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Probability Learning in Prey Selection with a Great Horned Owl and a Red-tailed Hawk

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PROBABILITY LEARNING IN PREY SELECTION WITH A GREAT HORNED OWL AND A RED-TAILED HAWK

by

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Deborah L. Mueller

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ABSTRACT

Probability Learning in Prey Selection with a

Great Horned Owl and a Red-tailed Hawk

by

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The purpose of this study was to examine the hunting strategies of birds of prey in a probability learning situation. One great horned owl and one red-tailed hawk served as subjects. Three boxes and associated perches, each representing different potential prey areas, were placed in a room adjacent to the birds' regular housing and served as test apparatus. One box was loaded with an available prey item (mouse) on each trial and the birds were required to land on a perch in order to gain access to the associated box and to the potential prey. A discrete-trial, self-correction procedure was used. In Experiment I, Box 1 was loaded with a live laboratory mouse on 60% of the trials, Box 2 on 30% of the trials, and Box 3 on the remaining 10%. A response requirement of sitting on the perch 5 seconds was programmed. In Experiment II, the probability of reinforcement was reversed for the 10 and 60% boxes and the response requirement was increased from 5 to 20 seconds. Experiment III returned the probability of reinforcement for each box to the

values used in Experiment I. In Experiment III the mice were euthanized prior to each trial.

The owl matched responses to probability of reinforcement in all three experiments while the hawk matched in Experiment II and showed matching toward two of the three boxes in Experiment III. In Experiment I the hawk had a Box 2 preference. This research extends the generality of the matching concept and suggests that predatory birds do not randomly hunt or hunt in only one location, but rather tend to search according to the probability of reinforcement for that location.

(50 pages)

INTRODUCTION

The study of predator-prey relationships has warranted much concern in recent years and led to extensive research. The interest ranges from concern over the indiscriminant shooting of eagles, to the coyote-sheep predation controversy. The initial focus on predator-prey relations sprang from observational studies of the predator in his natural habitat. Ethologists, but primarily ecologists, would observe and record information on a particular species in a pre-determined study area. Such was the case in Craighead and Craighead's (1956) work in Michigan and Wyoming. Out of this study, valuable information was gathered concerning the number of nesting pairs of raptors in the study area, their clutch size and number, whether they returned year after year to the same nesting spot, and their prey selection habits.

Data collected in the wild on prey selection habits from the Craighead and Craighead study and others like it have generated interest in predators from an experimental viewpoint. Today, the approach to predator-prey study is both ecological and psychological in nature.

SURVEY OF RELEVANT RESEARCH

Ecological Approach

As noted, much of the early work done in the predator-prey area was observational in nature. Out of such work, Leopold (1933) proposed the existence of four components to the predator-prey interaction:

1. Prey density,
2. Predatory density,
3. Behavior of prey,
4. Behavior of predator.

These four components were thus considered to govern predator density, prey density, and prey selection. Taking a somewhat different approach, but keeping these four components in mind, Solomon (1949) chose to focus on responses. He proposed that a predator's response was either numerical or functional. A numerical response was simply a change in predator density while a functional response was a change in the number of prey of a population consumed by individual predators. Today, much of the ecological research is based on either Leopold's or Solomon's proposed components of predator-prey relationship.

In a classic study, Holling (1959) looked at small mammal predation on the European pine sawfly. He concluded that prey density was regulated by the predators and that only the first two of Leopold's four components were

important in predation. Holling emphasized, however, that such components as prey characteristics, density and quality of alternate foods, and the characteristics of the predator were important, although secondary to functional and numerical responses. Holling (1966) expanded on the predator-prey relationship by concluding that even though prey density determined predation, predator deprivation and proximity of prey were also important factors.

Interest in raptors generated a great amount of observational research within an ecological/ethological framework. Fitch, Swenson, and Tillotson (1946) observed that red-tailed hawks on their study area in California preferred ground squirrels to other prey. This preference was attributed to a high density of ground squirrels since they were recently emerging from hibernation. McInvaille and Keith (1974) also reported a close correspondence between prey preference and prey density. When the snowshoe hare population in Alberta increased during 1970-71, great horned owls and red-tailed hawks responded by making the hare their preferred prey item.

Each of the above studies contributed strong support to the first two of Leopold's components and to Solomon's functional and numerical responses in explaining prey preferences. But recently the last two of Leopold's components, the behavior of the predator and prey, have begun to receive extensive investigation. Much of this research orients about Tinbergen's (1960) "specific searching image," or SSI theory, which suggests that

each time a predator hunts, it tends to seek out the same prey species it encountered last. Tinbergen thus places prey selection "within" the organism by attributing to the predator some mental image of the sought after prey. The importance of this hypothesis however, is that it emphasized the predator's behavior and the characteristics of the prey as instrumental in prey selection.

Royama (1970) has criticized the SSI theory on the basis that Tinbergen's observations "cannot be explained by assuming the existence of search images in the predator's mind, nor can one prove the existence of search images" (p. 656). The outcome of the SSI controversy has been a shift to a more quantitative approach, with the emphasis on characteristics and behavior of both the predator and prey species.

From a study with great tits, Royama (1970) suggested that predators may select larger and also more available prey items. Snyder (1975) studied both prey size and prey activity and found a clear interaction. Neither size nor activity alone, however, determined prey preference. Kaufman (1974b) presented a live and a dead mouse simultaneously to owls and found a preference for live (active) mice.

Mueller (1974, 1975) has suggested that kestrels may select "odd" prey, that is ones that differ in some manner from their conspecifics. "An odd animal in an aggregation might catch and hold the predator's attention more readily than the common animal" (Mueller, 1975, p. 953). Kaufman (1974a) on the other hand, proposed that predators select conspicuous prey,

rather than odd prey. He found that when barn and screech owls were presented both white and agouti mice in dense vegetation, they were more effecive in catching the conspicuous (white) mice. Wild shrikes showed similar behavior (Kaufman, 1973).

In an attempt to resolve some of the controversy over prey selection, Ruggero (1975) examined pelage color, morphology, activity, and the interaction of these three variables. He found that experience with a prey item faciltates selection and that there is an interaction between movement and morphology. The above studies suggest the need for further research on prey characteristics and behavior. Of further concern, though, is Leopold's fourth component in predation: the behavior of the predator.

Hunting Strategy

Eisenberg and Leyhausen (1972) studied the predatory sequence in smal mammals and defined three functional classes of behavior displayed by the predator: orientation and approach, seizing, and killing. These three classes could probably be applied to most, if not all predators, not just mammals. But prior to orientation (i.e., prey location), what strategy does the predator assume, that is, what factors determine where the predator will hunt? Does he randomly search the terrain for prey items or is there a pattern o his searching?

