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The Location and Capture of Prey by the
Great Horned Owl (Bubo virginianus)

By

John A. Mortenson

B.S., University of Montana, 1969


Presented in partial fulfillment of the requirements for the degree of

Master of Science

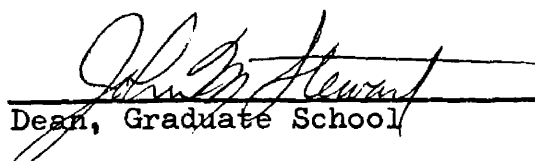
UNIVERSITY OF MONTANA

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Chapter 1

INTRODUCTION

The location of prey at night by various species of owls has been studied in several aspects. Vanderplank (1934, in Matthews and Matthews, 1939) stated that tawny owls (Strix aluco) are able to perceive infrared radiation and in this way can see prey by the heat waves radiated from them. This was shown to be incorrect for the tawny owl by Matthews and Matthews (1939) who found no retinal potential in response to infrared radiation. Dice (1945) studied the effect of light intensity on the ability of four species of owls to locate dead mice by sight. He found that a barred owl (Strix varia), a long-eared owl (Asio otus) and a barn owl (Tyto alba) were all able to see the dead mice at a lower light intensity than the more diurnal burrowing owl (Speotyto cunicularia). Dice was able to exclude the use of olfaction and infrared sensitivity by all owls even though these clues were available. Payne (1962) found that barn owls are able to locate prey by hearing alone. Both vision and audition have been implicated for locating prey by the great horned owl (Bubo virginianus) because of the sensitivity of these senses (Bent, 1938).

Movement is characteristic of most prey and increases the conspicuousness of the prey and thus increases its risk against predators (Cushing, 1939; Craighead and Craighead, 1956; Marler and Hamilton, 1966). Marler and Hamilton summarize from Cott (1957) the ways a prey animal conceals itself from predators before it is discovered. Once a prey animal is discovered it either feigns death (Marler and Hamilton, 1966), "freezes" (Craighead and Craighead, 1956) or dashes for cover

(Cushing, 1939). Cushing believes that "freezing" is ineffective once a prey is detected by a predator.

The purpose of this study was to determine:

- (1) what sense(s) the great horned owl uses to locate prey,
- (2) the influence of distance to prey on the ability of the owl to locate and capture prey,
- (3) the influence of height of the owl on the ability of the owl to locate and capture prey,
- (4) the effect of capturing prey on the owl's later predatory behavior,
- (5) whether prey response influences the ability of the owl to capture prey and
- (6) the importance of prey movement for prey recognition.

The scope of this study was to examine the functioning of the sensory apparatus used to locate prey and to study certain aspects of the prey-capturing behavior of the great horned owl by using the response of the owl to artificial prey. Artificial prey were used so that prey activity could be directly controlled.

Only one owl was used for this study. These experiments were conducted in a large flight cage outdoors. It was impractical to use more than one owl at a time because of difficulties that would be encountered in removing one owl from the cage and replacing it with another. More importantly, I believe that more valuable information could be obtained by studying one owl thoroughly than to make less detailed comparisons of several owls.

Chapter 2

THE APPARATUS

The experiments were done in a cage 100 feet long, 18 feet wide and from 18 to 24 feet high (Figure 1). The cage was located on privately owned land in a sparsely inhabited area about 15 miles south of Missoula, Montana. The cage was made of 2-inch poultry netting supported by wires and telephone poles. An observation blind was in the middle of one side of the cage. The blind was 8 feet long, 4 feet wide and 4 feet high. At the north end of the cage, where it was 24 feet high, three large ponderosa pines extended through the top of the cage. One of them was used as a corner of the cage. The branches of all the trees were cut inside the cage so that no natural perching places were available for the owl. The middle tree had four artificial perches which served as day roosting places. The canopy of the three trees provided the owl with shade during the day.

The four perches on the middle pine at the north end of the cage were at 5-, 10-, 15- and 20-foot heights. The perches were in the middle of the cage 7 feet from the end of the cage. Perches were made of 15-inch long 2x4's placed on their sides (Figure 2). A 1-inch by ½-inch piece of wood with a 3-inch metal strip on the underside at each end was held above the 2x4 by foam rubber pads. On the upperside of the perch and directly beneath each of the metal strips on the piece of wood was a metal strip nailed to the perch. The metal strips were part of an electrical circuit connected to a small light under each perch. When the owl sat on a perch, it pressed the sets of strips together and



Figure 1. The cage. The cage is 24 feet high on the left and drops down to 18 feet high on the right. The perches can be seen on the middle tree on the left. The 20-foot high perch is not clearly visible. The black object along the side of the cage at the middle is the blind.



Figure 2. A perch. The light is in the small box under the perch with the front covered with painted paper to reduce its illumination. On the right margin part of a burlap strip can be seen which was swung out from the tree to block the perch.

completed the electrical circuit which lit the light. The light was shielded so that it shone forward and was not visible to the owl perched above it. The light emitted less than 1 foot-candle as measured by a Weston Illumination Meter (Model 604). Thus it was possible to determine the position of the owl even though the owl was not visible. Another set of metal strips in the middle of each perch **was** connected to a tape recorder. When these two strips were in contact (by the owl sitting on the perch) the tape recorder would play and when the owl left the perch, the tape recorder would stop. This latter system was used for only some of the prey. During the experiments all the perches but one were blocked by movable strips of burlap.

Two-and-a-quarter inch Midland speakers (Model 21-383) broadcasted the auditory stimulus (Figures 3 and 4). Screening covered the speaker cones to protect them from talons. The speakers were hidden and were moved by being pulled along straight tracks. The speaker was mounted on stiff wire so that it could be placed on and slide along the tracks. The mounting was covered with oil soaked cloth to reduce friction and noise. The 19 sets of tracks which were 5 feet apart ran the width of the cage (Figure 5). Each set of tracks was made with two parallel $\frac{1}{8}$ -inch diameter steel rods 2 inches apart. They were supported by and glued to wood blocks placed in a ditch which was approximately 4 inches wide and 3 inches deep. Plastic, tarpaulin and burlap covered the ditches to hide the speakers and tracks. A 1-inch gap extended down the middle of the ditch covering. Only the burlap was visible and acted as the background color for the visible prey. A 2-inch wide strip of burlap was placed vertically behind most of the

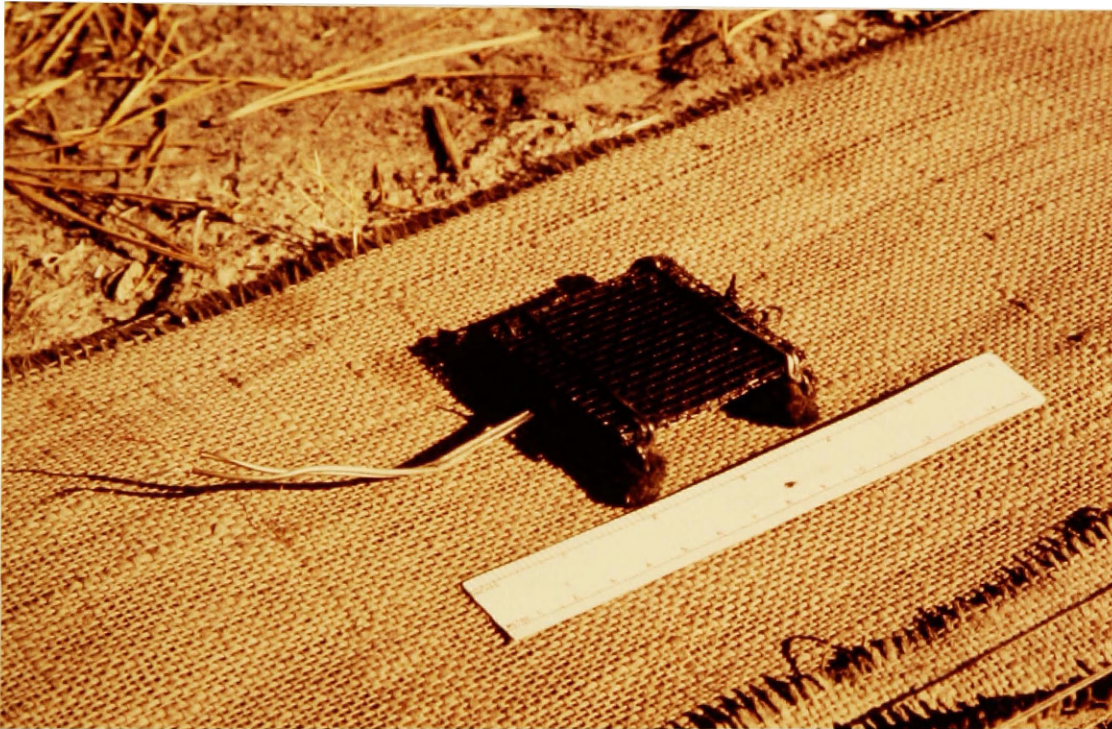


Figure 3. A speaker used for broadcasting the auditory stimulus. The speaker shown was used for prey that the owl could only hear.

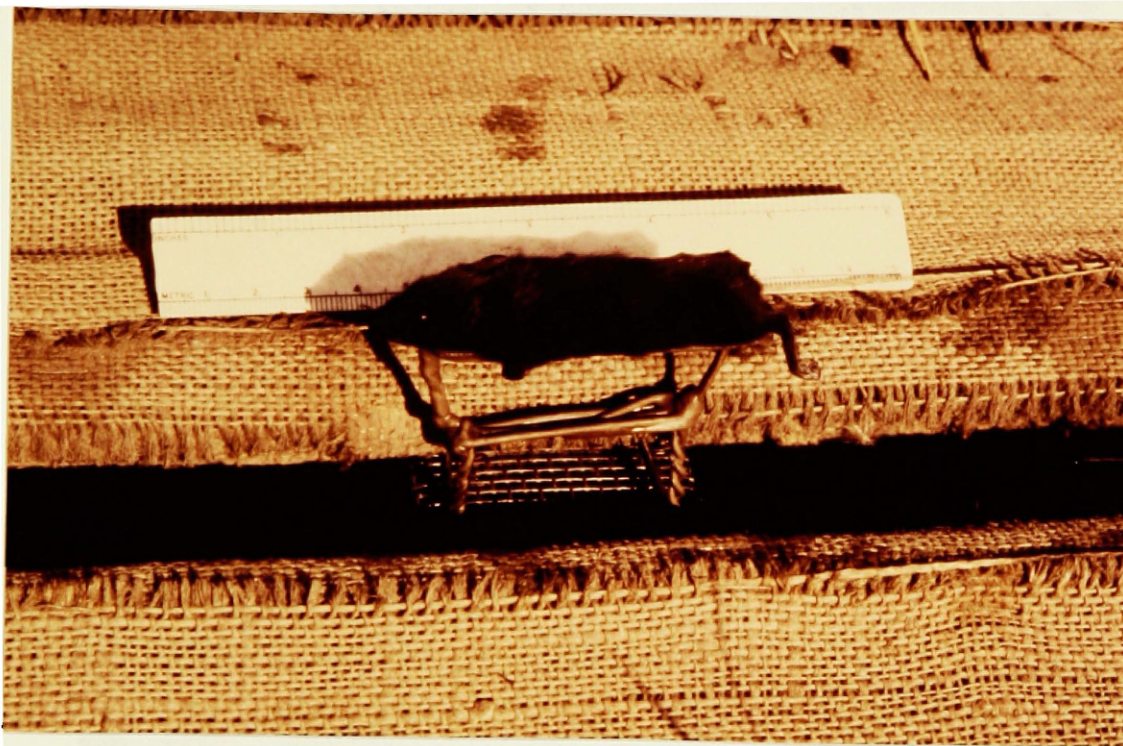


Figure 4. A mouse held by prongs above a speaker on a track. This was used for prey that the owl could both see and hear.



Figure 5. View of cage from the 15-foot high perch.

tracks. This was necessary so that the prey were outlined against the burlap. At the far end of the cage large pieces of burlap were laid on the ground because vertical strips would have obscured prey on farther tracks. The burlap was spray painted with Tree Bark colored Fuller Full-Stain thinned with an equal volume of turpentine. The top of the speaker was approximately 1 inch below the ditch covering. A dead mouse on top of the speaker was completely hidden and did not touch the covering (Figure 3). Also a dead mouse held by alligator clips attached to the speaker projected above the covering where the mouse was potentially visible to the owl. During the study wire prongs were substituted for the alligator clips (Figure 4). The speakers were put on the tracks at the edge of the cage. To insure that the owl did not collide with the sides of the cage when pursuing the prey, presentation was limited to the middle 15 feet of the cage. Removable padded blocks were placed at the ends of the tracks and dome-shaped pieces of tarpaper were set over the tracks at the sides of the cage so that only 15 feet of the tracks were exposed. Before presentation and after, if not captured, the prey remained inside the tarpaper dome, out of sight of the owl. The speakers were moved one way along the tracks by pulling the speaker wires attached to them from the tape recorder. The speaker wires were in the ditch between the two rods and were pulled by hand from within the blind. The speakers were moved the other way by pulling strings attached to them which went around a glass rod at the end of the track and then back down the track to the blind. One of the 19 tracks was only 11 feet long and 2 tracks were 14 feet long because one of the trees was in the way. There was a dip in the ground at the

southeast corner of the cage. To compensate for this the distance the speaker travelled could be varied on the last 4 tracks at the south end of the cage depending on the owl's height so that the prey did not go down the dip and out of potential sight of the owl.

In addition to these 19 sets of tracks, 8 other tracks were constructed to eliminate any noise that the sliding prey might make. These tracks were constructed with 10-inch wide pieces of painted burlap across the width of the cage. Over these burlap tracks moved sliders $2\frac{1}{4}$ inches long and $\frac{3}{4}$ inch wide made of stiff wire and glass rod (Figure 6). A thumbtack with its sharp point removed was soldered to each end of the slider. A dead mouse was impaled on these two thumbtacks. The slider was moved by brown heavy duty sewing thread in a manner similar to the speakers. The burlap tracks were placed in four pairs. Presentation of prey on the burlap tracks was also limited to the middle 15 feet of the cage as on the speaker tracks.

A 3-foot high tarpaper shield was placed along each side of the cage (Figure 5). A tarpaper roof extended 3 feet from the blind side of the cage (where most of the setting up was done) and $1\frac{1}{2}$ feet from the other side. A tarpaper strip on the ground inside the cage at the sides covered any holes where the shield met the ground. Although I was partly exposed while setting up the speakers and sliders, my hands and arms were always out of view.

