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Allocation of behavior by Northern blue jays in response to prey density changes in two foraging areas.

Jerrilynn Peters
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THE ALLOCATION OF BEHAVIOR BY NORTHERN BLUE JAYS IN RESPONSE TO PREY DENSITY CHANGES IN TWO FORAGING AREAS

A Thesis Presented
By
JERRILYNN PETERS

Submitted to the Graduate School of the University of Massachusetts in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

February 1982

Psychology
THE ALLOCATION OF BEHAVIOR BY NORTHERN BLUE JAYS IN RESPONSE TO PREY DENSITY CHANGES IN TWO FORAGING AREAS

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JERRILYNN PETERS

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Blue Jays in Response to Prey
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Jerrilynn Peters, A.B., Mount Holyoke College
M.S., University of Massachusetts
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The present research investigated the responses of Northern blue jays (*Cyanocitta cristata*) to prey density changes in two foraging areas by using complex operant procedures. Four blue jays previously trained to respond to the presence or absence of catocala moths in photographs were presented with sequences of slides which modelled constant and depleting density prey populations.

In the constant density experiment it was found that the jays were responsive to small density differences. The smaller the differences in density between the two areas, the longer it took the jays to adjust their behavior. These data suggest that this technique provides a sensitive way of measuring the preferences of jays for prey which vary along different dimensions.
In the depleting density experiment it was found that the jays did respond to prey depletion and that the jays appear to use a hunting by expectation rule. These data suggest that the rule a predator uses depends on the distribution of prey.
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CHAPTER I
INTRODUCTION

Variation in the spatial distribution and density of prey constitutes an important problem for predators. Since prey populations differ in their distributions (e.g., Odum, 1971; Taylor, 1961) predators would be most efficient if they could adjust their foraging behavior in response to various types of prey distributions (Kamil, 1978). Because of this, behavioral ecologists have become increasingly interested in the effects of learned behavior on foraging efficiency.

Profitability

A large amount of research has been conducted in the analysis of predator-prey interactions and the response of predators to changes in the density of prey populations. In order to exploit a given prey population, predators must concentrate their search in areas containing prey as compared to areas containing little or no prey, even though such areas may be similar in other aspects. Field data (Goss-Custard, 1970; 1977; O'Connor & Brown, 1977) suggest that predators respond to local variations in prey density by aggregating in areas where
the prey density is greatest.

On the basis of field data, Royama (1970) hypothesized that patch selection accounts for the concentration of searching behavior. He studied the hunting behavior of the great tit (Parus major) in mixed woods near Oxford, England, by measuring the frequency of various species of prey in the diet. Once each species of prey had been identified and the food plants from which they had been collected were located, one knew in what patch or area the tits found each prey item. From the high frequency of certain prey species in the diet, it could be concluded that the tits concentrated their hunting almost entirely on oak trees, searching the trunks but not the foliage. This exploitation of particular types of patches or niches led Royama to suggest that a predator tries to maximize its hunting efficiency by sampling the food available in different parts of its habitat and then spending most time where its success rate is high.

Evidence from several studies support Royama's suggestion. Smith & Dawkins (1971) found that a predator would spend a disproportionately large amount of foraging effort in the most profitable of several areas when offered a simultaneous choice. In these experiments, the great tits apparently did not discriminate between the various lower-density areas, although the density in each
area was different. Subsequent work in a similar, but slightly more complex laboratory environment has shown that great tits do learn to discriminate between lower density areas. In these experiments Smith and Sweatman (1974) set up six separate foraging areas or patches in a large aviary. Each patch consisted of 256 small holes covered with aluminum foil, under which a mealworm might be concealed. Great tits, which had learned to uncap the holes in order to find mealworms, were allowed to forage within the aviary.

In the experiment each patch was designated as a 0, 4, 8, 16, or 20 mealworm density area. Under these constant density conditions all six tits rapidly learned to concentrate their foraging behavior in the high density patches. Thus, tits were better than random in their choice from the six prey densities offered. Although most foraging occurred in the high density patches, three tits continued to visit the 0 patch throughout the 30 days of the experiment. This behavior appears inefficient, since it never resulted in prey and it certainly did not maximize the rate of obtaining prey. However, poor foraging areas may improve and this behavior might increase the sensitivity of the birds to any such changes.

In a second experiment the spatial distribution of prey was changed. The number of mealworms in the 0 den-
sity patch was gradually increased to 20 while the number of mealworms in the 20 patch was gradually decreased to 0. Two of the three "inefficient" tits learned to utilize the new high density patch, while none of the three "efficient" tits learned to utilize it even after 22 sessions. Thus, an inefficient behavior in the short run was quite efficient in the long run.