Craighead and Craighead (1956) noted that red-tailed hawks not only explore the geographic areas of high prey density, but they also explore areas

which rarely yield prey. Tinbergen (1960) explains switching as a function of SSI. The birds select one prey species for a period of time because of the searching image. When the image changes (how this occurs is not clear) then a predation switch occurs and a new prey species is selected for awhile. Tinbergen's (1960) study of great tits revealed "switching," that is, after preying on one species of lepidoptera larva for a period of time, the tits would "switch" to another larva species, apparently for no reason.

Smith and Dawkins (1970) also support the switching hypothesis in great tits. Although searching for prey occurred most often in high density areas, occasionally the tits searched (captured and consumed) in areas of lower productivity.

Royama (1970) attributes switching to a sampling of various geographic areas. After sampling, hunting is then concentrated in areas of highest prey density. Barnett (1963) reported what appears to be a laboratory correlate of switching. He (as have others) obtained spontaneous alternation, alternating left and right, with rats in a t-maze even with both arms always baited.

Not all the evidence supports the switching hypothesis. Murdoch (1969) concluded that no switching occurred with snail subjects when two prey species were presented. One prey species was always highly preferred and remained so. The probability of a snail eating a given prey species was increased if it had previously had several meals of that species. Murdoch and Marks (1973) also found no switching in ladybugs feeding on aphids.

Until now, the switching hypothesis has served as an explanation for the hunting strategy of predators. If a predator continually selects one prey species or continues to hunt in the same geographic area, then he supposedly has an SSI for that prey species. If the predator changes species or hunting location, then it is because he has "switched." But "switching" is not an explanation for predator behavior, rather only a description of behavior. Further insight into predatory behavior and hunting strategies may require removing the organism from his natural environment and testing under controlled conditions.

Psychological Research

A manipulative behavioral approach may answer some questions concerning the hunting strategies of predators. One approach has been to apply Herrnstein's (1961) matching law to the study of predator behavior. Using pigeon subjects, Herrnstein employed a two key concurrent procedure with variable-interval (VI) schedules of reinforcement on each key. The relative frequency of responding on a given key closely approximated the relative frequency of reinforcement for that key. Further studies using concurrent schedules of reinforcement extend the matching law beyond the two key situation. Miller and Loveland (1974), for example, used five keys with five concurrent VI schedules while Pliskoff and Brown (1976) studied matching with a trio of concurrent VI schedules. Both studies found that relative response rate on each key matched relative reinforcement rate.

The matching law has acquired the label "law" because the results of most concurrent VI schedule experiments tend to confirm Herrnstein's original report. But the data from discrete trial probability learning experiments do not always conform to the matching law. Although pigeons (Bullock & Bitterman, 1962), fish (Bitterman, Wodinsky, & Candland, 1958), and cockroaches (Longo, 1964) have shown matching; rats (Bitterman et al., 1958) and monkeys (Meyer, 1960; Wilson, 1960) maximize. That is, they select on almost all trials, the higher probability alternative (Graf, Bullock, & Bitterman, 1964). Additional investigations have revealed that not only are there species differences in probability learning, but procedural differences also determine whether the organism matches or maximizes. Graf et al. (1964) used correction, and guidance with correction, while manipulating whether a center key was present in a two-key discrete-trial experiment with pigeons. In non-correction procedures, an incorrect response terminates a trial, while in correction procedures, each incorrect response is followed by a timeout (TO) after which the two keys are reilluminated and the animal is given another opportunity to respond to the same configuration. In guidance procedures, an incorrect response produces a TO followed by the illumination of the correct key. In both correction and guidance procedures, each trial terminates in reinforcement. In the Graf et al. center-key procedure, a white key was turned on then turned off when pecked five times and then the two discrimination keys were turned on. The results are

summarized in Table 1. As depicted, correction procedures produced matching while non-correction procedures produced non-matching. The guidance procedure with center key produced maximizing while no center key resulted in matching. In the spatial problem, the authors report non-matching in the direction of maximizing.

The results of discrete trial procedures are thus equivocal with procedural and species differences seeming to determine the results. The matching "law" of the concurrent VI VI paradigm does not seem to generalize to all discrete-trial experiments. Naturally a controversy as to the source of these differences in results in discrete-trial problems has arisen. For a long time, Bitterman and associates (Bitterman & Mackintosh, 1969; Graf et al., 1964) argued that species differences in probability learning were due to differences in the mechanisms of response selection. That is, there are different learning processes at work in a pigeon than a rat or fish, or as Bitterman phrases it, there are qualitative differences in learning among fish, birds, and rats.

In opposition to Bitterman's point of view is that of Mackintosh and his colleagues (Bitterman & Mackintosh, 1969; Mackintosh, 1969; Sutherland & Mackintosh, 1971). Mackintosh argued that learning processes are in fact alike for all animals, thus no qualitative differences in learning exist, only quantitative ones. The differences in performance found among species is attributed to differences in the extent to which the organism can learn to attend to the relevant cue when it is not consistently correlated with

Table 1

Results from Visual and Spatial Discrete Trial Probability Problems with Pigeons

	Visual Problems		Spatial Problem
	Center Key	No Center Key	Center Key
Non-correction	Maximizing	Maximizing	
Correction	Matching	Matching	Maximizing
Guidance	Maximizing	Matching	

Source: Graf et al., 1964.

reinforcement. Thus in visual problems the animal must attend to key color and not key position. Mackintosh proposed that rats, which maximize, are thus more "efficient" because they are better able to attend to appropriate cues:

> From this it follows that the differences in the stability of attention between rats, birds and fish, . . . will equally account for the observed differences in performance in probability learning experiments. (Sutherland & Mackintosh, 1971, p. 456)

What Mackintosh acknowledges is the presence of species differences in performance on probability experiments without having to assume underlying qualitative differences in the learning process. Bitterman (1975) has recently hedged on his original hypothesis and now advocates further research before making conclusions about the learning processes of various species. What Bitterman does suggest is the continuance of comparative research to advance the understanding of learning processes and how these processes relate to behavior.

The purpose of the present experiment was to investigate the hunting strategies of two birds of prey, one great horned owl and one red-tailed hawk, by means of a discrete-trial, self-correction spatial probability paradigm. A self-correction procedure is the same as a guidance procedure except there is no TO following an incorrect response (Mackintosh, 1969). Three boxes, each representing spatially different hunting areas with a different probability of reinforcement, were utilized. Three boxes were used for two reasons. First, the natural environment is never an either/or

situation, thus a predator is never confronted with a situation whereby a non-reinforced response is automatically followed by a reinforced response at another location. Second, three boxes eliminate the possibility for spontaneous alternation. In reality, four, five, or more prey locations are preferable but three is more practical for control and analysis.

A self-correction procedure was chosen because it too might reflect more accurately the natural environment. When a predator hunts in one area and is unsuccessful, it either moves on to a second or third location or persists in the same until reinforcement is obtained.

The data were analysed to determine whether the two birds match, maximize, or randomly respond. Maximizing was defined as at least 90% of first responses occurring to the high probability box. Matching was defined as response frequency within a range of 15% of either direction of the probability for that box. Random behavior was considered responding to all three boxes within 15% of either direction of chance. Any responses not falling within the matching, maximizing, or random criteria were defined as non-matching. Figure 1 illustrates these criteria.