The tarpaper blind supported by a wooden frame was almost light-tight when the door flaps were closed (Figure 7). In the front of the blind was a $\frac{1}{2}$ -inch diameter hole through which I could view the tree

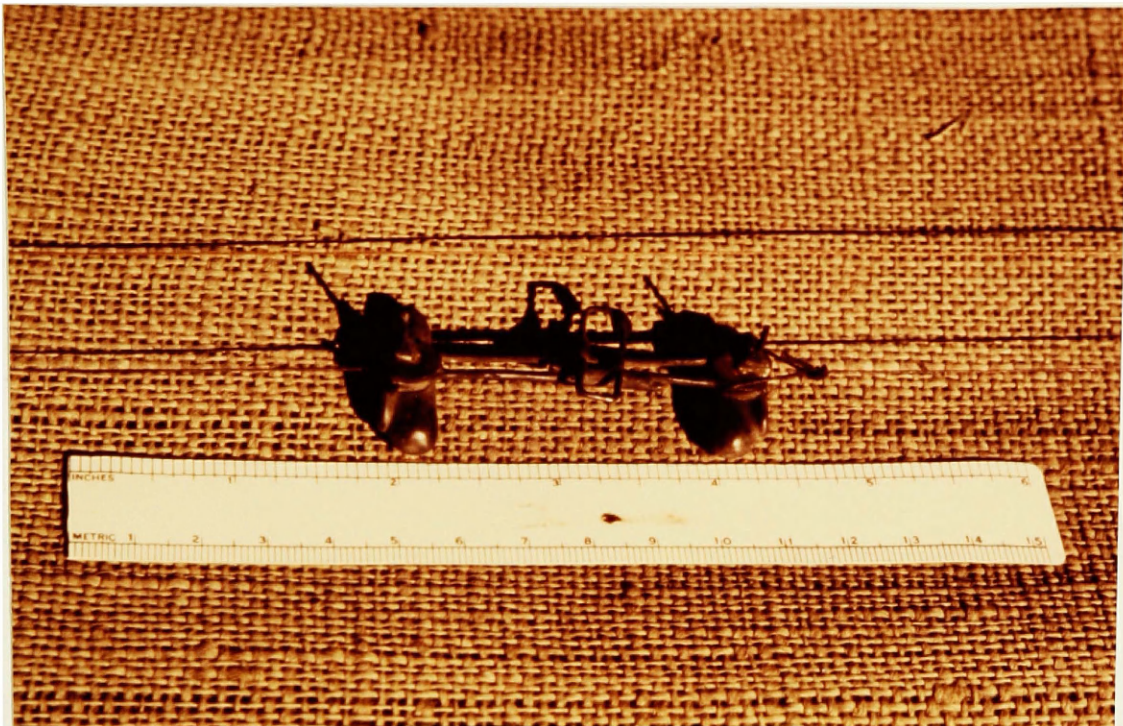


Figure 6. A slider on a burlap track on which a mouse was impaled. This was used for prey that the owl could only see.

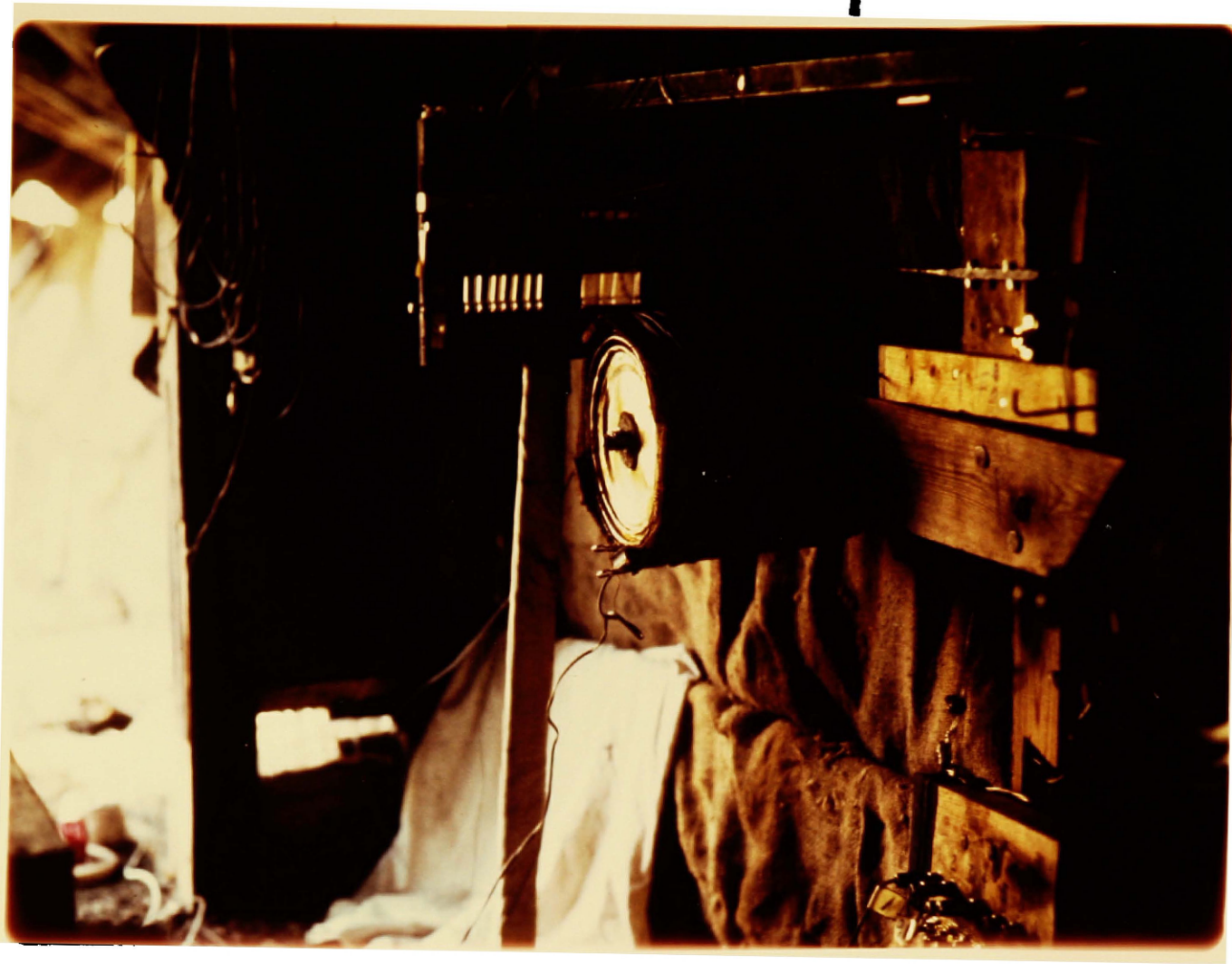


Figure 7. A view of the interior of the blind. The opening on the left was closed during trials by a door flap. The burlap and cloth on the wall are for reducing noise. The device above the gallon paint can is a divider for arranging strings and threads. The strings, threads and speaker wires enter and exit the blind through the hole to the right of the door.

perches but nothing else. During the study an infrared sniperscope was installed to observe the owl on the perch. Several dividers and sorters in the blind arranged the speaker wires, strings and threads coming from and returning to the 27 tracks. The wires, strings and threads made several bends between the tracks and inside the blind. The bends were made of either plastic, bare glass rod or cloth covered glass rod to reduce noise and friction. The speakers and sliders were moved at a constant speed of 1 foot per second by pulling the strings and threads across a 1-foot piece of wood in 1 second. The speakers were also moved by the speaker wires which were wound on padded, gallon paint cans. The cans were 2 feet in circumference and one revolution of the can was made in 2 seconds. A switch worked by my foot turned the tape recorder on and off and a panel of speaker jacks with switches controlled each speaker. A small shielded red light suspended from the roof illuminated the data sheets. A stopwatch in a small box with only the front open was illuminated by a small red light. Another small red light pointed downward directly in front of where I sat. This allowed me to pull appropriate wires, strings and threads. Another small red light in the blind turned on only when the owl was on a perch. All the lights in the blind and beneath the perches were radio lights powered by six volt batteries.

Chapter 3

METHODS

EXPERIMENT 1

History of Owl

The data reported here were gathered from the night of July 23 to the night of September 20, 1970. The owl was captured March 19, 1970 along the Bitterroot River in Ravalli County, Montana. It was released in the cage on March 22 before the apparatus was perfected. This allowed the owl to habituate to the cage and to my presence. Approximately 140 preliminary trials were run with the prey during this time to perfect the functioning of the apparatus and to train the owl to respond to the prey.

The Four Variables

This experiment was designed to test the owl's use of auditory and visual stimuli for locating and capturing prey. Four variables were tested simultaneously: Prey Activity, Height of Owl, Distance to Prey and Prey Response.

Prey Activity

This variable is what the prey did upon presentation and what sensory clues were available to the owl. The four types of Prey Activity and their methods of propagation were:

- a. stationary auditory prey - hidden mouse over stationary broadcasting speaker on speaker track,
- b. moving auditory prey - hidden mouse on broadcasting speaker sliding along speaker track,

- c. moving visual auditory prey - visible mouse over sliding broadcasting speaker and
- d. moving visual prey - visible mouse sliding along burlap track.

In all four Prey Activities the dead mouse served as a reward.

Height of Owl

The owl was tested at four heights: 5, 10, 15 and 20 feet. Only one height was tested each night by blocking all the perches but one just prior to starting the trials.

Distance to Prey

This was the horizontal distance from the ground beneath the perches to the prey. Distance was divided into four intervals which were: 0 - 20 feet, 20 - 45 feet, 45 - 70 feet and 70 - 95 feet. The first interval had four speaker tracks while the other longer intervals had five speaker tracks. There were two burlap tracks in each interval of distance.

Prey Response

This is what the prey did after the owl left the perch and started flying towards the prey. The three categories of Prey Response were:

- a. continuation of same Prey Activity,
- b. continuation of same Prey Activity but reversing the direction of movement or, if initially stationary, starting of movement and
- c. stopping both movement and auditory stimulus emission.

The first Prey Response is an attempt to simulate a prey that is unaware of the owl, the second to a change in the behavior of the prey when the owl took flight and the third to "freezing" of the prey when the owl took flight.

Auditory Stimulus

Possible choices of an auditory stimulus included gnawing, squeaking and rustling leaves. The sound of rustling leaves was used because of its ease in production and because I believed it to be the most frequent prey sound and characteristic of most prey.

The auditory stimulus was the recorded sound of a deer mouse (Peromyscus maniculatus) rustling dry leaves in a cage. A Uher 4000-Report L Tape Recorder was used to record the rustling leaves. A 3-second portion was transposed to a Panasonic Cassette Tape Recorder (Model RQ-209S) to form a recording 26 minutes long. The Panasonic tape recorder was used to play the auditory stimulus for the experiments.

The intensity of the auditory stimulus was chosen to approximate that of a wild mouse. All sounds were measured with a Scott Sound Level Meter (Type 450-B). A deer mouse walking and running in a cage with the floor covered with dry leaves produced intensities ranging from 42 to 55 dB on C weighting with the Sound Level Meter microphone approximately 6 inches from the mouse at a 45-degree angle. The intensities of the stationary auditory, moving auditory and moving visual auditory prey were all the same and varied from 40 to 55 dB on A weighting, from 40 to 53 dB on B weighting and from 44 to 55 dB on C weighting. The Sound Level Meter microphone was 6 inches from the speaker on the track and at a 45-degree angle to the speaker. The different weightings on the meter refer to the frequency sensitivities. The A weighting is less sensitive to frequencies below 1000 Hz than above 1000 Hz. The B weighting is slightly less sensitive to frequencies below 500 Hz than

above. The C weighting is equally sensitive to frequencies from 32 to 8000 Hz. Standing on the ground I could not hear the auditory stimulus beyond about 50 feet. The sound of the speakers moving along the tracks was masked by the auditory stimulus. The sound of rustling leaves fluctuates greatly which gave the auditory stimulus a variable intensity. The frequency of the auditory stimulus probably varied also but it was not measured. Before the experiment started the speakers were tested to make sure that they all emitted the same intensity of the auditory stimulus.

The moving visual prey made a sound as it moved over the burlap. The maximum auditory intensity of the moving visual prey was calculated to be 7 to 8 dB on all weightings at the same distance of 6 inches at which the intensities of the three types of auditory prey were measured. Over some parts of the burlap the slider made less noise. These measurements were the maximum intensities made along noisier portions of the burlap.

Visual Stimulus

The visual stimulus was a dead laboratory mus dusted with carbon powder with its tail cut off at the base. The mice were dusted by shaking them in a bag with carbon powder and then shaking the excess carbon off, thereby producing black mice. The black mice were presented against the brown background color of the burlap (Figure 4). Four sets of measurements were taken of the light reflected from the burlap, from

several black mice next to each other and from black paper outside in full sunlight and compared to the maximum reading of the sun. A Weston Illumination Meter (Model 603) was used with the light sensor held with a clamp at the same angle (approximately 30 degrees to ground) and about 4 inches above the ground. The light intensity of the burlap, the black mice and the black paper, respectively, were measured. The light sensor was then pointed directly at the sun and a maximum reading was recorded. The burlap reflected 5.0 per cent (4.3 to 5.5 per cent) of the light, the black mice 3.7 per cent (3.5 to 3.8 per cent) and the black paper 4.3 per cent (4.0 to 4.5 per cent). Black paper was included because the reading from the mice was possibly influenced by their shape and texture. From the standpoint of amount of light reflected, the black mice and black paper varied from the burlap by 0.7 to 1.3 per cent.

The mice used were weanlings that averaged 12.6 ± 1.4 g. The average body length of the mice was $7.5 \pm .2$ mm. The average width was $2.6 \pm .2$ mm across the widest part.

Weather Conditions

Eight nights of trials were run from July 23 to August 14 on starlit nights with no cloud cover, no moon and no wind. The light intensity on such nights is given by Dice (1945) as about 10^{-4} foot-candle. The background noise level was measured with the Scott Sound Level Meter. It varied from no response to 35 dB (A), from no response to 36 dB (B) and from 36 to 47 dB (C). Potential sources of background noise were the wind and the traffic on a highway one mile away and on a dirt road one-quarter mile away.

From August 16 to August 22 and then from September 12 to September 20, eight nights of trials were conducted on moonlit nights with the wind varying from none to a slight breeze. Moon size varied from more than a quarter to full. There was 100 per cent cloud cover on two nights. The sky was clear on all other nights. Dice (1945) reports that the light from a full moon is about 10^{-2} foot-candle while light from a quarter moon is about 10^{-3} foot-candle. He also says that 100 per cent cloud cover reduces light by a factor of about 10. Both cloudy nights had a full moon so the light intensity approximated 10^{-3} foot-candle. Thus on moonlit nights the light intensity varied from about 10^{-3} to 10^{-2} foot-candle or from 10 to 100 times that on starlit nights. On all nights including the three breezy nights the background noise level remained within the ranges reported for starlit nights. The data from September 16 were rejected because of the presence of a wild great horned owl. Between these two test periods of moonlit nights, moving visual auditory prey were presented in an attempt to improve the owl's performance with these prey. Also during this period the alligator clips on the speakers for holding the mice were replaced with wire prongs similar to those used on the sliders. Sometimes it appeared that the owl had difficulty in removing the mouse from the clips as evidenced by the displacement of the speakers from the tracks. It seemed to me that the alligator clips held the mice very firmly.