While this clearly demonstrates the adaptiveness of sampling, another approach to the problem is an optimality one since profitability could easily be re-defined as food intake per unit foraging time.

**Optimization Models**

In general, optimization models ask how the predator should behave in order to maximize its foraging efficiency (for reviews see Krebs, 1973; 1978; Pyke, Pulliam, & Charnov, 1979). The essence of the optimal foraging approach is the idea that individual predators who are more efficient at capturing prey will have greater fitness than those who are less proficient. Ultimately, fitness depends on genotype contribution to future generations, but in the models optimization is usually considered in terms of maximizing food intake per unit foraging time (MacArthur & Pianka, 1966; Schoener, 1971).

Optimal foraging models have dealt with various
aspects of predator behavior. They have most extensively dealt with optimal diet (MacArthur & Pianka, 1966; Emlen, 1966; Schoener, 1971; Pulliam, 1974; Werner & Hall, 1974; Estabrook & Dunham, 1976; Hughes, 1979), patch choice (MacArthur & Pianka, 1966), allocation of time to patches (Charnov, 1976), and pattern of movement (Cody, 1971; Pyke, 1978). One of the limitations of existing models is that they deal with steady state behavior in stable environments in which the predator behaves as if it has estimated the availability of different prey types or patches. Indeed, as several authors have pointed out (Oster & Heinrich, 1976; Oaten, 1977; Krebs, 1978; Green, 1980; McNamara & Houston, 1980) this is an unrealistic feature of the models (but see recent models by Hughes, 1979; McNair, 1980; Ollason, 1980). In a changing environment predators are faced with the problem of sampling in order to determine the relative availability of different food types and the profitability of different patches.

In order to investigate the problem of sampling Krebs, Kacelnik, and Taylor (1978) designed a laboratory situation. They placed two disk feeders within an aviary at which great tits could obtain rewards by hopping on a perch located in front of either feeder. Hopping was rewarded on a variable ratio schedule, and during experi-
mental sessions one of the feeders required fewer hops per reward. The values of the percentage reward rates used at the two feeders were 50:0, 40:10, 35:15, and 30:20.

The two armed bandit model which they tested views the behavior of the birds as consisting of two states: sampling and exploitation. During sampling the birds should respond equally often at each feeder. Once sufficient information has been acquired to determine which feeder is better, the bird should stop sampling and should exploit the better feeder. The model predicted that the birds should complete sampling sooner when the differences between the reward rate are large than when the differences are small.

Using the number of hops the bird made before selecting the better feeder as their measure, Krebs, Kacelnik, and Taylor found that the birds do indeed spend less effort in sampling the two feeders as the differences in reward rates between them increased. Although the birds' behavior supports the prediction of the two armed bandit model, there are no data presented on the patterning of hops between the two feeders or on the event(s) preceding switching from one feeder to the other. Such data would be important in determining whether or not the change from sampling to exploitation was learned in an all-or-none manner as implied by the model and what rules the birds use in making their decisions.
Present Study

The present experiments were designed to look at the question of how a predator exploits an environment in which food was patchily distributed. The predator was faced with several decisions concerned with the efficient exploitation of a patchy environment. The first decision arises from the fact that foraging areas are unlikely to be of equal worth, and the efficient predator must choose areas of high profitability (MacArthur & Pianka, 1966; Royama, 1970; Tullock, 1971). The second decision confronting the predator was at what point to leave one area and go to another. The efficient predator must estimate when it is no longer worthwhile to continue foraging in the current area. A number of solutions have been proposed for this problem and these can be broadly classified into three types: 1) number expectation (e.g., Gibb, 1962) - the predator should leave each area after a certain number of prey have been found; 2) time expectation (e.g., Krebs, 1973) - the predator should leave the area after a certain amount of time has been spent there; 3) rate expectation (e.g., Charnov, 1973) - the predator should leave the area when the rate of prey capture falls to a critical threshold level.

Since I hypothesize that both the number of prey available and the spatial distribution of these prey
determine which strategy is optimal, I have investigated these variables in two separate experiments. The first experiment investigated the response of the Northern bluejay to prey density changes in two constant density foraging areas, while the second experiment investigated the response of the Northern bluejay to a change in the spatial distribution of prey in one nondepleting foraging area and one depleting foraging area.
CHAPTER II

METHOD-GENERAL

Subjects

The subjects were 4 Northern blue jays (Cyanocitta cristata) obtained locally in the Amherst, Massachusetts area when 10-14 days old, and hand-raised in the laboratory. All subjects had prior experience in detection of C. relictta and C. resecta. The subjects were maintained at 80% ad lib. weight during the course of the experiment by controlled daily feeding.