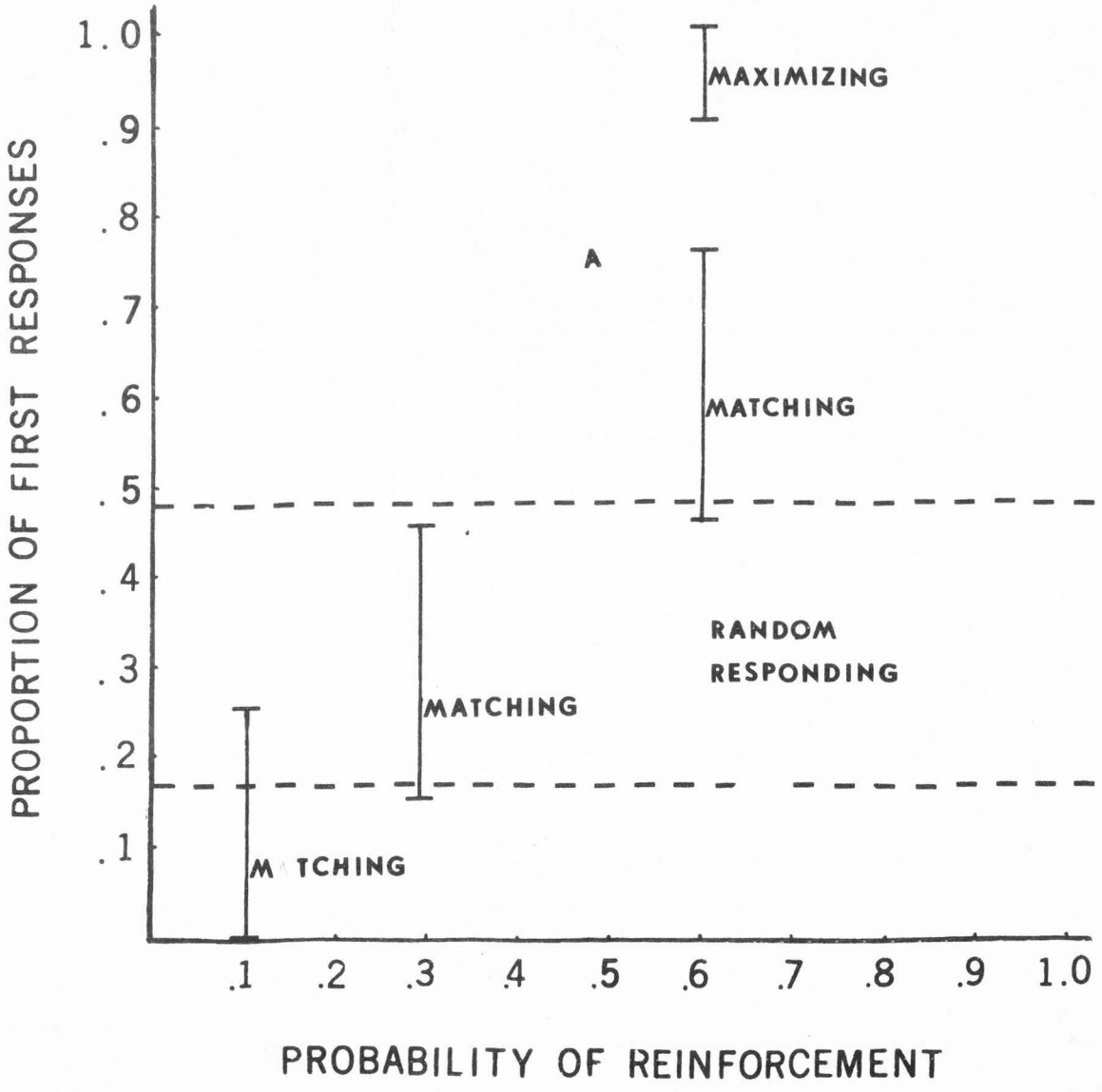

Figure 1. Response limits necessary to meet criteria for matching, maximizing, or randomizing.

METHODS AND RESULTS

Experiment I

Subjects

One, 2 year old great horned owl (Bubo virginianus) and one, 4 year old male red-tailed hawk (Buteo jamaicensis) served as subjects. White laboratory reared mice of undetermined age and sex served as prey items.

Apparatus

Each bird was housed outdoors in a 1 m x 1 m x 3 m wire cage. The cages were attached to opposite sides of a building which contained the experimental room (see Figure 2). Each cage had an access door to the experimental room which was operated from the equipment room. The experimental room measured 8 m x 10 m x 4 m.

Inside the experimental room were three 75.5 cm x 75.5 cm x 20 cm wooden prey boxes and three 1.3 m perches; one perch associated with each box. As shown in Figure 3, each prey box had two doors, an inner clear plexiglass door and an outer solid wooden door. The doors on the boxes were released by 28 volt solenoids. The perches and boxes were movable so as to allow them to be oriented to face each bird as he was tested. Each perch sat 5 m from the center of the access door and were thus in a semi-circular position facing the bird. A response (landing on a perch) closed a

