vibrotactile) in the location of mealworms buried in the soil.

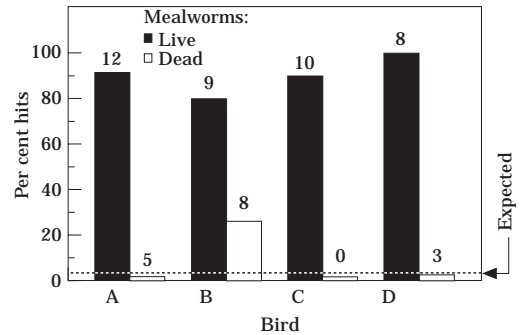
## EXPERIMENT 1: OLFACTORY CUES

### Methods

For this experiment, mealworms were buried in the square tray (A in Fig. 1). We buried two live and two freshly killed mealworms in randomly chosen grid squares, one in each of the four quadrants of the tray. Mealworms were killed by freezing overnight; this caused no apparent change in their odour. If olfaction was as useful as other cues in locating these mealworms, we expected no difference in the ability of the birds to locate live or dead mealworms.

### Results

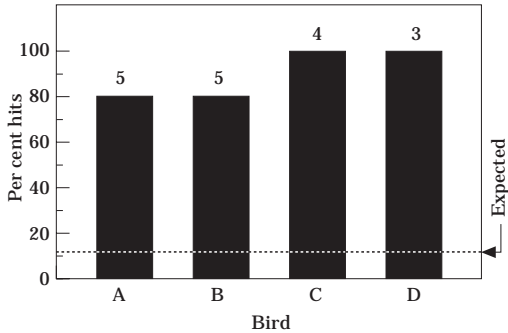
The test birds did significantly better than random expectation at finding live mealworms



**Figure 2.** Ability of the four test robins to find live and dead mealworms buried at random within quadrants on the square test tray (A in Fig. 1). Because 25 grid squares were available in each quadrant, 4% of the strikes would have been expected to hit grid squares containing mealworms by chance alone. Birds A, C and D had no hits on dead mealworms. Numbers above the bars indicate the number of trials in which the test bird struck (hit or miss) at any grid square in the quadrant containing a live or dead mealworm.

(replicated goodness-of-fit test,  $G_T=202.7$ ,  $P<0.0001$ ; Fig. 2) but no better than random at finding dead mealworms ( $G_T=1.61$ ,  $P=0.81$ ; Fig. 2). Sample sizes were low for quadrants containing dead mealworms, because the birds rarely struck at the ground in these quadrants and only twice (of 17 strikes) struck the grid square where a dead mealworm had been placed (Fig. 2). In contrast, the birds had 39 first strikes in quadrants containing live mealworms, and 35 (90%) of those strikes were in the same  $4.5 \times 4.5$ -cm grid square where a mealworm had been placed. In 32 of the 35 cases (91%) where robins hit the location of the live mealworm on their first strike, the mealworm was captured and eaten; even in two of the four cases where robins missed the location of a live mealworm on the first strike, they got it on the next strike.

Thus, when only olfactory cues might have been available (e.g. with dead mealworms), the test birds did no better than expected by striking at random, and we conclude that olfactory cues were not used by the birds in locating the mealworms. It is possible, of course, that the mealworms had less odour when they were freshly killed; this seems unlikely but might be worth further study in research on prey localization. That caveat aside, and because robins were able to find live, but not



**Figure 3.** Ability of test birds to find mealworms in the absence of vibrotactile cues. Because nine grid sections were available in the test tray, 11% of the strikes would have been expected to hit grid squares containing mealworms by chance alone. Numbers above the bars indicate the number of trials in which the test bird struck (hit or miss) at any grid section.

dead, mealworms buried under the soil, we assumed that auditory, visual or vibrotactile cues must have been used in locating the mealworms.

## EXPERIMENT 2: VIBROTACTILE CUES

### Methods

Here we used the rectangular tray (B in Fig. 1) suspended from an adjacent wall so that it was not in contact with the tray (A) where the test bird stood. Thus the test bird's feet and body were not in contact with the tray in which the mealworms were buried, and the prey could not have been localized using vibrotactile cues. We buried one mealworm in one randomly-chosen section of the suspended tray (Fig. 1). The birds were often reluctant to attempt feeding from this suspended tray, so sample sizes for each bird were relatively small.