Additional tests were made on five nights of poor weather conditions interspersed among the starlit and moonlit nights. These trials were run when it was cloudy with no moon (one night), windy and clear starlight (one night), windy and partly cloudy with starlight (one

night) and cloudy and no moon with light rain (two nights). Light intensity varied from starlight to very dark nights while the wind varied from calm to windy. On the windiest night the background noise measured 38 to 41 dB (A), 39 to 41 dB (B) and 41 to 66 dB (C). The background noise on the rainy nights was within the ranges reported on starlit nights.

Sequence of Prey

Three of the variables (Prey Activity, Height of Owl and Distance to Prey) tested the ability of the owl to locate prey. The fourth variable, Prey Response, tested the ability of the owl to capture prey. There are 64 combinations of the first three variables (four prey activities, four heights and four distances: $4 \times 4 \times 4 = 64$). Eight prey were presented in one night which required eight nights to test each combination once. The sequence of presentation of the prey was determined as follows. Only one height was used each night and each height was tested on two nights. The order of the heights was 15, 5, 20, 10, 15, 5, 20 and 10 feet. Each height had 16 combinations of prey activity and distance ($4 \times 4 = 16$). The order of these 16 combinations was mixed and determined separately for each height. Eight were run on the first night of that height and the second eight on the second night. The track used for each prey was chosen randomly as was the side of the cage from which the prey started. Prey response was also determined randomly for each of the 64 combinations. A prey response was selected for all prey presented but occurred only for those prey the owl attempted.

After two nights of trials the number of prey was increased from eight to twelve. This was possible because the owl did not attempt to capture either the moving or stationary auditory prey. All four additional prey were moving visual prey on the burlap tracks, one at each distance.

Only on starlit nights were all 64 combinations of Prey Activity, Height of Owl and Distance to Prey tested. Because the owl never made any attempts at the stationary auditory and moving auditory prey on starlit nights, only moving visual auditory and moving visual prey were presented on the moonlit nights. The owl was tested only at 5 and 20 feet high on moonlit nights. There are 16 combinations of Prey Activity, Height of Owl and Distance to Prey ($2 \times 2 \times 4 = 16$). Eight prey were presented each night and only one height was tested each night.

On nights of poor weather conditions only moving visual prey were presented because of the ease in setting them up on short notice. Eight prey were run each night using all eight of the burlap tracks. The owl was at 20 feet high for four nights and at 5 feet high for one night.

The speakers and sliders were placed in their correct positions on the tracks sometime during the day before the prey of that night were to be run. While doing this my movements at the tracks were hidden from the owl by the tarpaper shield but the owl possibly could have heard me.

The mice were placed on or over the speakers and on the sliders just prior to beginning the trials. This was also done from behind the tarpaper shield. I stopped at each track along each side of the cage

and made the movements necessary for installing the mouse whether or not a prey was to be run on that track. A head lamp was used while installing the mice. After placement of the mice I went to the blind where everything had been set up previously. After sitting for a randomly chosen period of time of from 5 to 10 minutes the first prey was started. Each prey was presented until (1) I felt the owl strike the prey, (2) the owl left the perch for the prey that "froze" or (3) 3 minutes of presentation had elapsed. The interval between the end of one prey and the beginning of the next was between 1 and 6 minutes. The length of any one interval was determined randomly.

After the trials a supply of food (mice, rats or hamsters) in excess of what the owl ate was left on a stool in the cage. The uneaten food was removed in the morning. Because the owl regularly placed food at the base of the telephone poles and under the tarpaper strips at the sides of the cage it was necessary to make a thorough search of the cage each morning. Occasionally the owl placed food on the 20-foot high perch where the owl spent the day. Trials were run every other night. The owl received no food on nights without trials. In preliminary trials the owl would not attempt the prey unless it had been deprived of food the previous night.

Data Collected

Several responses of the owl to the prey were recorded. Attempts and No Attempts were scored from within the blind. An Attempt was scored when the owl left the perch during a prey presentation. A No Attempt was scored when the owl remained on the perch during the entire 3-minute prey presentation. Success was scored by checking the

speakers and sliders after all the tests had been run for that night. Latency to Attempt was recorded by timing with a stopwatch the period from the introduction of a prey to the owl leaving the perch. Time off Perch was scored by subtracting Latency to Attempt from the total time to return to the perch. On several occasions when the owl remained off the perch for more than $3\frac{1}{2}$ minutes, I left the blind so the owl could see me. The owl flew against the cage and then to the perch. The Time off Perch for these occasions was scored as 3 minutes 38 seconds which was the minimum of these times. The infrared sniperscope was used to observe the owl on the perch on three moonlit nights and on one night of poor weather. On these nights in addition to the other data, Latency to Fixate the prey and whether the owl brought the mouse back to the perch to eat it were recorded. Latency to Fixate was often difficult to determine because the owl's head was sometimes oriented down the cage when a prey was presented. Only when the owl appeared to orient its head rapidly to the prey was Latency to Fixate recorded. On two moonlit nights the speakers for the moving visual auditory prey were turned on while the prey remained out of sight and stationary inside the tarpaper domes at the sides of the cage. Latency to Fixate just the auditory stimulus was then determined. After the auditory stimulus was fixated or after a few seconds, movement of the prey was started.

One criticism of my procedure may be the length of prey presentation. If no attempt was made the prey was presented for 3 minutes. This may seem unrealistic when compared to a wild situation where a prey may be exposed only briefly and the predator must react quickly. For part of the analysis the number of Latencies to Attempt of 10

seconds and less was compared to the combined number of both Latencies to Attempt longer than 10 seconds and No Attempts. In other words, for this part Latencies to Attempt longer than 10 seconds were considered as No Attempts.

Analysis of Data

The data from the three weather conditions were pooled. The observations were separated into the different categories of each variable for all variables. Thus any particular Latency to Attempt was placed in the correct category of Distance to Prey for the analysis of that variable and then placed in the correct category of Height of Owl for that variable and so on. All statistical tests came from Siegel (1956). The X^2 test (for 2 and k independent samples) were used for the analysis of Attempts and of Attempts within 10 Seconds. For the analysis of Time off Perch and Latency to Attempt the Kruskal-Wallis one-way analysis of variance was used for three or more samples and the Mann-Whitney U test for two samples. Other tests are mentioned specifically when used. The significance level was chosen as $P < .05$. All tests were two-tailed.

EXPERIMENT 2

The purpose of this experiment was to discover which of the potentially available sensory clues were not used by the owl to locate prey. One test procedure was used to test the owl's possible use of the following methods of prey detection: olfaction, infrared sensitivity and stationary visual stimuli. Mice were drugged with Surital (Sodium Thiamylal) so that they did not move or squeak. These mice were placed

individually on the burlap track covering throughout the cage. The mice were Peromyscus and mus dusted with carbon powder as in the previous experiment. While putting these mice out I hid my actions from the owl by wearing a poncho. After the drugged mice were set out I went to the blind and ran all eight moving visual prey as on the nights of poor weather conditions. This verified that the owl was responsive to these prey. It took about 30 minutes to run the moving visual prey. After they had been run I checked on the drugged mice and recorded which ones had been taken by the owl.

Shortly after Experiment 1 was completed the owl failed to respond to the moving visual auditory and moving visual prey or when it did respond it did so very slowly. I do not know the reason for this. Because of this decrease in responsiveness, the owl received no food for two nights prior to the running of Experiment 2 rather than only one night as in Experiment 1. Trials were run on October 11 and October 14, 1970. The owl was 15 feet high for the first night and 20 feet high for the second. On the first night two drugged Peromyscus and four drugged and dusted mus were set out while on the second night two Peromyscus and five dusted mus were used. Four of the drugged mice died during presentation and were excluded from the analysis. The owl was released after the second night of trials.

Chapter 4

RESULTS

EXPERIMENT 1

The owl made a total of 99 Attempts and 31 No Attempts at moving visual auditory and moving visual prey. Twenty-two prey did not function properly and are excluded from the analyses. The frequency distribution for the Latencies to Attempt shows that the Latencies tended to be clustered around a time shorter than the average Latency of 35 seconds (Figure 8a). Thirty-one per cent of all Attempts occurred in the first 5 seconds of prey presentation and 50 per cent occurred in the first 10 seconds. The average Time off Perch was 67 seconds. The periods of Time off Perch also tended to be grouped around a point shorter than the average (Figure 8b).

Prey Activity

The owl made no Attempts at all 32 moving auditory and stationary auditory prey. The owl made Attempts at 60 per cent of the moving visual auditory prey and 81 per cent of the moving visual prey. The two types of auditory non-visual prey were presented only on starlit nights and are excluded from the following analyses.

Latency to Attempt. The Latencies for the moving visual prey and the moving visual auditory prey are not significantly different ($P > .05$, Figure 9a). Comparing the Latencies to Attempt for the moving visual and moving visual auditory prey over Distance to Prey reveals no significant differences between the Latencies for the two types of Prey Activity at any of the Distances ($P > .05$ at all Distances, Table 1).

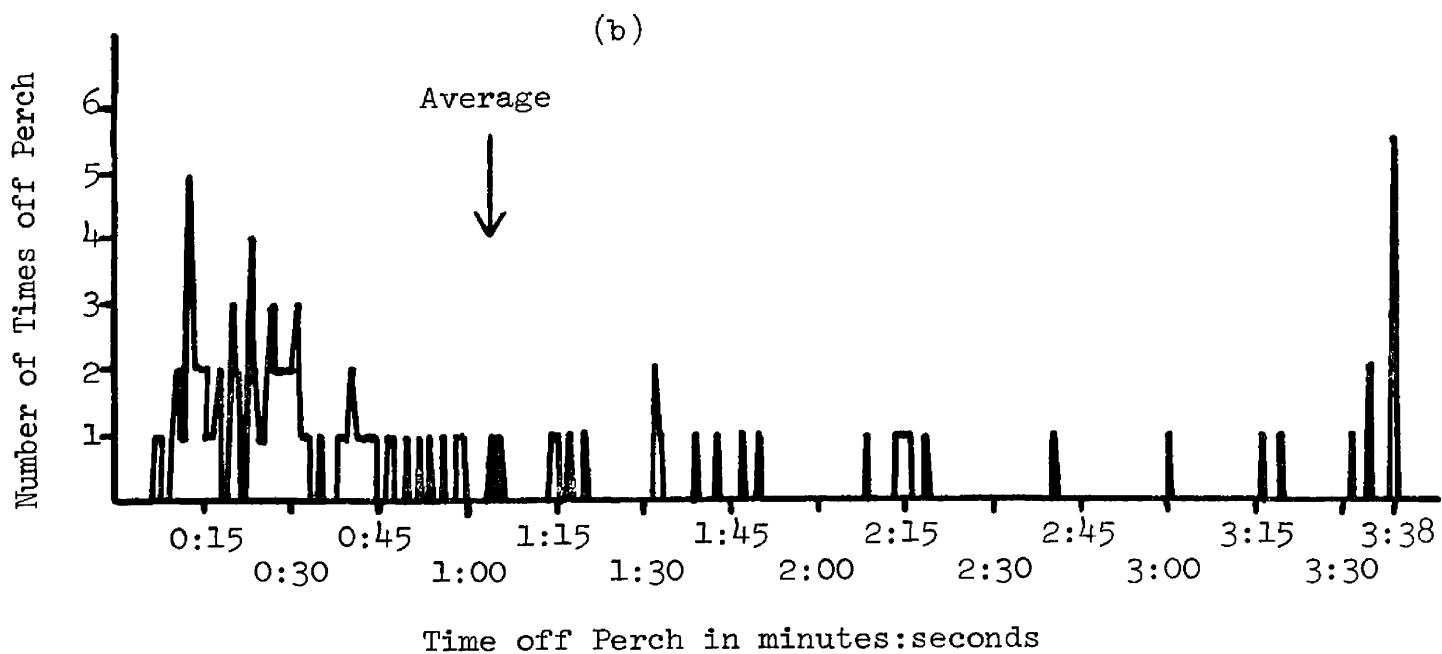
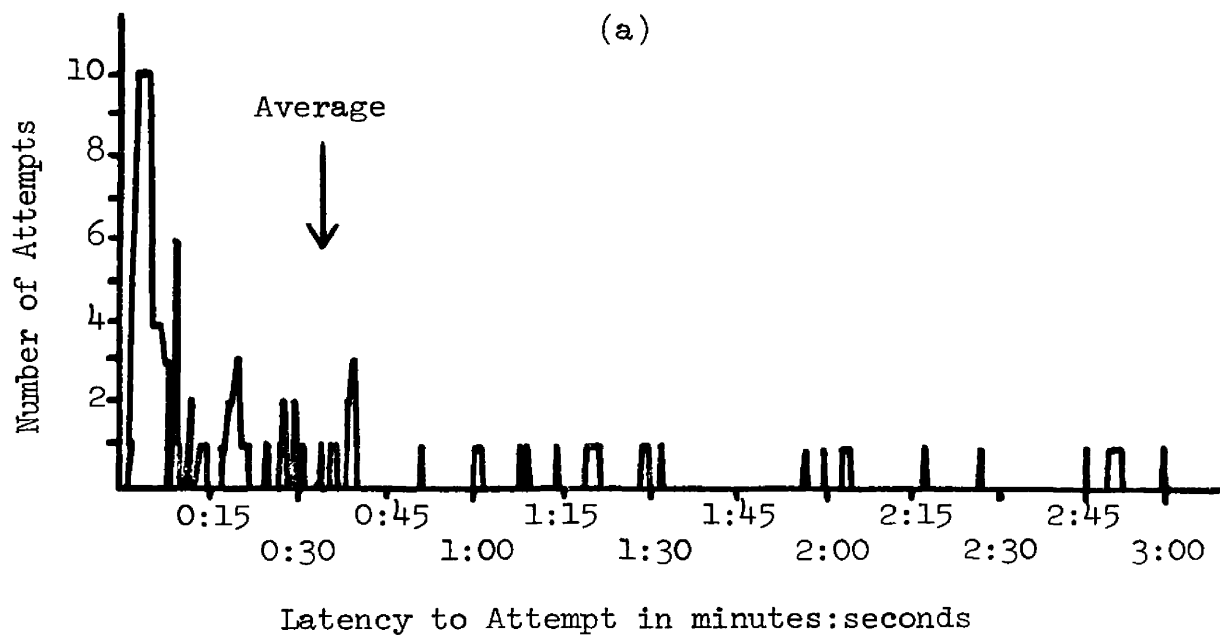


Figure 8. Frequency distribution of Latency to Attempt(a) and Time off Perch(b).