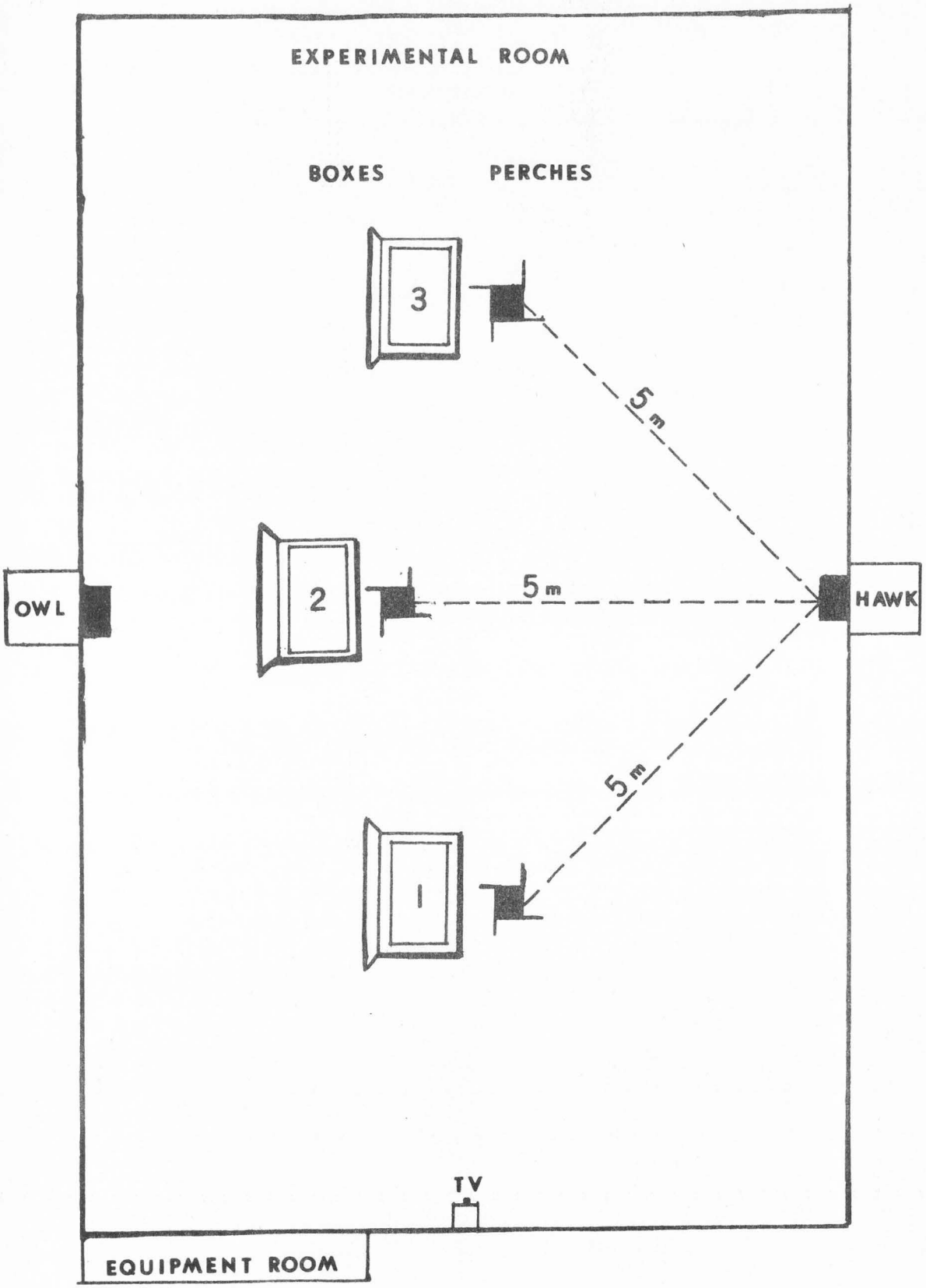

Figure 2. Apparatus as positioned when testing the hawk. Boxes and perches were turned and appropriately placed for testing the owl.

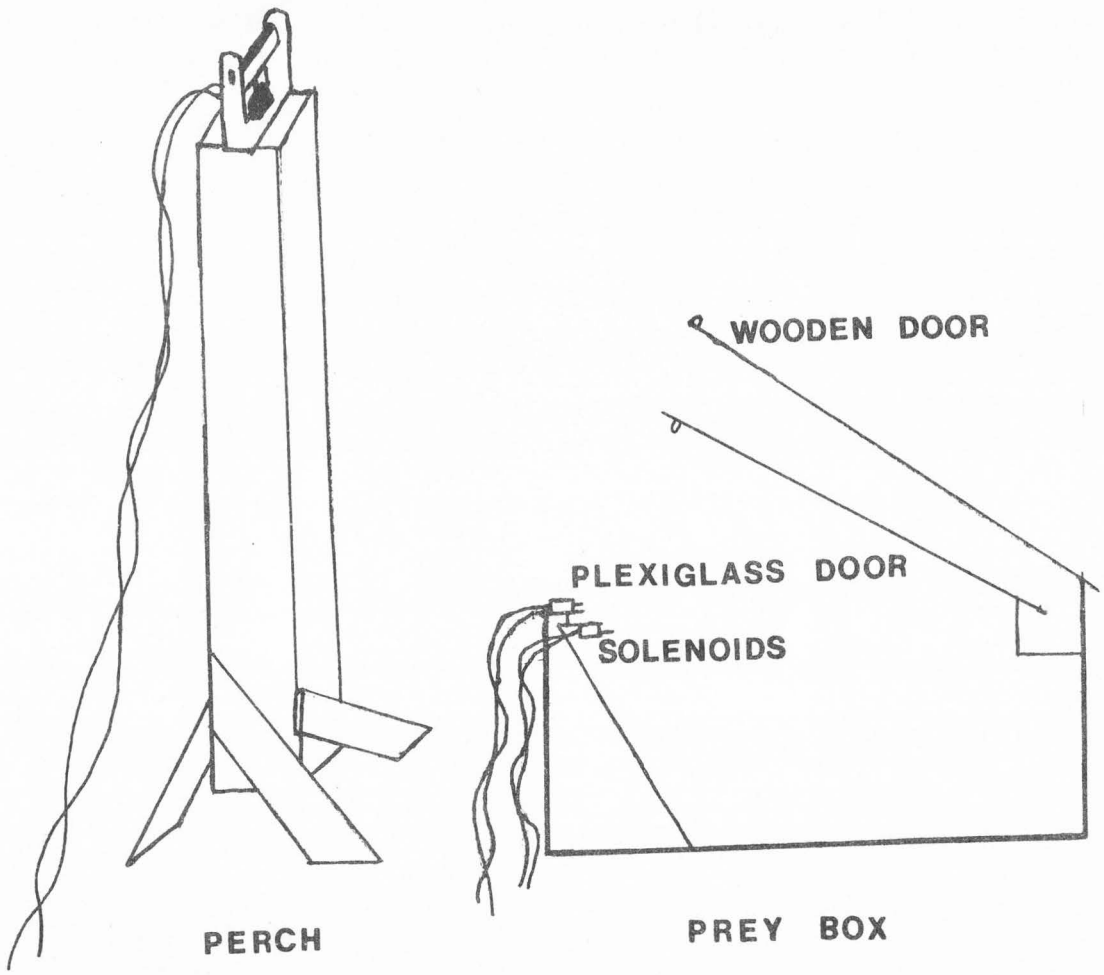

Figure 3. Apparatus used in all three experiments.

microswitch and started a constant ground timer. Upon timing out, the timer operated the solenoids for both doors on the box associated with that perch, allowing access to the inside of the box. A closed circuit TV was used by the experimenter to monitor each trial from outside the experimental room.

Procedure

Training. Each bird was offered one mouse per trial from one of the boxes with both doors initially open. This series was done in random sequence. Once familiarized with the experimental boxes (three consecutive trials of taking a mouse within 5 minutes), the plexiglass door on each box was closed. A mouse was placed in each box prior to setting the closed plexiglass door. The bird was then required to land on a perch which immediately operated the door and allowed access to the mouse. A criterion of landing on a perch and obtaining a mouse within 5 minutes, for five consecutive trials was set for this phase. Finally, a mouse was placed in each box and both doors were shut so there was no visual contact with the mice. Again the birds were required to land on a perch which immediately opened both doors. Three trials were run under this condition.

Testing. Upon completion of training, the birds began experimental trials. First, six randomized trials with only one box loaded were run. After these six trials, each box was assigned a different probability of reinforcement with Box 1 containing a mouse on 60% of the trials, Box 2 on 30%

of the trials, and Box 3 on 10% of the trials. A predetermined, 10 trial block sequence (see Appendix for the sequence used) was repeated for a total of 46 trials. Each bird was run three or four trials per day depending on the total weight of the mice. Each bird received 50-60 grams of mice per day.