### Results

All of the test birds found mealworms much better than expected if they were striking at random (Fig. 3), and their overall success was significantly better than random expectation (replicated  $G$ -test,  $G_T=56.7$ ,  $P<0.0001$ ,  $N=4$  birds with 3–5 strikes each). The birds missed on only two of 17 first strikes altogether, and in one of these cases the bird obtained the mealworm on the second

strike. We concluded that vibrotactile cues were not required for robins to locate buried mealworms.

## EXPERIMENT 3: VISUAL CUES

### Methods

For this experiment a live mealworm was buried at a random location in two of the four quadrants in the square test tray (A in Fig. 1). We placed each mealworm in a hole 2 cm deep. The entire surface of the soil in the tray was covered with a  $42 \times 42$ -cm sheet of 1-mm-thick cardboard. We then covered this cardboard sheet to a depth of 2 cm with more soil. In this way we eliminated any slight visual cues that might be available on the soil surface that would allow a robin to locate a buried mealworm. In preliminary trials, we noticed that mealworms moving even 2 cm below the soil surface could be detected by movement of surface particles. Thus, although the cardboard might have dampened or distorted auditory cues, it was needed to ensure that no visual cues to the mealworm's location were detectable. This procedure may thus also have eliminated vibrotactile and olfactory cues. As before, we allowed each test bird to forage for 15 min per trial, and we scored only the first strike in each quadrant as a hit or a miss.

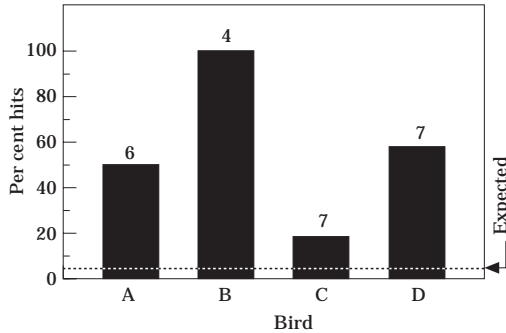
### Results

All four test birds found mealworms more often than expected by chance (Fig. 4), and their overall ability to find mealworms was significantly better than random expectation ( $G_T=54.6$ ,  $P<0.001$ ,  $N=4$  birds with 4–7 strikes each). Bird C had the lowest success rate (1 hit out of 7 first strikes) and spent most of the time during trials trying to dig up the cardboard, having several times struck the cardboard when attempting to strike buried mealworms. We concluded that robins are able to find buried mealworms in the absence of visual cues.

## EXPERIMENT 4: AUDITORY CUES

### Methods

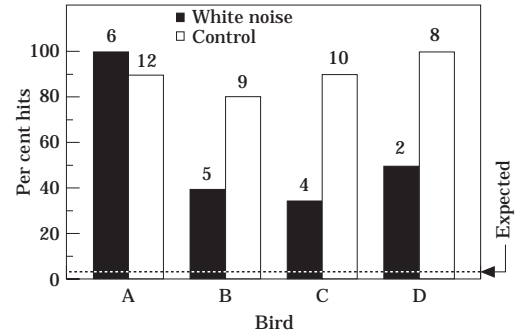
Because experiments 1–3 collectively suggested that hearing was the most likely method by which



**Figure 4.** Ability of test birds to find mealworms in the absence of visual cues. Expected values as in Fig. 2. Numbers above the bars indicate the number of trials in which the test bird struck (hit or miss) at any grid square in the quadrant containing a mealworm.

robins located buried mealworms, we designed this experiment to make auditory cues difficult to detect while other cues to mealworm location remained available. We tested birds on the square tray (A in Fig. 1) with one mealworm buried at a random location. White noise (50–20 000 Hz) was generated using SoundEdit software on a Macintosh microcomputer and recorded on a continuous loop cassette tape. We initially mounted a small speaker (Aiwa SC-A8, output 100–18 000 Hz) beside the tray with its centre at the level of the soil surface and about 30 cm away from the buried mealworm. The sound pressure level (SPL) for the white noise played from this speaker was 61 dB (Slow Reading; Realistic Sound Pressure Meter) at 1.0 m. This white noise had little effect on the first test bird's ability to locate mealworms; this bird found mealworms on the first strike for all six trials (goodness-of-fit,  $G_1 = 21.5$ ,  $P < 0.001$ ).