Apparatus

The apparatus consisted of an operant conditioning chamber and automatic programming equipment interfaced with a Lehigh Valley Electronics INTERACT system. The inside dimensions of the chamber were 34.0 cm. x 30.0 cm. x 35.5 cm. A food magazine was located centrally on one wall, and was illuminated whenever food was delivered. Two large rectangular stimulus keys measuring 11.5 cm. x 7.5 cm. were also located on this wall. Each key was mounted 12.5 cm. above the floor—one 0.5 cm. to the left of the feeder and the other 0.5 cm. to the right of the feeder. A small, round pecking key 2.5 cm. in diameter
was mounted 3.1 cm. below the left corner of the left stimulus key and another small, round pecking key 2.5 cm. in diameter was mounted 3.1 cm. below the right corner of the right stimulus key.

A programmable Kodak Carousel projector which projects slides onto the key was located behind each large, rectangular stimulus key. An IEE multiple stimulus projector which projected chromatic and geometric stimuli was located behind each small, round key.

Reinforcement consisted of halves of mealworms (Tenebrio larvae) which were delivered into the magazine by a Davis Universal feeder (Model UF-100) located on top of the chamber. A wooden perch was located 9.0 cm. in front of the intelligence panel, 5.0 cm. above the floor, so the subject's eye level was approximately at the midpoint of the rectangular stimulus key. White noise was delivered through a speaker mounted behind the intelligence panel, and a ventilating fan at the rear also provided masking noise. A houselight was mounted above the feeder opening and was illuminated throughout all experimental sessions.

All stimulus presentations, contingencies, and data recording were controlled by a Lehigh Valley Electronics INTERACT system located in an adjacent room.

Two sets of stimulus slides were used: one set
containing the species *C. relictia* and the other set containing *C. retecta*. Both sets were prepared in the laboratory by pinning a dead moth into position and taking a picture of the scene, then removing the moth and taking several more pictures. All sets were taken at a subject-to-camera distance of 1.4 m. Each slide consisted of two upright, artificial gray-colored logs against a white background. In each slide set the moth appeared equally often on each log and in each vertical third of a log.

**General Procedure**

Figure 1 presents a flow chart of the response requirements used to simulate the foraging situation. The jays were introduced into the chamber with the houselight on and the response keys off. Each trial began with the illumination of both start keys. (The left with a white horizontal line and the right with a white vertical line.) When the jay pecked one start key, the other start key was turned off and made inoperative for the remainder of the trial. This first peck also initiated a signalled 5 second travel time interval on the start key. On completion of the travel time interval the start key was illuminated with a yellow chromatic stimulus. The next peck on the start key caused a slide to be projected onto the appropriate stimulus key and a red chromatic stimulus to
Figure 1. Flow diagram depicting events occurring during each trial.
Fig. 1.
be displayed on the small round key, which now functioned as an advance key. This search stage could be terminated by either of two responses: 1) a peck on the advance key or 2) a peck on the stimulus key.

If the jay pecked the advance key once, then both the advance key and the stimulus key were turned off and the trial ended. There was a 2 second intertrial interval during which the slide projector advanced, and then the next trial began with the illumination of both start keys.

If the jay pecked the stimulus key once, then the red stimulus on the advance key was turned off and the advance key became inoperative while the stimulus key remained unchanged. This first peck also initiated a 20 second handling time interval on the stimulus key. The first peck after the completion of this interval turned off the stimulus key. Then, a mealworm was delivered if there had been a moth in the slide. No mealworm was delivered if there had been no moth in the slide. Following either event the next trial began with the illumination of both start keys after a 2 second intertrial interval during which the slide projector advanced.