On each trial, one mouse was placed in the predetermined box and both doors closed on all boxes. The cage access door was then opened and the bird was required to enter the room and choose one of the three perches. The bird had to remain on the perch for 5 consecutive seconds in order to open the doors of the associated box and thereby gain access to the potential prey. Since a self-correction procedure was used, the bird was free to move to a second and third perch until it finally obtained reinforcement. Fifteen minutes per trial was allowed to locate the prey item. Upon locating the prey, the bird was ushered to its home cage in order to consume the mouse. Two minute inter-trial intervals (ITI's) were used. All responses were recorded by an experimenter watching the TV monitor. However, only first responses were considered in the data analysis. First response was defined as that response per trial which successfully opened the doors on one of the boxes first. Also, only the last 30 trials were considered in the data analysis.

Results

The results are plotted in Figures 4 and 5. The owl matched first responses to reinforcement probability according to the criteria set in

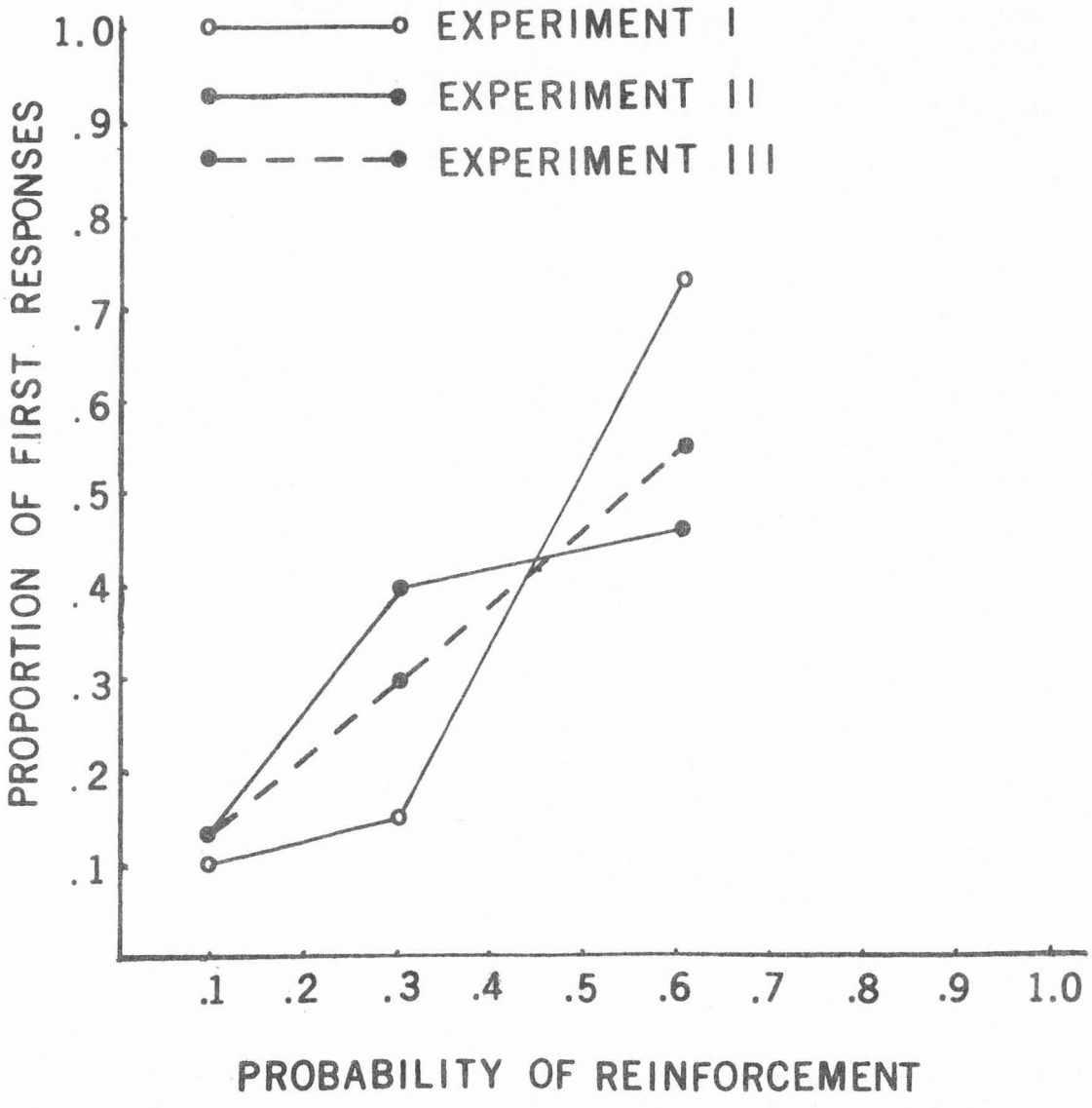

Figure 4. Owl data from Experiments I, II, and III.