We then placed a 2-cm-diameter speaker (same frequency range and SPL) inside a small cotton bag and buried it at a depth of 3 cm in the centre of the experimental tray, facing upward. White noise was played from this speaker continuously during each 15-min trial. Because this speaker was buried in the soil and played some sounds at low frequency, vibrotactile cues may also have been affected by this method. If the robins were locating mealworms by sound in the previous experiments, however, then the white noise should have made prey detection more difficult. Because olfactory, visual and possibly vibrotactile cues should not have been affected by white noise, robin



**Figure 5.** Ability of test birds to find mealworms in the presence of white noise. Control results here are taken from experiment 1 (see text). Expected values as in Fig. 2. Numbers above the bars indicate the number of trials in which the test bird struck (hit or miss) at any grid square in the quadrant containing a mealworm.

foraging success should have remained high in this experiment unless they used auditory cues.

## Results

All of the test birds found mealworms more often than expected by chance alone (Fig. 5), and overall the pattern of strikes was significantly different from random expectation ( $G_T = 50.9$ ,  $P < 0.001$ ,  $N = 4$  birds making 2–6 strikes each). In this experiment, however, the test birds attempted to strike at the soil on only 50% ( $N = 34$ ) of the trials (presumably because they could not locate any mealworms) and were successful on only 59% of first strikes compared to an attempt rate of 87% ( $N = 45$ ) and 90% success on live mealworms in the olfactory cues experiment. The difference in success rate between these two experiments was significant only for bird C (Fisher's exact test:  $P = 0.04$ ) and was not significant overall (Fisher's method of combining probabilities:  $\chi^2_3 = 12.5$ ,  $P = 0.13$ ). Comparing the success of trials (hits versus misses or no response) between the auditory and olfactory experiments, trials in the olfactory experiment were significantly more successful overall (Fisher's method of combining probabilities:  $\chi^2_3 = 21.9$ ,  $P = 0.005$ ). This result suggests that the white noise hampered the birds' abilities to locate buried mealworms although they were often able to catch the mealworms successfully despite the noise. Thus the white noise did not appear to completely mask the sounds being made by the mealworms (see below).



## MEALWORM SOUNDS

### Methods

Because robins appeared to be able to locate mealworms by auditory cues, we recorded the sounds made by buried mealworms in an attempt to describe the actual cues available to the birds. We placed a mealworm 2 cm below the soil surface in a small pot and, using a directional microphone (AudioTechnica 835a, frequency response 40–20 000 Hz) directed at the soil surface from a distance of 10 cm, recorded the sounds made on to audiotape (using Sony UCX tape in a Sony Walkman WD6 recorder, frequency response 40–15 000 Hz). We repeated this procedure for 10 mealworms. We made all recordings in a large ( $3 \times 3 \times 3$  m) anechoic chamber and analysed the resulting sounds on a Kay DSP 5600 Sonagraph (using the sonagram display with a wide (600 Hz) band filter).

### Results

The frequency at maximum amplitude of the sounds made by mealworms buried in the soil ranged from 6400 to 7920 Hz (mean  $\pm$  SE =  $7480 \pm 154.2$  Hz,  $N=10$ ). Sounds generally covered a broad frequency range, on average 4850–10 980 Hz ( $N=10$ ), and had an average duration of 3.01 ms with intervals as short as 1.0 ms between sounds. These sounds were presumably made only when the mealworm was moving and, when amplified, sounded to us like a person walking on gravel. Although songbirds are most sensitive to sounds in the 1–5 kHz range, most species studied so far can hear sounds up to 10 kHz (Dooling 1982). Thus the sounds made by mealworms should have been audible to the robins we studied, although it is surprising that they could detect sounds of such low amplitude.

## EARTHWORMS VERSUS MEALWORMS

### Methods

To determine whether the test birds could find earthworms as readily as mealworms, we conducted an experiment using 2-cm-long pieces of live earthworms, *Lumbricus terrestris*, instead of mealworms. We randomly selected two quadrants

of the square tray (A in Fig. 1) and within each, randomly selected a grid square where we buried one piece of live earthworm using the same procedure as we used for mealworms (see General Methods). We used earthworm segments instead of whole adult earthworms to ensure that they would stay close to where we buried them and that they would represent a target equivalent in size to a mealworm. Using a  $\times 10$  hand lens, we could detect no visual cues on the soil surface (movement of tiny soil particles) that might have revealed an earthworm's location.