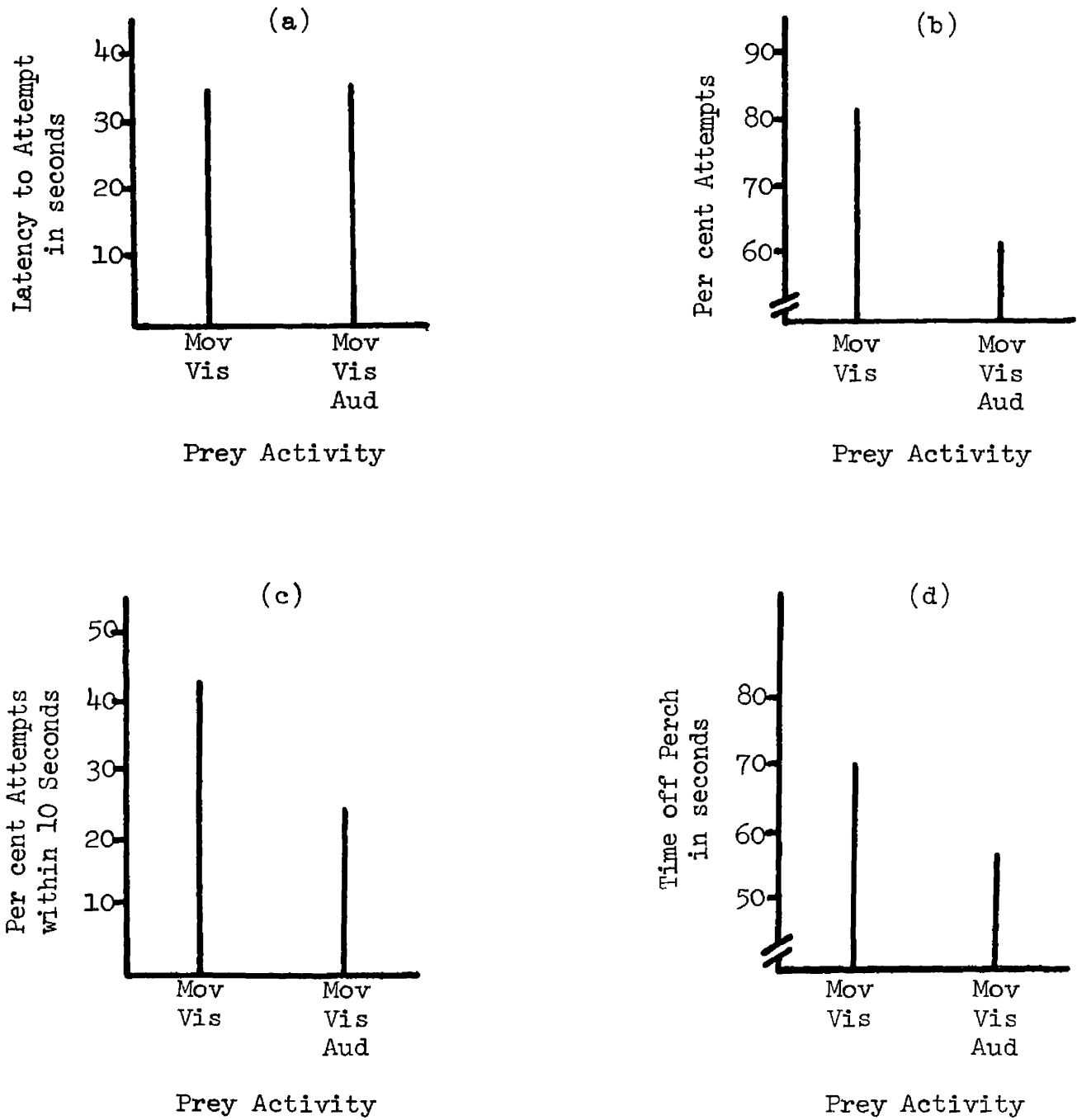


Figure 9. Prey Activity compared to Latency to Attempt(a), per cent Attempts(b), per cent Attempts within 10 Seconds(c) and Time off Perch(d). Mov Vis and Mov Vis Aud represent moving visual prey and moving visual auditory prey, respectively. $P < .05$ for b and c.

TABLE 1

LATENCY TO ATTEMPT IN SECONDS FOR MOVING VISUAL PREY
AND MOVING VISUAL AUDITORY PREY AT THE
FOUR DISTANCES TO PREY

Latency to Attempt in seconds				
	Distance to Prey in feet			
	0-20	20-45	45-70	70-95
Moving Visual Prey	29	26	38	58
Moving Visual Auditory Prey	30	34	38	44

Attempts and Attempts within 10 Seconds. Significantly fewer Attempts of both kinds were made for the moving visual auditory prey than for the moving visual prey during both the first 10 seconds of exposure and the entire test ($P < .05$ for both, Figure 9b and c).

Time off Perch. The Time off Perch was slightly longer for the moving visual prey than for the moving visual auditory prey but the difference was not significant ($P > .05$, Figure 9d).

Weather Conditions

There were no significant differences in Latency to Attempt, proportions of Attempts and Attempts within 10 Seconds and length of Time off Perch between the starlit, the moonlit and the poor weather condition nights ($P > .05$ for all, Figure 10). However, Time off Perch tended to be shorter for moonlit nights than for starlit and poor weather condition nights. Latency to Attempt showed the opposite trend and was somewhat longer for moonlit nights than for starlit and poor weather condition nights.

Distance to Prey

Latency to Attempt. Latency to Attempt shows a general increase as Distance to Prey increased but the trend is not significant ($P > .05$, Figure 11a).

Attempts and Attempts within 10 Seconds. The proportions of Attempts and of Attempts within 10 Seconds are both significantly different with Distance to Prey ($P < .01$ and $P < .05$ respectively, Figure 11b and c). The highest proportion of both types of Attempts occurred at 20-45 feet. The lowest proportion occurred at 70-95 feet while at 0-20 and at 45-70 feet the proportions were intermediate and about equal.

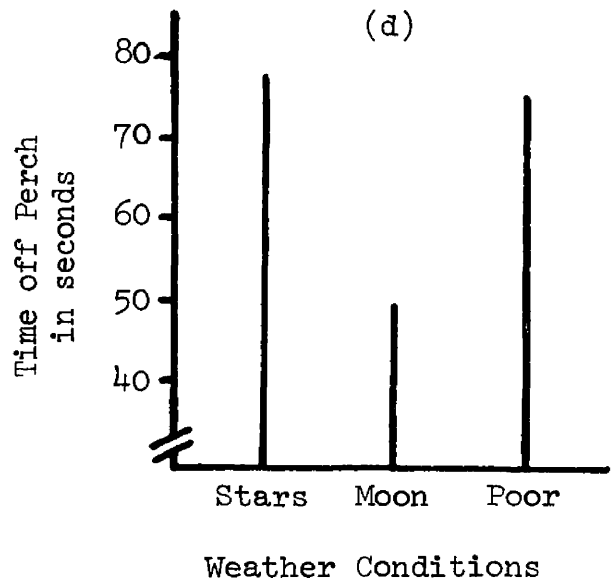
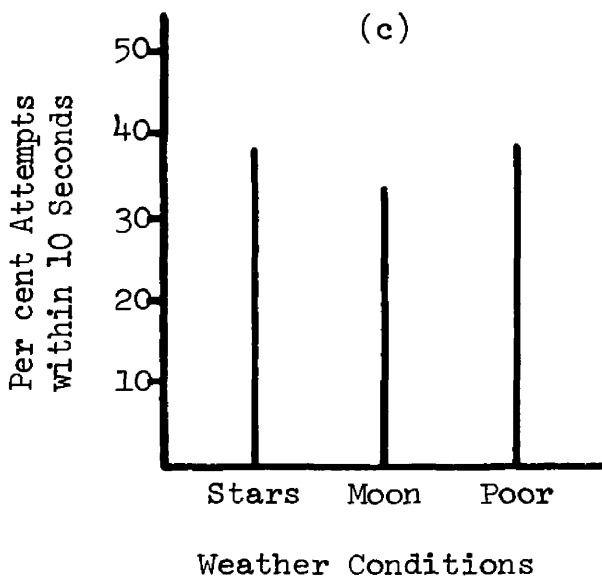
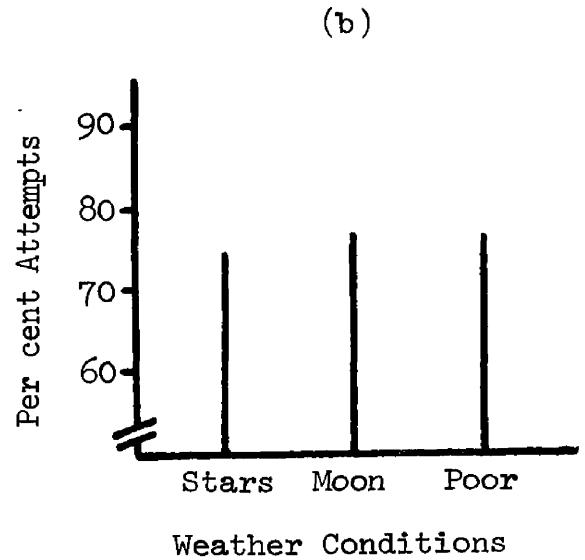
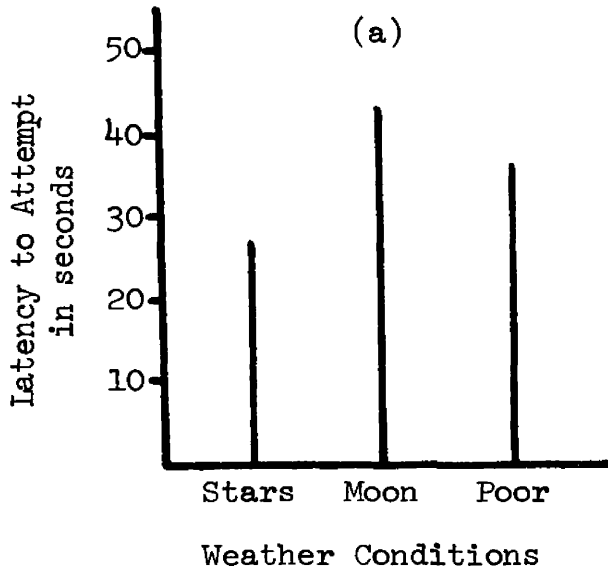


Figure 10. Weather Conditions compared to Latency to Attempt(a), per cent Attempts(b), per cent Attempts within 10 Seconds(c) and Time off Perch(d). The Weather Conditions were starlit nights (Stars), moonlit nights(Moon) and cloudy, rainy and windy nights (Poor).

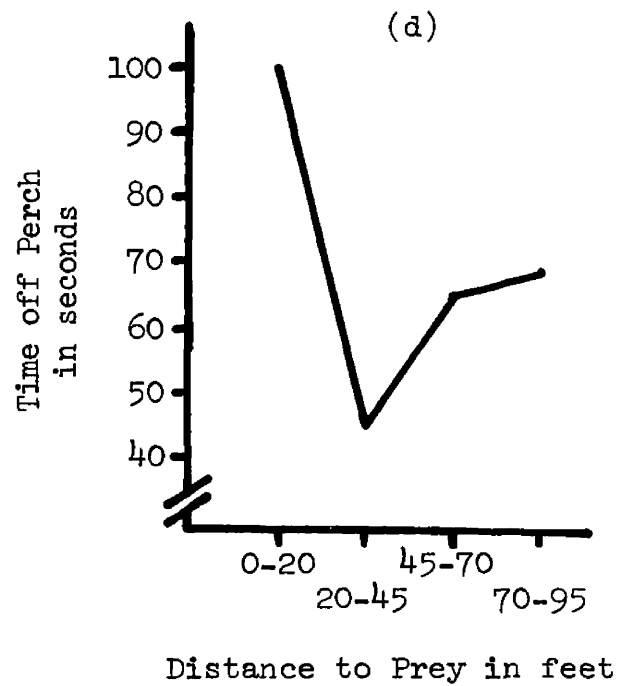
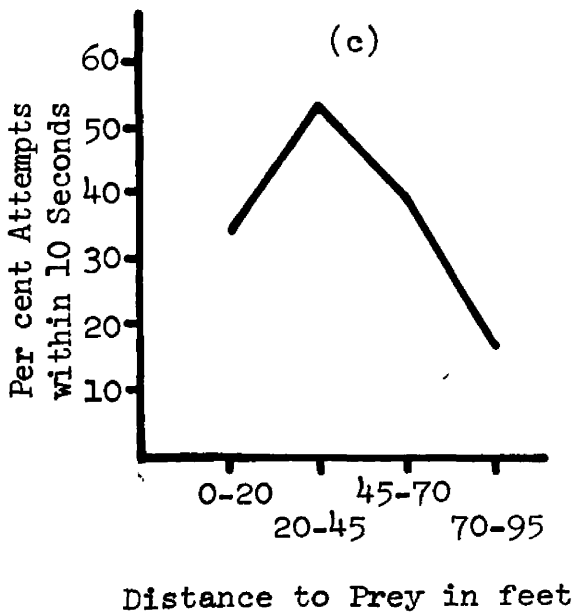
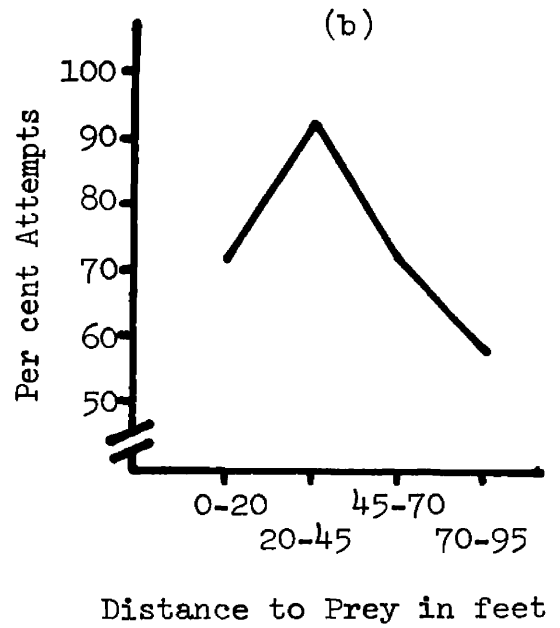
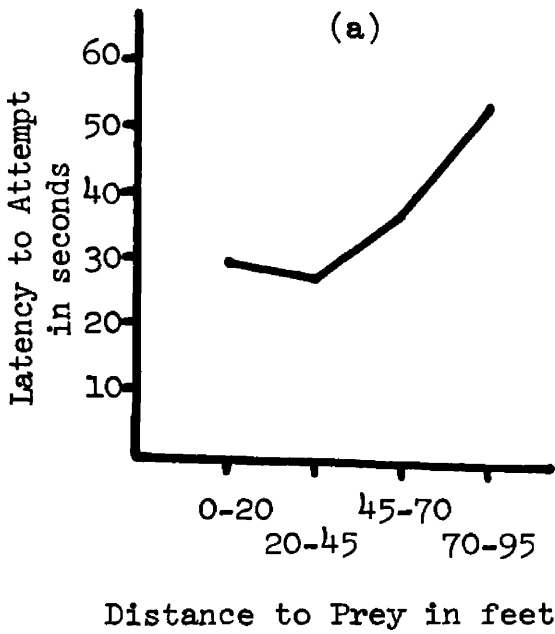


Figure 11. Distance to Prey compared to Latency to Attempt(a), per cent Attempts(b), per cent Attempts within 10 Seconds(c) and Time off Perch(d). $P < .01$ for b and $P < .05$ for c and d.