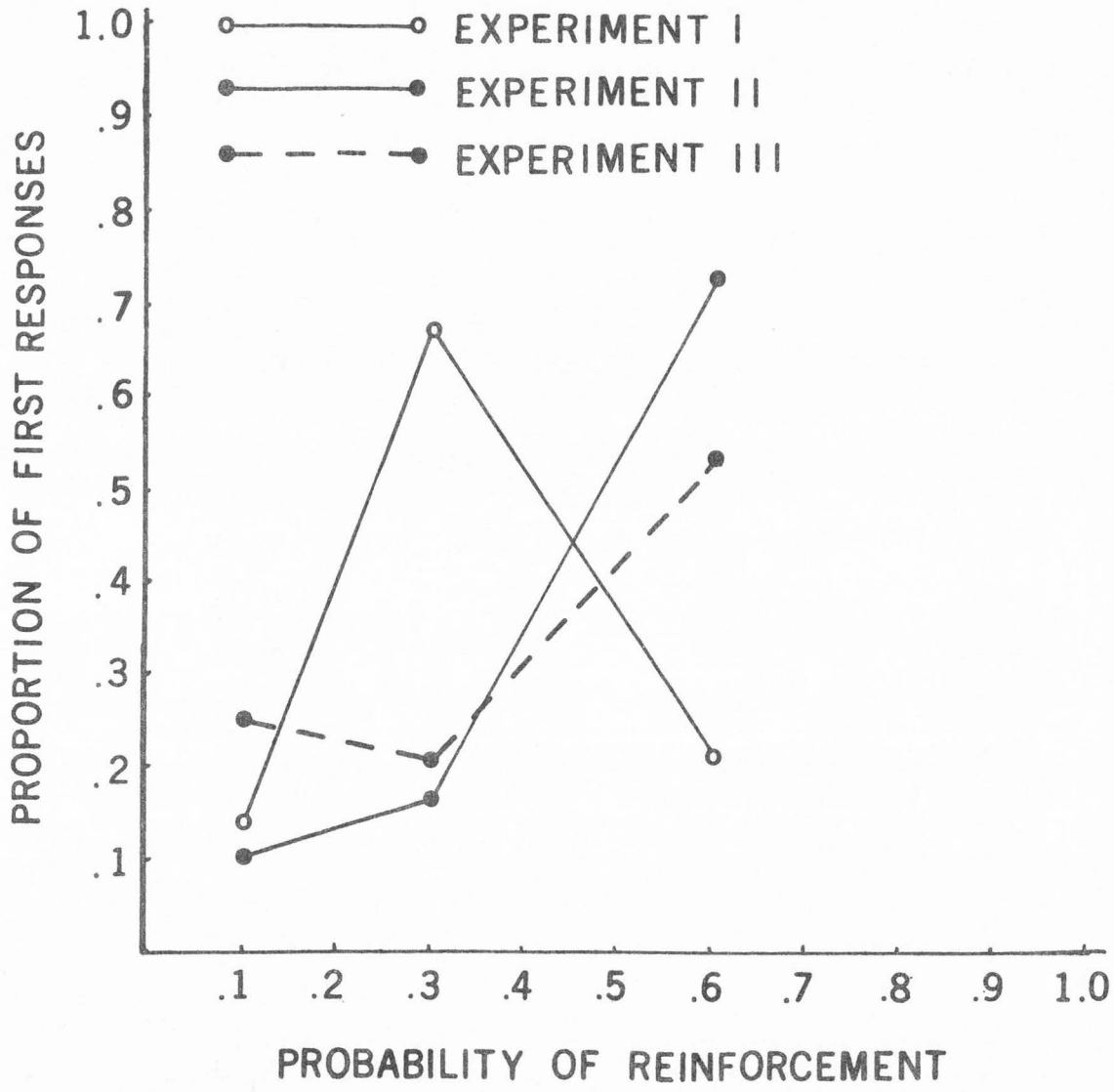

Figure 5. Hawk data from Experiments I, II, and III.

Figure 1. He[1] responded exactly 10% of the time to Box 3 which is perfect matching for that box. He was, however, slightly over on first responses to Box 1 with 73.33% responses there. This high response rate to Box 1 meant a correspondingly lower rate to Box 2.

The hawk by definition did not match, maximize, or randomize his responses. He showed a definite bias toward Box 2 with 66.67% of his responses made to that location. Responses to the other two boxes appeared to be random in nature with 20% of his responses to Box 1 and 13.33% to Box 3.

Experiment II

The probabilities were reversed from Experiment I for the two end boxes in this experiment, thus Box 1 contained a mouse on 10% of the trials, Box 2 on 30% of the trials, and Box 3 on 60% of the trials. A second change increased the response requirement from 5 seconds to 20 seconds. That is, each bird was required to sit on the perch 20 seconds before gaining access to the box. This was done in an attempt to eliminate the position bias by the hawk.

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[1]Although the sex of the owl was not known, the masculine gender is used for convenience.

Subjects

The subjects were the same as those in Experiment I.

Apparatus

The apparatus was the same as that of Experiment I.

Procedure

Since the birds were already familiar with the procedure, no further training was necessary. As mentioned, two changes were made from Experiment I. The probabilities for the end two boxes were reversed and the response requirement was increased from 5 to 20 seconds. As in Experiment I, six random trials were run first followed by the 46 experimental trials. Again, only the last 30 of the 46 trials were considered in the data analysis.

Results

The results of this experiment are found in Figures 4 and 5. The hawk produced good matching in this experiment with his responses to the 10%, 30%, and 60% boxes being 10%, 16.67%, and 73.33%, in that order. The owl did not match as well in Experiment II as Experiment I, but the pattern (13.33%, 40%, and 46.67%) is correct and responses fell within the set criteria. The poorer matching is due to a lower number of responses to Box 3 than expected.

Experiment III

In this experiment, the probabilities of reinforcement for each box were reversed back to those in Experiment I. In this experiment, however, the mice were euthanized by a blow to the head before being placed in the appropriate box. The purpose of killing the mice was to assure that they were not revealing their position by making noise and thus influencing choices of the birds. A comparison between the number of correct first responses among the three experiments would indicate if the birds had in fact been detecting the mice. If they were detecting the mice, then the number of correct first choices in Experiments I and II would greatly exceed those of Experiment III and better matching would be expected in Experiments I and II than III.

Subjects

The subjects were the same as those of Experiment I.

Apparatus

The apparatus was the same as that of Experiment I.

Procedure

The procedure was the same as that of Experiment II but with the two noted exceptions; the probabilities were the same as those of Experiment I and the mice were killed prior to each trial.

Results

The results are in Figures 4 and 5, and a summary of data from all three experiments is found in Table 2. The owl again matched first responses to reinforcement probability well within defined limits. In fact, his matching performance was better in Experiment III than in either of the prior two experiments, thus not supporting the hypothesis that he had been detecting the presence of the mice in Experiments I and II. The hawk matched responses within criteria for two of the three boxes (Boxes 2 and 3) but over-responded to Box 1.

Table 3 lists the number of correct first responses for each bird in all three experiments. The results indicate no evidence for either bird ever detecting the mice in a closed box. As mentioned, the owl matched better in Experiment III than either of the other two experiments, thus refuting this concern. The owl did have 15 correct responses in Experiment I and the hawk had 14 correct first choices in Experiment II, but in each of these experiments, the bird responded for 10 consecutive trials to the high probability box (maximized), thus producing six correct first choices for that 10 trial block alone.

Further evidence that the birds were not detecting the mice lies in the "reward following" data (Table 3). "Reward following" is defined as making a response to the location or box which had been reinforced on the previous trial. As seen in Table 3, a high number of correct first choices was associated with a high frequency of reward following. If the birds had

detected the mice, then they should have responded to the appropriate box and not followed reward. The high number of correct first choices may be attributed to reward following on the high probability box.

DISCUSSION

The results of this experiment indicate that birds of prey in a discrete trial, spatial probability experiment employing a self correction procedure do match. The owl matched responses to reinforcement probability in all three experiments while the hawk did so in Experiment II and matched for two of the three boxes in Experiment III. The hawk showed a box bias in Experiment I which was eliminated by increasing the response requirement from 5 to 20 seconds. Through casual observation during Experiment I, it was noted that the hawk immediately flew into the room to perch 2 when the access door was opened. Since perch 2 was directly in front of the access door, it was probably most readily observed. With the response requirement being only 5 seconds, the hawk gained almost immediate feedback as to whether a mouse was in Box 2 or not, and he could then select another perch with little effort. By increasing the response requirement to 20 seconds, immediate feedback was not possible and this procedure eliminated the box bias.