### Results

The test birds found earthworms significantly more often than expected by chance overall ( $G_T=151.1$ ,  $P<0.0001$ ,  $N=4$  birds with 5–10 strikes each), missing on only 7% of first strikes ( $N=27$ ) in quadrants containing earthworms. The distribution of hits and misses did not differ significantly from those in experiment 1 (olfactory cues) in which we used live mealworms (Fisher's exact tests:  $P>0.49$  in each case) nor was the difference significant overall (Fisher's method of combining probabilities:  $\chi^2_8=2.59$ ,  $P=0.96$ ). We concluded that the test birds had a similar ability to find earthworms as mealworms.

## GENERAL DISCUSSION

Collectively, these results strongly suggest that the robins located buried mealworms and earthworms by using auditory cues. Robins did not locate dead mealworms (experiment 1) and located live mealworms when olfactory cues were unavailable (experiment 3), indicating that olfactory cues were not used to locate mealworms. When vibrotactile cues were eliminated (experiment 2 and probably experiments 3 and 4), the robins were still successful at finding mealworms, indicating that they were not finding mealworms from vibrations in the soil. Similarly, the robins found mealworms in the absence of visual cues (experiment 3). Thus, experiments 1–3 demonstrated that robins can find mealworms at a relatively high success rate when auditory cues are available and some or all of the other sensory cues are eliminated. In experiment 4, we showed that, when other sensory cues were available and auditory cues were obscured, robins made fewer feeding attempts and were less

successful when they did attempt to feed than they were when auditory cues were available (experiment 1), although the differences were not significant. Even though white noise reduced foraging success, three of the four birds still performed much better than expected by chance, suggesting either that the birds were still able to detect auditory cues or that, in the absence of auditory cues, the birds used other cues to locate the mealworms. Unfortunately, our attempts to get the birds to strike at artificially produced sounds were unsuccessful, but such experiments will be needed to fully understand which auditory cues are important and how they are used to localize sounds. Our attempts to mask mealworm sounds with white noise were also relatively unsophisticated in that our playback equipment probably did not have a flat frequency response.

Studies of auditory mechanisms suggest that small birds might have a variety of methods available for localizing sounds (reviewed in Knudsen 1980). One possibility is that they use the differential sound pressure reaching each side of the tympanum through the ear canal and the interaural pathway (Figure 10-1 in Knudsen 1980). Such a mechanism could account for the characteristic 'head-cocking' of foraging robins, which would maximize the distance that worm-generated sound would travel to each side of the tympanum (B. Frost, personal communication). The sounds made by mealworms are short, repeated and contain a range of frequencies, making them more readily localizable, whatever the mechanism.

An alternative explanation for 'head-cocking' is that robins attempt to focus the apparent source of sound on the fovea of their eye to improve visual acuity (Sillman 1973). Examination of both the location of the fovea in the robin and the videotapes of foraging birds suggests to us that the angle of head-cocking is consistent with this explanation. Thus although this head-cocking behaviour makes the bird appear to be listening, it may actually result from visual searching for movement before the bird finally strikes.

How do we reconcile our findings with Heppner's (1965, p. 253) conclusion that the American robin locates earthworms exclusively by visual clues? Heppner's (1965) carefully conducted experiments showed, in fact, that robins were able to capture earthworms, when they could see them, in the absence of auditory and olfactory cues. He

did not directly test whether they could use these other cues in the absence of visual cues.

Our experiments have focused on different sensory modalities, one at a time, but it is possible that birds use more than one modality when localizing food. For example, different sensory modalities may be used simultaneously or in a hierarchy where the use of one cue interferes with, or supersedes, the use of others. Robins, for example, seem to use auditory cues when locating earthworms and other prey buried in the soil but certainly use visual cues when these are available. Since visual cues are likely to be more accurate for localizing prey, we expect that robins use such cues in preference to auditory cues when their prey is visible. More complicated experiments will be required to elucidate the hierarchy and interaction of sensory modalities used by these birds.

These results show that field observations of foraging birds are insufficient to allow us to determine the sensory modalities that they use and even simple experiments can be misleading. Indeed, a thorough knowledge of perceptual abilities and the interaction between different modalities, as has been worked out for barn owls (Knudsen 1980), is needed for studies of foraging by passerine birds. Without such information, we might assume, for example, that American robins cannot forage on prey that they cannot see.

## ACKNOWLEDGMENTS

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