Time off Perch. Time off Perch was longest at 0-20 feet, shortest at 20-45 feet and intermediate at 45-70 and 70-95 feet ($P < .05$, Figure 11d).

Height of Owl

Latency to Attempt. The Latencies to Attempt were not different at the various Heights ($P > .05$, Figure 12a).

Attempts and Attempts within 10 Seconds. The proportions of Attempts did not vary with Height of Owl ($P > .05$, Figure 12b). The 10- and 15-foot Heights had to be combined because of their small sample sizes. The proportion of Attempts within 10 Seconds was slightly lower for the 20-foot Height than for the 5-, 10- and 15-foot Heights but is not significant ($P > .05$, Figure 12c).

Time off Perch. Time off Perch shows a general increase as Height increased but is not significantly different ($P > .05$, Figure 12d).

Distance to Prey - Height of Owl

Latency to Attempt. The interaction between Distance to Prey and Height of Owl for Latency to Attempt has an overall significance level of $P < .05$ (Figure 13a). The 10- and 15-foot Heights were combined because of their small sample sizes. When the owl was at the 5-foot high perch the average Latency to Attempt increased as Distance to Prey increased. At both the 10-15- and 20-foot high perches the average Latency to Attempt decreased from the 0-20-foot Distance to the 20-45-foot Distance and then increased as Distance increased further. The greatest differences between the three Height categories at any one Distance appear to occur at the 0-20- and 20-45-foot Distances.

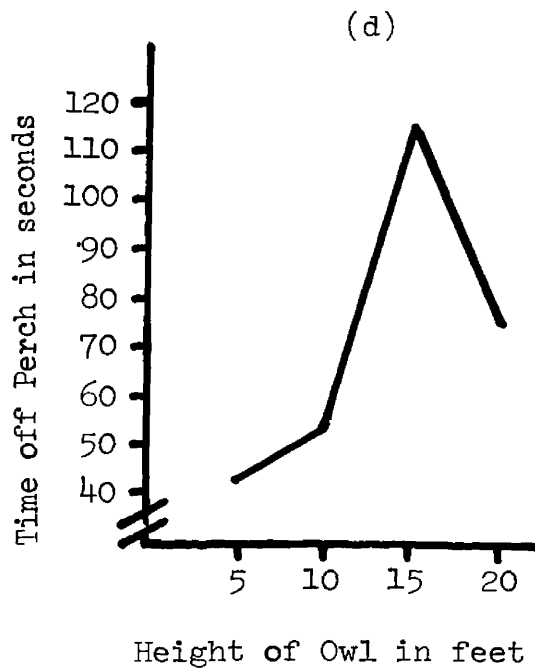
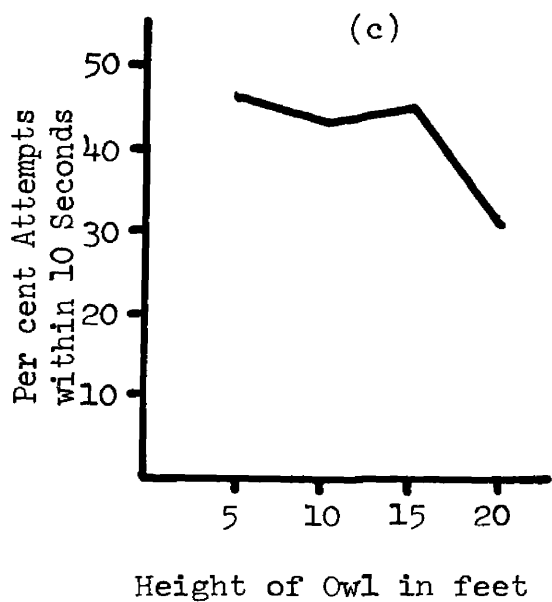
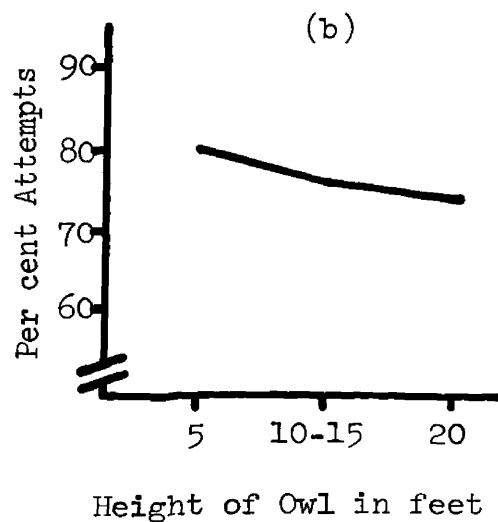
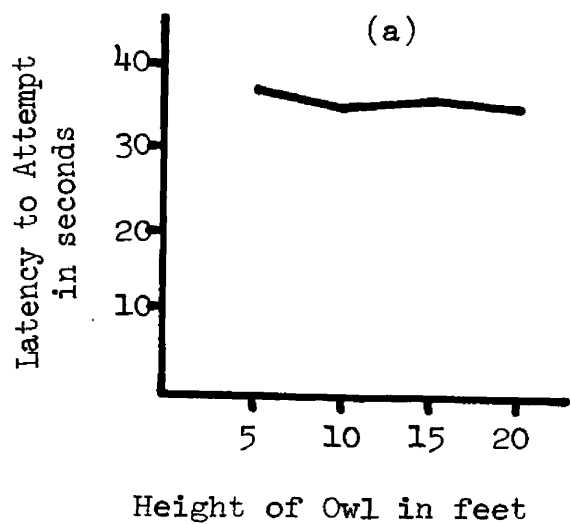


Figure 12. Height of Owl compared to Latency to Attempt(a), per cent Attempts(b), per cent Attempts within 10 Seconds(c) and Time off Perch(d).

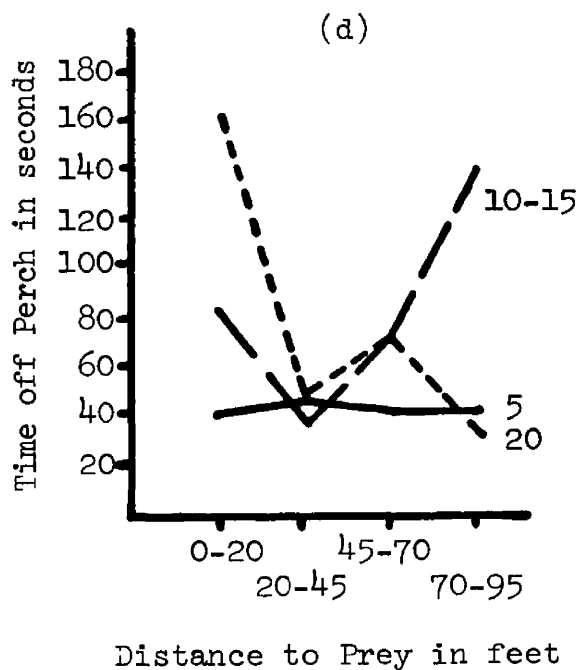
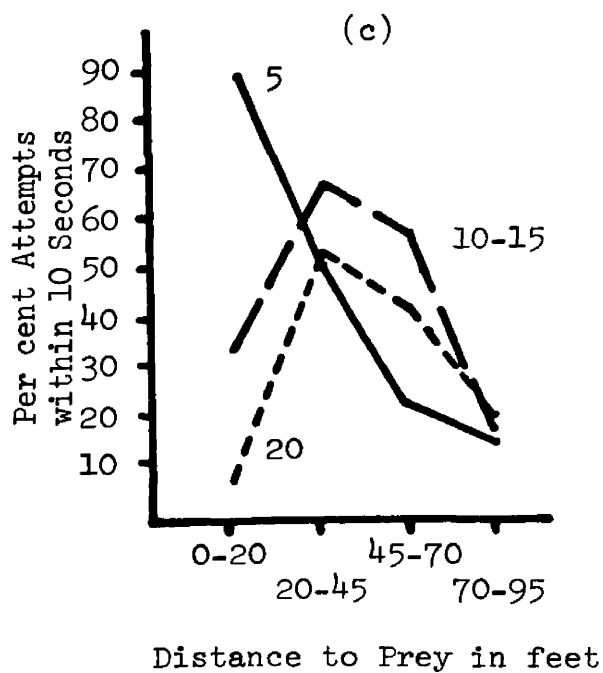
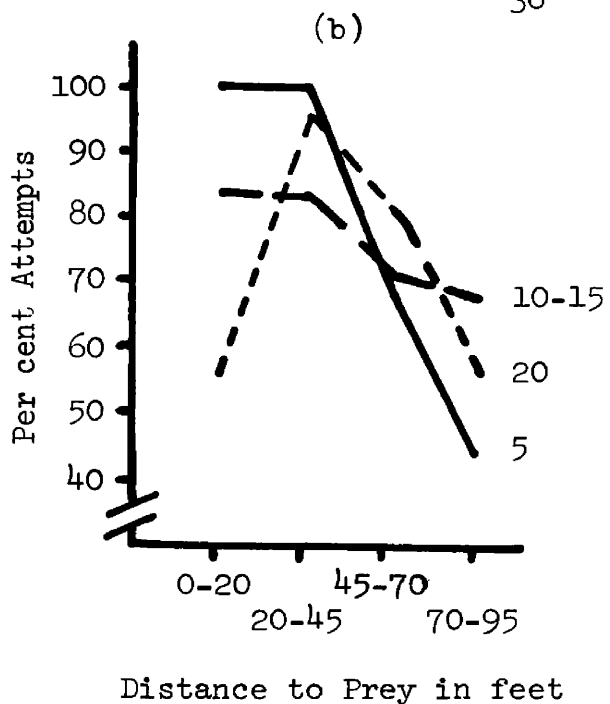
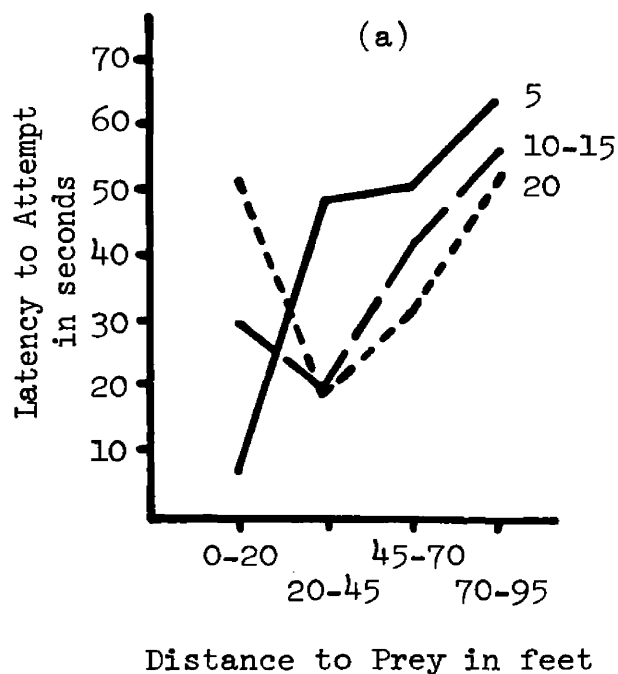


Figure 13. Distance to Prey and Height of Owl compared to Latency to Attempt(a), per cent Attempts(b), per cent Attempts within 10 Seconds (c) and Time off Perch(d). Each line represents a different Height in feet with the 10- and 15-foot Heights combined. $P < .05$ and $P < .01$ for a and d, respectively. No tests were computed for b and c.

Attempts and Attempts within 10 Seconds. No statistical tests were computed for these data because of too many low expected values. The 10- and 15-foot Heights were combined. The proportions of Attempts generally decreased with Distance when the owl was on the 5- and 10-15-foot high perches (Figure 13b). At the 20-foot Height the proportions of Attempts increased from the 0-20-foot Distance to the 20-45-foot Distance and then decreased as Distance increased further. The proportions of Attempts within 10 Seconds decreased with Distance when the owl was at the 5-foot Height (Figure 13c). When the owl was 10-15 feet and 20 feet high the proportions of Attempts within 10 Seconds increased from the 0-20-foot Distance to the 20-45-foot Distance and then decreased as Distance increased further. The greatest differences in the proportions of both Attempts and Attempts within 10 Seconds between the three Heights at any one Distance appear to occur at the 0-20-foot Distance.

Time off Perch. The overall significance level for Time off Perch for all combinations of Distance to Prey and Height of Owl is $P < .01$ (Figure 13d). The 10- and 15-foot Heights were combined. The average Time off Perch remained short at all Distances when the owl flew back to the 5-foot high perch. When the owl flew back to the 10-15-foot high perches the average Time off Perch decreased from the 0-20-foot Distance to the 20-45-foot Distance and then increased as Distance increased further. At the 20-foot Height the average Time off Perch decreased from the 0-20-foot Distance to the 20-45-foot Distance, increased at the 45-70-foot Distance and finally decreased at the 70-95-foot Distance. With the exception of the 10-15-foot Height at the

70-95-foot Distance, the greatest differences in Time off Perch between the Heights at any one Distance appear to occur at the 0-20-foot Distance.

Number of Prey Already Captured and Total Number of Prey Captured in One Night

The number of prey captured is used instead of number eaten because the number captured could be measured whereas the number eaten could not. However, it is probably safe to assume that every prey captured was eaten because the owl had nothing to eat the previous night.

Latency to Attempt. There is a significant change in Latency with the Number of Prey Already Captured ($P < .02$, Figure 14a). As the owl captured more prey the average Latency first increased and then decreased. Latency to Attempt shows no distinct trend when compared to the Total Number of Prey Captured in One Night ($P > .05$, Figure 15a). Latency to Attempt appears to be affected by both Total Number of Prey Captured in One Night, and Number of Prey Already Captured (Figure 16a). On nights when only three or four prey were captured the Latency increased sooner as more prey were captured than when a total of five or six prey were captured. On nights when seven prey were captured the Latency was erratic. The decrease in Latency to Attempt when four, five and six prey had already been captured (Figure 14a) is a result of variations between nights when the owl captured different numbers of prey and not the result of decreased Latency per se.