If generalized to natural behavior, the results of this research suggest that predatory birds do not randomly hunt, nor do they maximize by responding to one location. Rather they search different locations according to the probability of reinforcement in that area. These results are in agreement with Smith and Dawkins (1971) and Craighead and Craighead (1956). Smith and Dawkins manipulated prey density (meal worms in four feeding

areas) and studied the responses of great tits to these four areas. About 75% of foraging time was spent in the highest prey density area with the remaining 25% spread fairly equally over the other three areas. Although the birds were not precisely matching, they were very close while exploring all other potential prey areas. Smith and Dawkins add that in natural settings, great tits probably do more exploratory foraging since time limits do not occur in nature as they did in the experiment. Therefore, they would predict a very close approximation to matching in wild great tits. Craighead and Craighead (1956) lend further support to this idea in their observations that red-tailed hawks tend to search all parts of their territory.

The results of the present study, however, do not agree with those of Graf et al. (1964). In their spatial problem with pigeons, they report maximizing (Table 1). The discrepancy between the two results could be attributed to either procedural or species differences. This leads to the question of whether birds of prey differ in strategy from other birds or other species such as rats? As mentioned, Mackintosh proposed that maximizing is the optimal or most efficient strategy and that the non-maximization found in some species is a result of an inability to attend to the relevant cues. He considers responses to low probability areas as errors. But should responses to low probability locations be considered errors and should maximization be considered optimal for predators? Several factors suggest that this need not be the case. First, a predator would quickly diminish his resource if he continually preyed in one area or "maximized." Second, the prey

(i. e., mice) may learn the predators' hunting pattern and become "efficient" at escaping the predator. And third, as Smith and Dawkins (1971) suggest, the natural environment of a predator does not identically resemble the typical laboratory discrete trial procedure, or the environment of non-predators (i.e., pigeons). In equating the predators' environment to a probability learning experiment, they note:

> This (probability learning experiment) is effectively the problem encountered by a predator whose food occurs at differing densities in different spatial locations in its habitat, except that the predator is faced with more than two choices and that the situation is inherently less stable, and hence less "predictable." (Smith & Dawkins, 1971, p. 696)

Thus matching (as opposed to maximizing) may result from a checking process wherein the predator samples low density areas to determine if fluctuations in prey density are occurring. Also, there is always the possibility of an opportunistic chance kill in a low probability area, making an infrequent search of that area efficient in terms of energy expenditure.

The above arguments were not intended to undermine Mackintosh's hypothesis about probability learning. He may well be correct in his assumptions but their applicability need to be limited to either certain species or procedures. Maximizing may be the most efficient strategy for rats but perhaps matching is more "naturally" efficient or adaptive for birds of prey. However, Mackintosh's attentional theory would seem to apply to both predators and non-predators; laboratory and non-laboratory situations. Wild predators probably learn certain relevant cues about their habitat to indicate

prey density. Smith and Dawkins (1971) note this:

> It is likely that great tits in the wild may have secondary cues to the density of their prey species, e.g. leaf damage, or webs spun by some species of prey such as Acantholyda nemoralis. (p. 696)

A bird of prey may have to learn the relevant cues before he will optimally respond. But as suggested, optimal responding for the predator may be matching, not maximizing.

Several interesting findings are noteworthy from the three experiments reported here. In Experiment I, the owl responded to the high probability box on 10 consecutive trials early in the experiment (trials 3-12). In other words, the owl maximized initially and then stabilized responding to more closely approximate matching. The hawk did not display such behavior in Experiment I, but he did not match in Experiment I either. However, in Experiment II, the hawk did maximize over trials 11-20. Thus both birds, when initially learning the probabilities, maximized before stabilizing into a matching pattern. A possible explanation for such a phenomenon is that initial maximizing confirms that location as the high probability location. Such an explanation does not explain why each bird initially maximized only once and did not repeat such behavior in future experiments. It is possible that the original maximizing was necessary for learning the probabilities and thereafter changes in density (reversals) were rapidly detected, therefore not necessitating a period of maximizing.

A second phenomenon of interest comes from an analysis of reward following and correct first choices. For each bird, the experiments in which

there was a high percentage of reward following tended to also produce a high number of correct first responses, and these experiments also tended to be the ones in which matching was the most prevalent. The only strategy which could produce both high reward following and high correct first choices would be one of: respond again to the high probability box if reinforcement was just obtained there but if a response to the high probability box was not reinforced, then change to a new area or box. That is, when a response is made to the high probability area, a win-stay, lose-shift strategy is adopted toward that location. This suggests that matching occurs when a win-stay, lose-shift strategy is adopted toward the high probability reinforcement area. In generalizing to the wild condition, a predator may hunt at high density areas until unsuccessful, then begin to explore other known prey areas on following days or hunts, then returning to the former high density area.

The reward following data is of further interest because of its relationship to matching. Matching is a descriptive term which relates overt behavioral patterns to the observer. Matching, however, may be a function of one of several processes. One of those processes could be reward following. If an organism reward follows then the outcome is manifested as "matching." In these experiments, the function of reward following is unclear because it occurred only at a chance level in three of the six possible instances. Furthermore, where reward following did occur above chance level (on greater than 10 of the 30 trials/experiment) its impact is unclear. Matching tended to

still prevail when reward following trials were removed from the data analysis.

Thus, if birds of prey do perform in nature as they did in this experiment, they would match responses toward a given location according to the probability of reinforcement in that area. This matching behavior can partly be explained as a function of "reward following."

REFERENCES

Barnett, S. A. The rat, a study in behavior. Chicago: Aldine, 1963.

Bitterman, M. E. The comparative analysis of learning. Science, 1975, 188, 699-709.

Bitterman, M. E., & Macintosh, N. J. Habit-reversal and probability learning: rats, birds, and fish. In R. M. Gilbert & N. S. Sutherland (Eds.), Animal discrimination learning. New York: Academic Press, 1969.

Bitterman, M. E., Wodinsky, J., & Candland, D. K. Some comparative psychology. American Journal of Psychology, 1958, 71, 94-110.

Bullock, D. H., & Bitterman, M. E. Probability matching in the pigeon. American Journal of Psychology, 1962, 75, 634-639.

Craighead, J. J., & Craighead, F. C. Hawks, owls, and wildlife. New York: Dover Publications, Inc., 1956.

Eisenberg, J. K., & Leyhausen, P. The phylogenesis of predatory behavior in mammals. Zeitschrift fur Tierpsychologie, 1972, 30, 59-93.

Fitch, H. S., Swenson, F., & Tillotson, D. E. Behavior and food habits of the red-tailed hawk. Condor, 1946, 48, 205-237.

Graf, V., Bullock, D. H., & Bitterman, M. E. Further experiments on probability-matching in the pigeon. Journal of the Experimental Analysis of Behavior, 1964, 7, 151-157.

Herrnstein, R. J. Relative and absolute strength of response as a function of frequency of reinforcement. Journal of the Experimental Analysis of Behavior, 1961, 4, 267-272.

Holling, C. S. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist, 1959, 91, 293-320.

Holling, C. S. The functional response of predators to prey density. Memoirs of Entomological Society of Canada, 1966, 48, 1-86.

Kaufman, D. W. Shrike prey selection: color or conspicuousness. Auk, 1973, 90, 204-206.

Kaufman, D. W. Differential predation on white and agouti Mus musculus. Auk, 1974a, 91, 145-150.

Kaufman, D. W. Differential predation on active and inactive prey by owl. Auk, 1974b, 91, 172-173.

Leopold, A. Game management. New York: Charles Scribner's Sons, 1933.

Longo, N. Probability learning and habit reversal in the cockroach. American Journal of Psychology, 1964, 77, 29-41.

Mackintosh, N. J. Comparative studies of reversal and probability learning: rats, birds, and fish. In R. M. Gilbert & N. S. Sutherland (Eds.), Animal discrimination learning. New York: Academic Press, 1969.

McInvaille, W. B., & Keith, W. B. Predator-prey relations and breeding biology of the great horned owl and red-tailed hawk in central Alberta. Canadian Field Naturalist, 1974, 88, 1-20.

Meyer, D. R. The effects of differential probabilities of reinforcement on discrimination learning by monkeys. Journal of Comparative and Physiological Psychology, 1960, 53, 173-175.

Miller, H. L., & Loveland, D. H. Matching when the number of response alternatives is large. Animal Learning and Behavior, 1974, 2, 106-110.

Mueller, H. C. Factors influencing prey selection in the American Kestrel. Auk, 1974, 91, 705-721.

Mueller, H. C. Hawk select odd prey. Science, 1975, 188, 953-954.

Murdoch, W. W. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs, 1969, 39, 335-354.

Murdoch, W. W., & Marks, R. J. Predation by coccinellid beetles: experiments on switching. Ecology, 1973, 54, 160-167.

Pliskoff, S. S., & Brown, T. G. Matching with a trio of concurrent variable-interval schedules of reinforcement. Journal of the Experimental Analysis of Behavior, 1976, 25, 69-73.

Royama, T. Factors influencing the hunting behavior and selection of food by the great tit. Journal of Animal Ecology, 1970, 39, 619-658.

Ruggiero, L. F. The influence of movement, pelage color, and morphology on prey selection by kestrels with emphasis on interaction. Unpublished doctoral dissertation, Utah State University, 1975.

Smith, J. P., & Dawkins, R. The hunting behavior of individual great tits in relation to spatial variations of their food density. Animal Behavior, 1971, 19, 695-706.

Snyder, R. L. Some prey preference factors for a red-tailed hawk. Auk, 1975, 92, 547-552.

Solomon, M. E. The natural control of animal populations. Journal of Animal Ecology, 1949, 18, 1-35.

Sutherland, N. S., & Mackintosh, N. J. Mechanisms of animal discrimination learning. New York: Academic Press, 1971.

Tinbergen, L. The natural control of insects in pinewoods: 1. Factors influencing the intensity of predation by songbirds. Archives Neerlandaises De Zoologie, 1960, 13, 265-343.

Wilson, W. A. Two-choice behavior of monkeys. Journal of Experimental Psychology, 1960, 59, 207-208.

APPENDIX

Table 3

A Summary of Number of Correct First Responses and Reward Following Data from all Three Experiments for the Hawk and Owl

Experiment	Reward Following	Percent of Total	Correct First Response	Percent of Total
Hawk				
I	10	33.3	10	33.3
II	15	50.0	14	46.67
III	9	30.0	11	36.67
Owl				
I	17	56.67	15	50.0
II	9	30.0	13	43.33
III	14	46.67	14	46.67

Table 4

Raw Data for the Owl for Experiments I, II, and III

Trial	Experiment I		Experiment II		Experiment III	
	Correct Location	First Response	Correct Location	First Response	Correct Location	First Response
1	3	3	2	3	3	2
2	1	1	3	1	1	1
3	2	1	2	2	2	3
4	1	1	3	3	1	1
5	1	1	3	2	1	1
6	2	1	1	2	2	2
7	1	1	2	2	1	2
8	1	1	3	2	1	1
9	1	1	3	3	1	2
10	2	1	3	2	2	2
11	3	1	2	3	3	2
12	1	2	3	1	1	1
13	2	1	2	3	2	1
14	1	2	3	3	1	3
15	1	3	3	1	1	1

Table 2

Data from all Three Experiments for the Hawk and Owl

Box	Probability of Reinforcement	Hawk		Owl	
		Number of First Responses	Percent of Total	Number of First Responses	Percent of Total
Experiment I					
1	.60	6	20	22	73.33
2	.30	20	66.67	5	16.67
3	.10	4	13.33	3	10.0
Experiment II					
1	.10	3	10.0	4	13.33
2	.30	5	16.67	12	40.0
3	.60	22	73.33	14	46.67
Experiment III					
1	.60	16	53.33	17	56.67
2	.30	6	20.0	9	30.0
3	.10	8	26.67	4	13.33

Table 4

Continued

Trial	Experiment I		Experiment II		Experiment III	
	Correct Location	First Response	Correct Location	First Response	Correct Location	First Response
16	2	1	1	2	2	1
17	1	2	2	3	1	3
18	1	1	3	3	1	1
19	1	1	3	2	1	2
20	2	3	3	3	2	1
21	3	1	2	3	3	3
22	1	1	3	3	1	1
23	2	1	2	2	2	1
24	1	2	3	1	1	1
25	1	1	3	3	1	2
26	2	2	1	2	2	1
27	1	1	2	2	1	1
28	1	1	3	3	1	2
29	1	1	3	3	1	1
30	2	1	3	2	2	1

Table 5

Raw Data for the Hawk for Experiments I, II, and III

Trial	Experiment I		Experiment II		Experiment III	
	Correct Location	First Response	Correct Location	First Response	Correct Location	First Response
1	3	2	2	1	3	1
2	1	2	3	3	1	3
3	2	2	2	1	2	2
4	1	2	3	2	1	1
5	1	1	3	3	1	3
6	2	1	1	3	2	2
7	1	2	2	3	1	3
8	1	2	3	3	1	3
9	1	2	3	2	1	2
10	2	2	3	3	2	2
11	3	2	2	3	3	1
12	1	1	3	3	1	1
13	2	2	2	3	2	3
14	1	2	3	3	1	3
15	1	2	3	3	1	1

Table 5

Continued

Trial	Experiment I		Experiment II		Experiment III	
	Correct Location	First Response	Correct Location	First Response	Correct Location	First Response
16	2	3	1	3	2	1
17	1	2	2	3	1	1
18	1	1	3	3	1	2
19	1	3	3	3	1	3
20	2	2	3	3	2	1
21	3	1	2	2	3	1
22	1	2	3	3	1	1
23	2	3	2	3	2	1
24	1	1	3	1	1	3
25	1	3	3	3	1	2
26	2	2	1	3	2	1
27	1	2	2	3	1	1
28	1	2	3	2	1	1
29	1	2	3	2	1	1
30	2	2	3	3	2	1

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