Attempts and Attempts within 10 Seconds. The proportions of Attempts and of Attempts within 10 Seconds appear to increase as more prey were captured but not significantly ($P > .05$ for both, Figure 14b

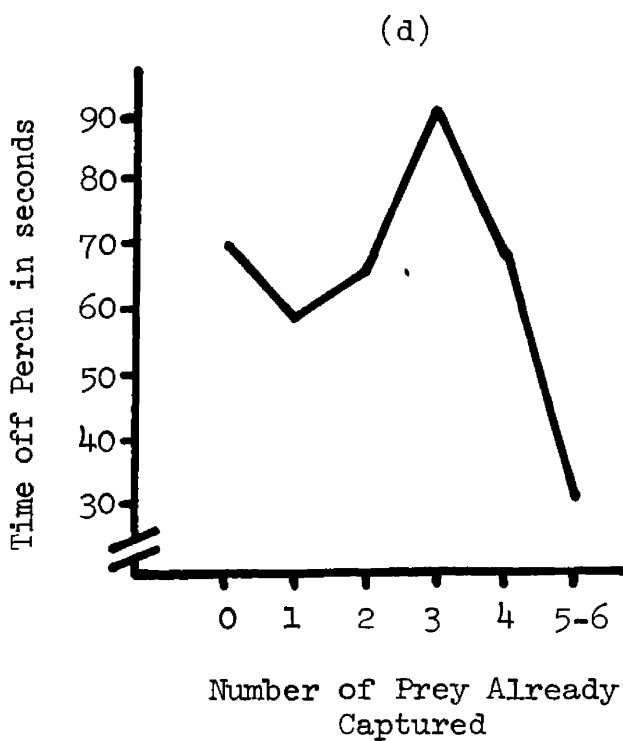
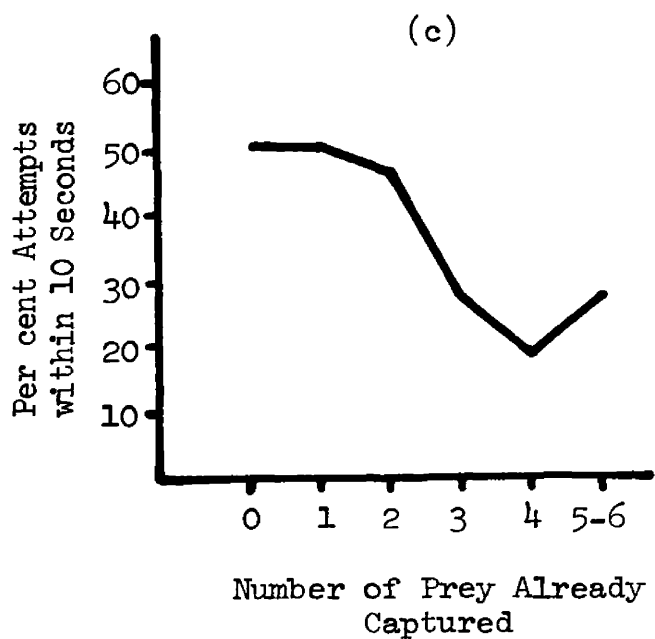
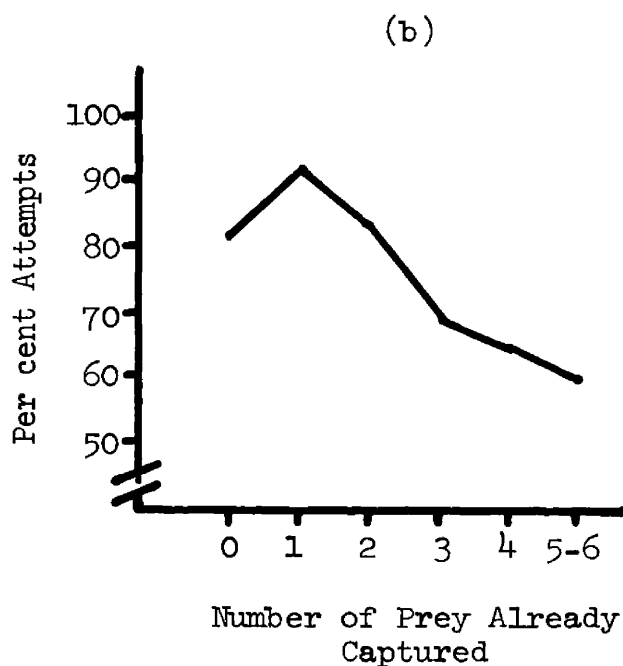
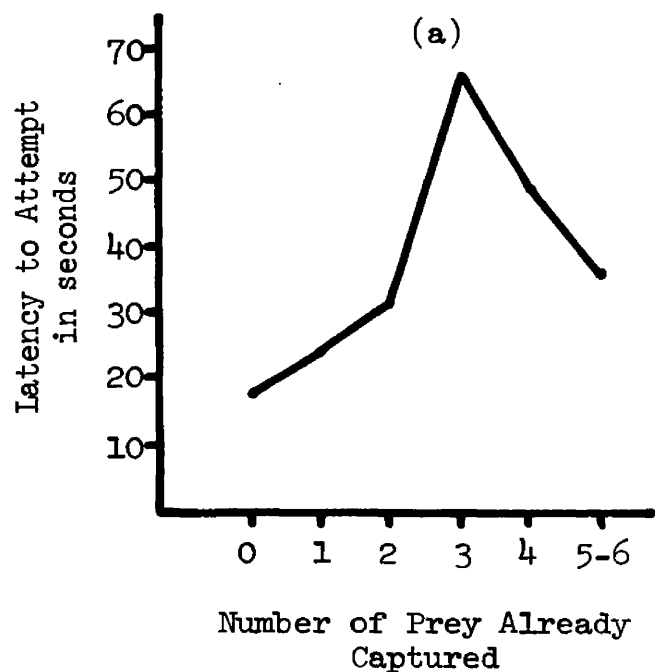
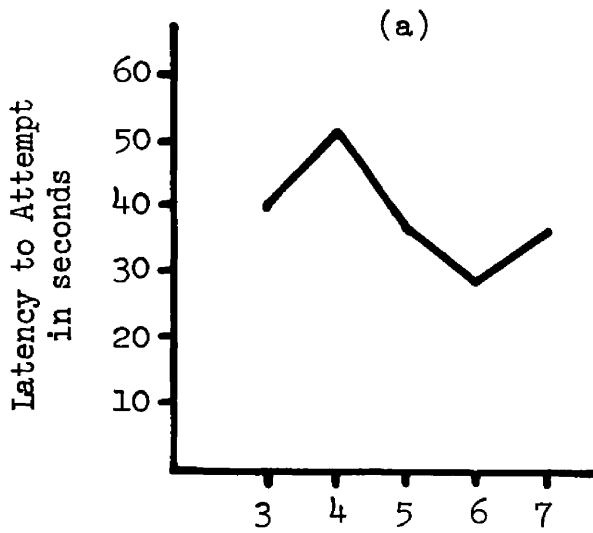
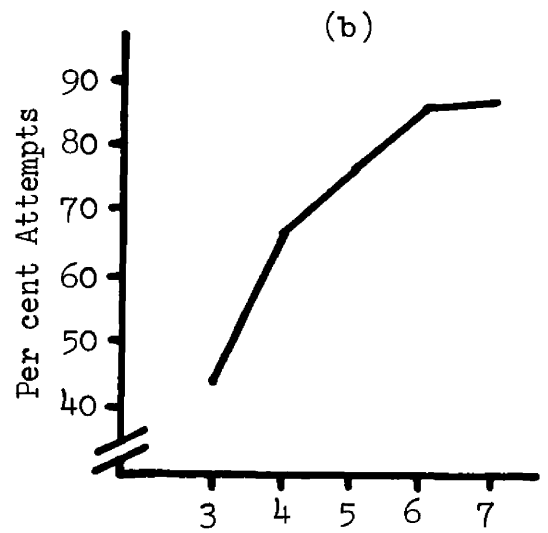


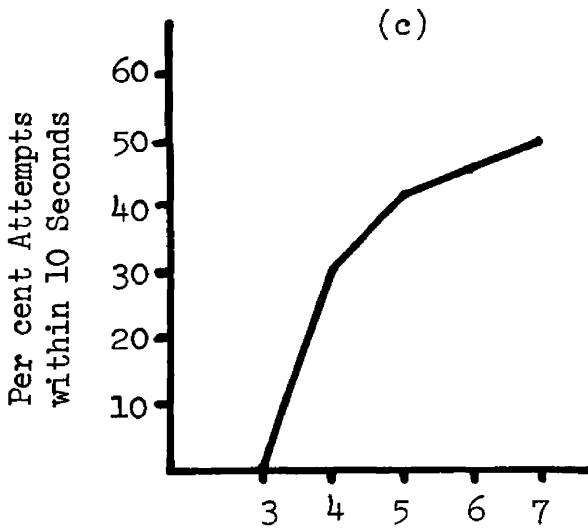
Figure 14. Number of Prey Already Captured compared to Latency to Attempt(a), per cent Attempts(b), per cent Attempts within 10 Seconds(c) and Time off Perch(d). $P < .02$ for a.



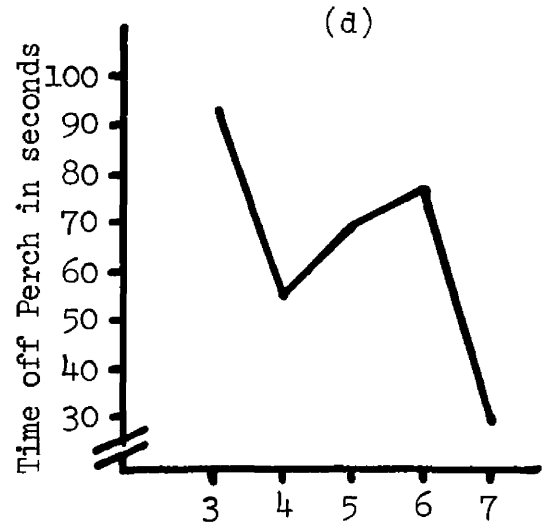
Total Number of Prey Captured in One Night



Total Number of Prey Captured in One Night



Total Number of Prey Captured in One Night



Total Number of Prey Captured in One Night

Figure 15. Total Number of Prey Captured in One Night compared to Latency to Attempt(a), per cent Attempts(b), per cent Attempts within 10 Seconds(c) and Time off Perch(d). $P < .01$ and $P < .05$ for b and c respectively.

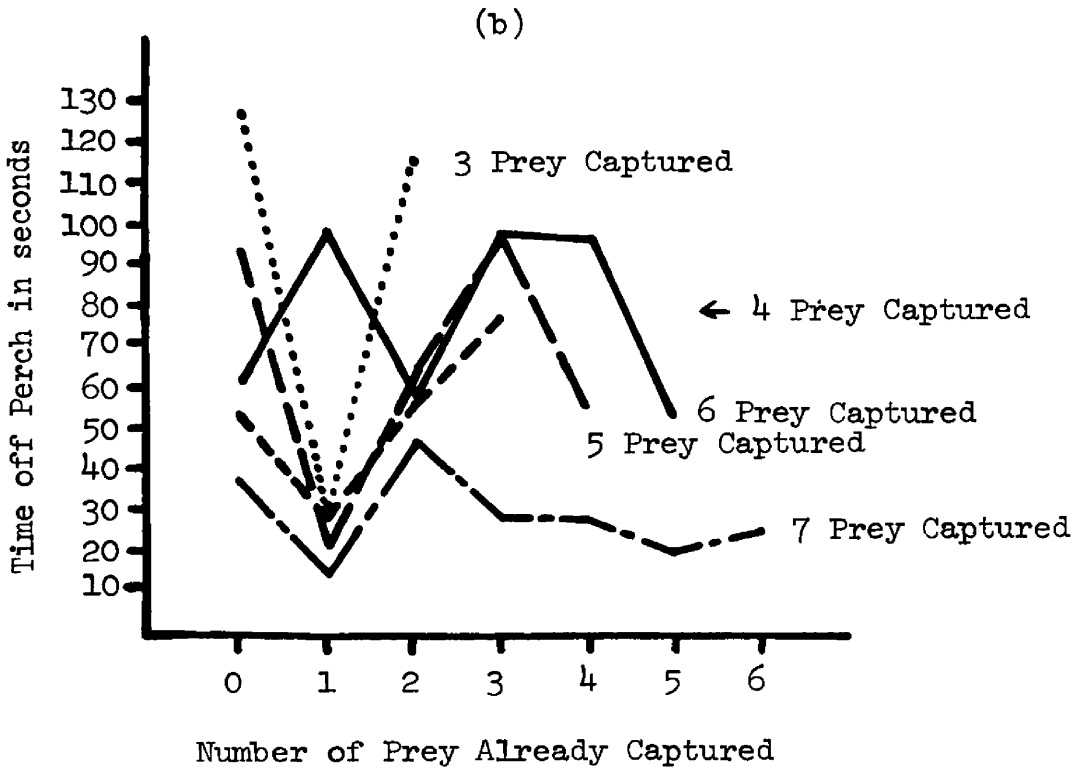
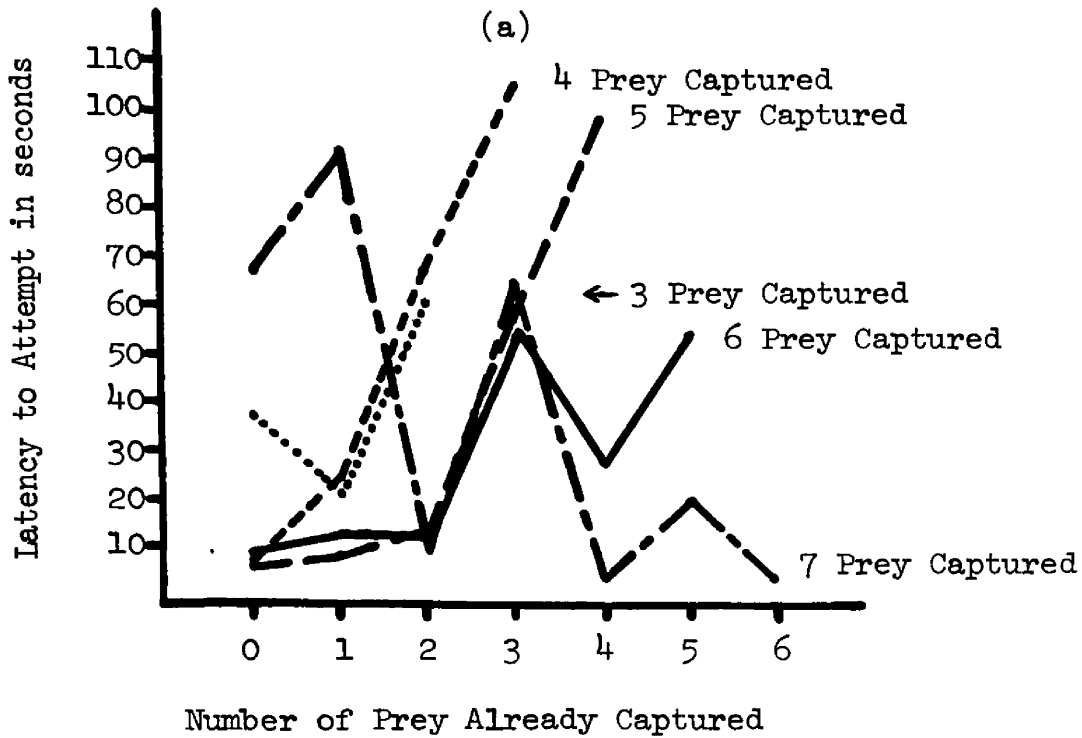


Figure 16. Number of Prey Already Captured and Total Number of Prey Captured in One Night compared to Latency to Attempt(a) and Time off Perch(b). Each line represents those nights when the owl captured the same total number of prey.

and c). There is of course a positive relationship between the proportion of Attempts and the Total Number of Prey Captured in One Night ($P < .01$, Figure 15b). A positive relationship also exists between the proportion of Attempts within 10 Seconds and Total Number of Prey Captured in One Night ($P < .05$, Figure 15c).

Time off Perch. Time off Perch appears to follow the same basic pattern as Latency over Number of Prey Already Captured but is not significant ($P > .05$, Figure 14d). As more prey were captured Time off Perch tended first to increase and then to decrease. Time off Perch shows no distinct pattern with Total Number of Prey Captured in One Night ($P > .05$, Figure 15d). Unlike Latency, Time off Perch did not appear to be influenced by an interaction between Total Number of Prey Captured in One Night and the Number of Prey Already Captured (Figure 16b).

Total Amount of Food Captured and Eaten. The total amount of food eaten on nights when different numbers of prey were captured does not appear to be different (Table 2). The total amount of food eaten two nights earlier (the last time the owl ate before the trials) also does not appear to be related to the number of prey captured. The owl captured an average of 29 per cent of the total weight of food eaten (Table 2).

Correlation Between Latency to Attempt and Time off Perch

There is a significant, positive correlation between Latency to Attempt and Time off Perch ($P < .05$, Spearman rank correlation coefficient, $r_s = .243$).

Time Between Successive Attempts

Latency to Attempt was not significantly correlated with elapsed

TABLE 2

PER CENT OF FOOD CAPTURED AND AVERAGE TOTAL WEIGHT
OF FOOD EATEN BOTH THAT NIGHT AND TWO NIGHTS
EARLIER, COMPARED TO THE TOTAL NUMBER
OF PREY CAPTURED IN ONE NIGHT

Total Number of Prey Captured in One Night	Per cent of Weight of Food Eaten That Night that was Captured	Average Total Weight of Food Eaten	
		That Night	Two Nights Earlier
3	18	206 g	246 g
4	23	213	186
5	29	216	239
6	38	199	198
7	36	246	210
Total Averages			214 g

time since returning to the perch after a capture ($P > .05$, Table 3).

Owl Returned to Perch With or Without Mouse After A Capture

On five nights the owl was observed on the perch with the infrared sniperscope. The number of times the owl returned to the perch with the mouse did not differ significantly from the number of times without the mouse ($P > .05$, Table 4). However, on any one night it appears that the owl did predominately one or the other (Table 4). No relation was found between Height of Owl, Distance to Prey or Weather Conditions, and whether the owl returned to the perch with or without the mouse. The sample sizes may be too small to bring out any of these relations.

The Time off Perch was significantly longer when the owl returned without the mouse ($P < .002$, U Test, Table 4). The owl averaged 55 seconds on the perch before completely eating the mouse. The 55 seconds for eating the mouse plus the Time off Perch when the owl ate the mouse on the perch agrees closely to the Time off Perch when the owl ate the mouse on the ground (87 and 74 seconds respectively).

Latency to Fixate

Latency to Fixate was determined primarily for the moving visual prey. The average Latency to Fixate was 8 seconds. The Latency to Fixate was the same for the 0-20-foot and 20-45-foot Distances and tended to increase as Distance increased further though no overall significant difference exists ($P > .05$, Table 5). The ranges of Latency to Fixate appear to be much shorter for the 0-20-foot and 20-45-foot Distances than for the further Distances. No significant correlation was found between Latency to Fixate and Height of Owl ($P > .05$, Table 5). The only Latencies to Fixate longer than 5 seconds occurred at the 45-70- and

TABLE 3
MINUTES BETWEEN SUCCESSIVE ATTEMPTS COMPARED TO
LATENCY TO ATTEMPT

	Minutes Between Successive Attempts						
	1	2	3	4	5	6-7-8-9	10 & +
Latency to Attempt in seconds	43	16	26	24	31	30	58

TABLE 4

NUMBER OF TIMES THE OWL RETURNED TO PERCH WITH AND
WITHOUT THE MOUSE, EACH NIGHT AND TOTAL,
AND TIME OFF PERCH

	Owl Returned to Perch	
	With Mouse	Without Mouse
Number of Times Dur-	1	1
ing Each Night	4	1
(5 Nights)	0	6
	2	5
	3	0
Total Number of Times	10	13
Time off Perch in seconds	32	74

TABLE 5
 AVERAGES AND RANGES OF LATENCY TO FIXATE MOVING VISUAL
 PREY COMPARED TO DISTANCE TO PREY
 AND HEIGHT OF OWL

Latency to Fixate Moving Visual Prey in seconds				
	Distance to Prey in feet			
	0-20	20-45	45-70	70-95
Average Latency	2	2	21	31
Range of Latency	1-5	1-5	1-78	18-43
	Height of Owl in feet			
	5	10	15	20
Average Latency	2	.6	5	15
Range of Latency	2	1-18	1-27	1-43

70-95-foot Distances before the owl had captured any prey.

Latency to Attempt the moving visual prey on the nights when Latency to Fixate was observed does not show the same trends as Latency to Fixate (Table 6). Latency to Attempt was roughly the same for all Distances except the farthest one where the Latency to Attempt appeared to be shorter. At the 70-95-foot Distance the average Latency to Fixate was 31 seconds and the average Latency to Attempt was 8 seconds. The reason for this discrepancy is that Latency to Fixate was not always possible to determine especially when the owl's head was oriented towards the prey upon presentation. Latency to Fixate would probably be short in these cases. In addition, fixated prey were not always attempted.

On two nights the Latency to Fixate the auditory stimulus was determined (Table 7). The owl did not fixate the auditory stimuli at the 0-20-foot Distance but should have been able to hear the stimuli because it did fixate the stimuli at the 20-45-foot and 45-70-foot Distances. When the owl did fixate the stimulus it did so almost immediately.

Prey Response

The owl succeeded in capturing 96 prey in 99 Attempts. Fairly equal numbers of the three Prey Responses (continue, change direction of movement, and stop movement and auditory stimulus emission) were tested. All three misses were at prey that stopped movement or stopped movement and auditory stimulus emission. This Prey Response is analogous to a prey "freezing." The three misses occurred at the 45-70- and 70-95-foot Distances for both moving visual prey and moving visual auditory prey on starlit and moonlit nights.

TABLE 6

LATENCY TO ATTEMPT MOVING VISUAL PREY COMPARED TO
 DISTANCE TO PREY WHEN LATENCY TO FIXATE
 WAS OBSERVED

	Distance to Prey in Feet			
	0-20	20-45	45-70	70-95
	Latency to Attempt Moving Visual Prey in seconds			
Average Latency	25	38	32	8
Range of Latency	3-51	7-92	4-120	3-12

TABLE 7
 LATENCY TO FIXATE AUDITORY STIMULUS COMPARED
 TO DISTANCE TO PREY

Latency to Fixate Auditory Stimulus				
Distance to Stimulus in feet				
0-20	20-45	45-70	70-95	
- ^a	1 ^b	1	-	
-	? ^c	1	?	

^aOwl did not fixate stimulus.

^bNumber of seconds to fixate.

^cCould not be determined if owl fixated stimulus.

EXPERIMENT 2

A total of nine drugged mice and thirteen moving visual prey were presented. Four of the drugged mice (three mus and one Peromyscus) were captured and seven of the moving visual prey were captured. The proportions of captures for the drugged mice versus the moving visual prey are not significantly different ($P > .05$, Fisher exact probability test). On the first night the owl captured two drugged mice at the same time, 24 minutes after the start of the trials. During the second night it was not possible to determine exactly when the owl captured the other two drugged mice. The owl remained on the perch for 6 minutes after the drugged mice were set out until the first moving visual prey was captured. The drugged mice then were not captured before 6 minutes. The average Latency to Attempt for the seven moving visual prey was 16 seconds. The Latency to Attempt for the drugged mice was therefore much longer than that for the moving visual prey.

Chapter 5

DISCUSSION

THE ROLE OF AUDITORY CLUES

On the starlit nights the owl did not make any Attempts at prey it could hear but not see. It could hear the prey because it fixated the auditory stimulus. There are several possible reasons for this. Before the start of Experiment 1 when the tracks were being worked on, the owl made two Attempts at the auditory prey without receiving the reward either time. These two trials may have conditioned the owl not to make any more Attempts. The burlap covering that hid the auditory prey may have appeared impenetrable to the owl. The quality of the auditory stimulus coming from the small speakers could have been unnatural. The significantly greater proportion of Attempts for moving visual prey than for moving visual auditory prey could have been due to some inhibitory effect of the auditory stimulus. It is also possible that the owl was unable to accurately locate prey when only auditory clues were available.

Different species of owls have different anatomical and physiological adaptations which are believed to increase the sensitivity of audition. These adaptations are described and discussed by Pumphrey (1948 and 1961), Pycraft (1898), Schwartzkopff (1955 and 1963) and Voous (1964). Four genera of owls are included in this group: Aegolius, Asio, Strix and Tyto. The most obvious anatomical adaptation of all four genera is the bilateral asymmetry of the external ears. Pumphrey (1948) believes that this asymmetry improves the local-

ization of a sound in space. The great horned owl and certain other species of owls have symmetrical rather than asymmetrical external ears. When the number of auditory neurons in the different nuclei of the medulla are plotted against body weight, the little owl (Athene noctua) and the eagle owl (Bubo bubo) fall in the same distribution as diurnal birds (Schwartzkopff, 1963). The eagle owl and the great horned owl belong to the same genus. On the other hand, the barn owl (Tyto alba), the tawny owl (Strix aluco) and the long-eared owl (Asio otus) all have many more auditory neurons in proportion to their body weight than the diurnal birds. The number of neurons may influence the efficiency of processing auditory information. Other adaptations have been reported for the above four genera but have not been compared to other genera. These two adaptations (asymmetry of the external ears and increased number of auditory neurons) occur only in some species of owls, not all. On the basis of morphology the great horned owl appears to belong to the group of owls with fewer adaptations.

Behavioral evidence shows that some species of owls can capture prey by audition alone. Payne (1962) demonstrated that the barn owl could capture prey by hearing alone. Dice (1947) during experiments on the selection by owls of deer mice which contrast in color with their background found that the owls could catch the living deer mice in complete darkness. Dice used a long-eared owl, a barn owl and a barred owl (Strix varia). These three species of owls that Dice used and the one that Payne used belong to the group of four genera of owls that have the greatest anatomical and physiological adaptations for hearing.

I cannot say whether the great horned owl can capture prey by hearing alone. In any case it should be realized that more special adaptations for hearing are found in some species of owls than others. The work on hearing in owls seems to center on those with the greatest adaptations and the results are incorrectly generalized to include all species of owls. It, of course, could be said that the individual owl that I used was not representative of all great horned owls. Other individuals may be able to capture prey by hearing alone. I do not exclude the possibility that any owl uses hearing in prey location. I believe hearing is used by these species for determining the general location of the prey and then vision is used for the exact location.

LIGHT INTENSITY

The trials were conducted under light intensities varying from about 10^{-2} foot-candle on moonlit nights to about 10^{-4} foot-candle on starlit nights. On cloudy and rainy nights light intensity was even lower. The owl apparently had no difficulty in seeing the prey at all Distances at these light intensities. Dice (1945) found that a barred owl, a long-eared owl and a barn owl could see dead mice at a distance of 6 feet or more at a light intensity of 7.3×10^{-7} foot-candle. When the light intensity was reduced to 5.3×10^{-7} foot-candle the three owls could not see the dead mice beyond a distance of about 1 foot. Two burrowing owls (Speotyto cunicularia) which are more diurnal in habits were unable to find the dead mice when the light intensity was reduced below 2.6×10^{-5} foot-candle. Dice (1947) forced owls to depend on vision to capture live deer mice (Peromyscus maniculatus)

by use of a mouse "jungle." The mouse "jungle" was a latticework made from sticks about 4 inches above the floor of the room with 8 inch by 8 inch openings. With the mouse "jungle" he found that a barn owl could capture the live mice readily at a light intensity of 8×10^{-8} foot-candle. The distance at which the prey were seen was not known. Dice points out that moving prey are probably more easily seen than stationary prey and that the owls probably used hearing to determine the general location of the live mice. This explains why the owls were able to see the live mice at a lower light intensity than the dead mice. Dice (1945) concludes from calculations of the light intensity in nature that on dark nights the light intensity is probably too low for these owls to see prey in shady habitats. The cage in my experiments was completely open except for three pines at one end where the perches were. There was no vegetation on the ground of the cage to obscure the prey or produce shade so the light intensities in the cage were probably maximal.

RESPONSES OF OWL

The proportion of Attempts within 10 Seconds generally follows the same trends as the proportion of Attempts. The results of the experiments then are not influenced greatly by the long period of presentation, but the average Latency to Attempt is increased.

A negative relationship appears to exist between both Attempts and Attempts within 10 Seconds, and Latency to Attempt. Generally where the average Latency to Attempt is short the percentages of both Attempts are high. It appears then that in the test situation, prey that are most

frequently attempted are also attempted soonest and conversely, prey that are less often attempted are attempted longer after presentation. This suggests that common causal factors underlie the two behaviors, i.e., whether or not to make an Attempt and when to make the Attempt.

PREY ACTIVITY

The proportions of Attempts and of Attempts within 10 Seconds are both significantly greater for the moving visual prey than for the moving visual auditory prey. No significant difference exists in Latency to Attempt or Time off Perch. One reason for this significant difference in both Attempts could be that the owl had difficulty in removing the mice from the alligator clips. After the alligator clips were replaced by the wire prongs only nine more moving visual auditory prey were presented. Another cause for this difference could have been due to the speakers, often hard to pull, traveling with a jerking motion. The speaker wire even though fairly flexible would kink, making it difficult to pull the speaker. The moving visual prey on the other hand moved with a constant speed. The jerking movements may have inhibited the owl in making Attempts. In addition, as previously stated, the auditory stimulus may have also inhibited Attempts by the owl.

THE EFFECT OF WEATHER

No significant differences were found in the owl's behavior for the three weather conditions. One would expect that the average Latency to Attempt would be shorter on the moonlit nights because supposedly the prey are more easily seen on such nights. However, the opposite

trend occurred, that is, the average Latency was longest for moonlit nights, though not significantly. The proportions of Attempts and of Attempts within 10 Seconds are about the same for all three weather conditions. Therefore the longer average Latency to Attempt on moonlit nights is not due to relatively fewer short Latencies but to an increase in the length of those Latencies longer than 10 seconds. In addition, the average Time off Perch was shortest on moonlit nights, though not significantly. The high light intensity on moonlit nights apparently inhibited leaving the perch and once the prey was captured inhibited a long stay on the ground. On moonlit nights the owl may be more vulnerable to some factor.

DISTANCE TO PREY AND HEIGHT OF OWL

Both the average Latency to Attempt all prey and the average Latency to Fixate the moving visual prey tend to be shorter at the 0-20- and 20-45-foot Distances than at the 45-70- and 70-95-foot Distances, though neither of these trends is significant. The simplest explanation is that the owl sees the closer prey sooner and makes an Attempt sooner, but data gathered on the nights when both Latency to Fixate and Latency to Attempt were recorded do not support this explanation (Table 6).

The sharp differences in Latency to Fixate the moving visual prey at the 0-20- and 20-45-foot Distances compared to the 45-70- and 70-95-foot Distances suggest that the owl could hear the moving visual prey at the 0-20- and 20-45-foot Distances. This would explain the shorter Latencies at these Distances when the owl's head might be oriented in any direction including directly away from the prey. The owl

could probably not hear the moving visual prey at the 45-70-foot Distance or at least not hear it as easily as at the closer Distances. If Latency to Fixate does primarily influence Latency to Attempt then one would expect a shorter Latency to Attempt for moving visual auditory prey than for moving visual prey at the 45-70-foot Distance. At this Distance it is improbable that the owl heard the moving visual prey but it did hear the moving visual auditory prey (Table 7). Surprisingly, the Latency to Attempt the moving visual auditory prey at the 45-70-foot Distance is not shorter than that for the moving visual prey (Table 1). This means that something other than Latency to Fixate caused the owl to respond faster to the close prey than to far prey. In addition, the great differences in Latency to Attempt between the 5- and 20-foot Heights at the 0-20- and 20-45-foot Distances (Figure 13) cannot be explained by Latency to Fixate which was uniformly short for all Heights at these Distances.

The interaction between Distance to Prey and Height of Owl leads to the explanation of the differences in Latency to Attempt. After fixating the prey the owl pauses before making an Attempt. During this pause the owl apparently evaluates the situation taking into account its height and the distance to the prey. Whether an Attempt is made or not and how long it takes the owl to decide whether to attempt is related to how much effort the owl must expend in order to capture the prey.

When the owl is 20 feet high and the prey is at the 0-20-foot Distance, the owl must break its speed in flight in order to capture the prey. Few such Attempts are made, few Attempts within 10 Seconds are made and the average Latency to Attempt is long. When the owl is 5

feet high and the prey is at the 0-20-foot Distance, the owl merely hops off the perch onto the prey. More Attempts and more Attempts within 10 Seconds are made and the average Latency to Attempt is short.

Once the owl has captured the prey and is on the ground it can stay and eat the mouse or return to the perch and eat it there. Unfortunately the data on where the owl ate the mouse are inadequate to allow analysis for the effects of Distance to Prey and Height of Owl. If the owl eats the mouse on the ground it must still return to the perch. Time off Perch also depends on how much effort the owl must expend in order to reach the perch. It takes a long time for the owl to return to the 20-foot high perch from the 0-20-foot Distance. In four of nine such cases the owl had to be chased off the ground. The owl returns shortly to the 5-foot high perch from the 0-20-foot Distance.

When the owl is 20 feet high and the prey is at the 20-45-foot Distance, the owl has momentum from its height to reach the prey with little effort. The average Latency to Attempt is short and more Attempts and more Attempts within 10 Seconds are made. Returning to the 20-foot high perch from the 20-45-foot Distance apparently is not as difficult as it is from the 0-20-foot Distance and the owl spends a short period of time on the ground. At a Height of 5 feet and with the prey at the 20-45-foot Distance, the owl does not have momentum from height and more effort is required to reach the prey than at the 0-20-foot Distance. The average Latency to Attempt is long, and though the same proportion of Attempts is made as at the 0-20-foot Distance, fewer Attempts within 10 Seconds are made than at the 0-20-foot Distance. Returning to the 5-foot high perch from the 20-45-foot Distance is not

difficult because there is little height to regain and the owl returns promptly.

At the 20-foot Height and with the prey at the 45-70- and 70-95-foot Distances the owl has momentum from height but a longer distance to fly. The Latency to Attempt increases and fewer Attempts and fewer Attempts within 10 Seconds are made. The owl returns to the perch after a longer period of time on the ground at the 45-70-foot Distance but after an unexplainably short period of time at the 70-95-foot Distance. At the 5-foot high perch the owl has no height for momentum and it requires more effort to reach prey at the 45-70- and 70-95-foot Distances. The Latency to Attempt increases and fewer Attempts and Attempts within 10 Seconds are made. Since the owl has no height to regain it spends only a brief period of time on the ground in spite of the distance.

The data from all sources (Latency to Attempt, Attempts, Attempts within 10 Seconds and Time off Perch) support the hypothesis that the effort required to reach the prey and to return to the perch correlates with and may actually determine whether an attempt will be made, how soon the attempt is made and how long the owl remains on the ground after an attempt. It would also explain the positive correlation between Latency to Attempt and Time off Perch. A more direct measure of the effort expended by the owl in attempting the prey at the various Distances from the different Heights and in returning to the perch would be helpful. Effort expended could be measured by the number of wing beats required to reach the prey. This suggests an alternative hypothesis. Even though a great horned owl's flight is generally silent, the sound of beating wings is audible to a

person nearby. The owl might be slower to respond and make fewer attempts in situations where its wing-beating might frighten the prey or mask the sound the prey makes. This however does not explain Time off Perch and the positive correlation between Time off Perch and Latency to Attempt.

Sparrows (1969) studied the effects of experience, duration of prey exposure, contrast of prey to background and density of cover over prey on the capture of prey by the American kestrel (Falco sparverius). Hand-reared kestrels made attempts indiscriminately whereas adult-captured kestrels made fewer attempts at those prey for which they were less successful. The kestrels did not capture all prey attempted and apparently estimated the probability of capturing the prey. The height of the kestrels was fixed at 7 feet and the air distance to the prey was always 14 feet from the perch so the effort expended by the kestrels in making a capture was probably constant. The owl captured almost all prey attempted and apparently estimated the effort required to capture the prey.

Latency to Fixate the prey is an important parameter because the prey must be fixated before the owl has the choice to attempt or not. If some prey are fixated sooner than others the choice to attempt or not can be made sooner. In these experiments Latency to Fixate was short compared to Latency to Attempt, 8 seconds compared to 35 seconds. Therefore Latency to Fixate does not appear to be the most important factor determining Latency to Attempt. In this connection it is important to note that prey that could be heard were fixated on the average much sooner than prey that could just be seen. The reason is that the

owl could hear in all directions but could see only where its eyes were oriented. I believe the important function of hearing in the great horned owl and some of the other species of owls is to establish the presence of a prey animal and its general location. The area of search for the eyes then is much reduced. Walker (1964) observed two domestic cats (Felis domestica) hunting singing Orthopteran prey and experimented with a speaker broadcasting the songs in the presence of one of the cats. The cats were attracted to the singing prey and to the broadcasting speaker but apparently depended on visual or other clues to make the capture.

THE ROLE OF HUNGER

Number of Prey Already Captured and Total Number of Prey Captured in One Night are measures of the owl's hunger. As more prey were captured the average Latency to Attempt increased and fewer Attempts and Attempts within 10 Seconds were made. These changes suggest that as the owl ate more prey it became less hungry and its responsiveness decreased. Latency to Attempt increased sooner as more prey were captured on nights when a total of three and four prey were captured than on nights when a total of five and six prey were captured. Hunger then seems to influence the responsiveness of the owl in three ways. First, hunger determines the number of prey captured. Secondly, Latency to Attempt increases and the proportions of both Attempts and Attempts within 10 Seconds decrease as hunger is reduced by eating prey. Thirdly, the first two effects interact so that when hunger is low and the owl attempts few prey, Latency to Attempt increases sooner than

when hunger is high. The owl ate about the same total weight of food every night regardless of how many prey it captured that night. Total Number of Prey Captured in One Night is a valid measure of how much work the owl will do in order to get something to eat.

Latency to Fixate and Number of Prey Already Captured were not related except in one case. The Latencies to Fixate the moving visual prey at the 45-70- and 70-95-foot Distances were relatively long before the owl had captured any prey. The owl could not hear these prey and could fixate them only visually. The long initial Latency to Fixate indicates that the owl was probably caught "unawares" by the beginning of the trials, i.e., looking elsewhere than down the cage. The changes in Latency to Attempt related to hunger then are not due to changes in Latency to Fixate but rather to the owl taking more time on the perch before choosing to attempt or not.

Beukema (1968) working with the three-spined stickleback (Gasterosteus aculeatus) found similar results related to hunger. The probability of a stickleback fixating a prey was not dependent on hunger except at a very low hunger when fewer prey were fixated. The probability of a stickleback eating a prey was dependent on hunger and decreased as hunger decreased. Mueller and Berger (1970) found that the wild sharp-shinned hawks (Accipiter striatus) which struck the lure birds had a lower incidence of food in their esophagi and had a lower mean weight than those that just passed low over the lures. They believe that hunger caused these differences. These two studies support my conclusions with the owl that hunger influences the responsiveness to prey.

Time off Perch shows no distinct trends when compared to Number of Prey Already Captured and the Total Number of Prey Captured in One Night. One exception is the uniformly short Time off Perch when seven prey were captured in one night. The relation between Time off Perch and hunger is not as clear as with Latency to Attempt. This is probably to be expected though because functionally Time off Perch does not influence the capturing and eating of a prey as directly as Latency to Attempt.

PREY RESPONSE

The owl captured all but three prey attempted and consequently no differences could be noted for the three Prey Responses. This extraordinarily high success rate is probably the result of the simplicity of the prey. No cover obscured the prey from the owl and prey movement was constant. Rudebeck (1950) found an overall success rate of 7 per cent for four species of raptors preying on migrating birds in Sweden. Jenkins (1970) reports a success rate of 39 per cent for wintering American kestrels in Costa Rica capturing insects. The success rate for kestrels in Michigan was 33 per cent catching mice and insects (Sparrowe, 1969). These field studies show that most attempts end as failures. The reason for the failures is most likely a change in the behavior of the prey as a result of becoming aware of the predator.

DRUGGED MICE

The proportions of drugged mice and moving visual prey captured did not differ. However, the Latency to Attempt was much longer for the drugged mice than for the moving visual prey. The owl took a much

longer time to see, recognize or react to the drugged mice. This points to the ineffectiveness of olfactory stimuli and infrared sensitivity as has already been shown for four other species of owls by Dice (1945). It also suggests that prey movement is important for prey recognition. After the trials each night a surplus of dead mice, rats or hamsters was left on a stool for the owl. Recognition of the non-moving mice, rats and hamsters as food was apparently limited to the stool where it had been learned; a live mouse was wired to the top of the stool along with some dead mice. This Experiment suggests that prey movement is important for prey recognition; movement separates the prey from its background and indicates a living object. This agrees with the importance of movement mentioned by Cushing (1939), Craighead and Craighead (1956) and Marler and Hamilton (1966).

Chapter 6

SUMMARY

This individual great horned owl required either visual or both visual and auditory sensory clues to attempt to capture the artificial prey. The owl made no attempts at prey it could only hear. Some species of owls are able to capture prey by hearing alone. The role of hearing in this individual and in some species of owls is believed to determine the general location of prey and subsequently restrict the area of visual search. The owl apparently had no difficulty capturing the prey at all distances under light intensities that varied from moonlight to dark, cloudy, rainy nights. The behavior of the owl indicates that the amount of effort needed to capture the prey and return to the perch determines whether an attempt is made, how soon the attempt is made and how long the owl remains off the perch after the attempt. The owl's hunger also influences whether an attempt is made and how soon the attempt is made but not how long it remains off the perch. No differences were noted for the three prey responses because the owl captured almost all prey attempted. The importance of prey movement for prey recognition and the ineffectiveness of olfactory and infrared stimuli were demonstrated by presenting motionless, drugged mice.

Chapter 7

LITERATURE CITED

- Bent, A. C. 1938. Life histories of North American birds of prey, Part II. Dover Publications Inc., New York. 482 pp.
- Beukema, J. J. 1968. Predation by the three-spined stickleback (Gasterosteus aculeatus L.): the influence of hunger and experience. *Behaviour*, 31:1-126.
- Craighead, J. J., and F. C. Craighead. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Penn. 443 pp.
- Cushing, J. E. 1939. The relation of some observations upon predation to theories of protective coloration. *Condor*, 41:100-111.
- Dice, L. R. 1945. Minimum intensities of illumination under which owls can find dead prey by sight. *Amer. Nat.*, 79:385-416.
- _____. 1947. Effectiveness of selection by owls of deer mice (Peromyscus maniculatus) which contrast in color with their background. *Contributions from the Laboratory of Vertebrate Biology, Un. of Mich., Ann Arbor, Mich.* No. 34, 20 pp.
- Jenkins, R. E. 1970. Food habits of wintering sparrow hawks in Costa Rica. *Auk*, 82:97-98.
- Marler, P. R., and W. J. Hamilton III. 1966. Mechanisms of animal behavior. John Wiley & Sons, New York. 771 pp.
- Matthews, L. H., and D. H. Matthews. 1939. Owls and infra-red radiation. *Nature*, 139:983.
- Mueller, H. C., and D. D. Berger. 1970. Prey preferences in the sharp-shinned hawk: the roles of sex, experience and motivation. *Auk*, 87:452:457.
- Payne, R. S. 1962. How the barn owl locates prey by hearing. *The Living Bird*, No. 1. Cornell Univ., Ithaca, New York. pp. 151-159.
- Pumphrey, R. J. 1948. The sense organs of birds. *Annual Report Smithsonian Inst.* pp. 305-330.
- _____. 1961. Sensory organs: hearing. In *Biology and Comparative Physiology of Birds*, ed. by A. J. Marshall, Vol. 2:69-86. Academic Press, New York.

- Pycraft, W. P. 1898. A contribution towards our knowledge of the morphology of owls. Trans. Linnean Soc., 7:223-275.
- Rudebeck, G. 1950 and 1951. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. Oikos, 2:65-88 (Part I), and 3:200-231 (Part II).
- Schwartzkopff, J. 1955. On the hearing of birds. Auk, 72:340-347.
- _____. 1963. Morphological and physiological properties of the auditory system in birds. Proc. 13th Int. Orn. Congr., 2:1059-1068.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312 pp.
- Sparrowe, R. D. 1969. Prey-catching behavior in the American kestrel (Falco sparverius). Unpub. Ph. D. thesis, Mich. St. Un. 47 pp.
- Voous, K. H. 1964. Wood owls of the genera Strix and Ciccaba. Zool. Med., 39:471-478.
- Walker, T. J. 1964. Experimental demonstration of a cat locating Orthopteran prey by the prey's calling song. Florida Entomol., 47:163-165.