Pretraining. Blue jays who were experienced in using an apparatus with one set of keys were trained to use the apparatus with two sets of keys. The training sessions consisted of forced choice trials such that the probabi-
lity of left key and right key trails each equalled 0.5. At the beginning of a forced choice trial only one start key was illuminated and the other remained inoperative. Once the jay pecked the illuminated start key the trial proceeded as previously described. Training continued until the jay responded with an average latency of 5 seconds or less, on each start key.
CHAPTER III

EXPERIMENT I

In nature the jay has many areas in which to forage. These areas may contain patches differing in the number of prey available. The simplest choice a predator could face is between two areas of different prey density with no depletion or other changes in prey quality over time. The optimal solution for such a problem is trivial: if a predator knows the sign of the difference in prey availability between the two areas, then the predator should expend all its effort foraging in the most profitable area (since foraging in the less profitable area can only reduce the rate of food intake). The two armed bandit model predicts that the optimal solution (exploitation) should occur sooner as the difference in reward probabilities between the foraging areas becomes larger. Krebs, Kacelnik, and Taylor (1978) tested this prediction by allowing great tits to forage in an aviary containing two feeding disks. Tits could obtain food from the disks by completing a variable number of hops. The number of hops at each disk was recorded. It was found that the tits made fewer hops to exploitation as the difference in reward probabilities between disks increased.
Experiment I simulated two constant density areas as in Krebs, Kacelnik, and Taylor (1978). Data were collected to determine how rapidly the jays reached exploitation and how the jays modified their patterning of movements.

Method

Each jay was given 45 minute sessions on an equal density baseline condition in which the percentage reward rate was 25% on each key (25:25) until the jay chose each set of keys equally often. Then the proportion of positives on each key was varied. Three differential density conditions were used--40:10, 35:15, 30:20.

Each jay was given sessions on each density condition until the jay chose one key 27 times in 30 consecutive trials. In the next session the jay was returned to the 25:25 baseline condition. The jay remained on the baseline until the jay was again choosing the two keys equally often (+ 5%). Then another density condition was presented. The higher density was always assigned to the key chosen less often at the end of the baseline. Each jay received each density condition three times (see Table 1).
<table>
<thead>
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<th>First</th>
<th>Second</th>
<th>Third</th>
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</tr>
<tr>
<td>Block 2</td>
<td>40:10</td>
<td>35:15</td>
<td>30:20</td>
</tr>
<tr>
<td>Block 3</td>
<td>30:20</td>
<td>35:15</td>
<td>40:10</td>
</tr>
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</table>
Results

Each of the panels of Figure 2 present individual data on the choice of foraging area during consecutive sessions. Beginning at the top and continuing downward each point represents the choice made on Trial 1, Trial 2, and so on. When the left foraging area was chosen on any trial the point for that trial was entered under the column labelled L; when the right foraging area was chosen on any trial the point was entered under the column labelled R. From the left most panels it can be seen that each bird shows a distinctive and recurring pattern of choices during equal density baseline condition. A bird spent a typical number of trials foraging in one area before switching to the other area where an equal number of trials was then spent foraging. By looking at the next panels it can be seen that birds continued this pattern of alternating equal length foraging bouts when the differential density condition 40:10 was first begun. Only gradually did the number of trials spent per foraging bout in the 40 area increase and the number of trials spent per foraging bout in the 10 area decrease. When criterion behavior was reached each bird spent a long foraging bout in the 40 area then switched to the 10 area for one trial and immediately switched back to the 40 area for another long foraging bout. The switches to the 10 area occurred
Figure 2. Trial by trial choice of foraging area by each jay on 25:25 and 40:10 conditions.
following trials on which prey were obtained, while switches back to the 40 area occurred regardless of whether or not a prey had been obtained (see Table 2).

On each differential density condition the pattern of choices followed this same overall process of change. The rate at which the pattern changed varied as a function of the differences in density between the two foraging areas. The smaller the differences in density between areas, the longer it took the birds to adjust their behavior (see Figure 3). Although there was considerable variation between jays in the number of trials required to meet criterion, each jay was remarkably invariant in how long it took to adjust to each density condition across replications of the experiment.

The number of prey obtained during criterion sessions was found to vary as a function of density (see Table 3). The higher the density in the more profitable area, the greater the number of prey the jays obtained; and, the less time the jays required to select foraging areas (see Table 4).

Discussion

The results of this experiment provide information on the manner in which blue jays adjust their behavior when offered a choice between two foraging areas con-
TABLE 2

PERCENTAGE OF SWITCHES DURING CRITERION SESSIONS ON WHICH EACH JAY CHANGED FORAGING AREAS IMMEDIATELY AFTER OBTAINING A PREY

<table>
<thead>
<tr>
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<th>35 : 15</th>
<th>30 : 20</th>
<th>25 : 25</th>
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<tr>
<td>Jay 20</td>
<td>93</td>
<td>13</td>
<td>91</td>
<td>19</td>
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<tr>
<td>Jay 31</td>
<td>89</td>
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<td>85</td>
<td>17</td>
</tr>
<tr>
<td>Jay 34</td>
<td>96</td>
<td>25</td>
<td>96</td>
<td>12</td>
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</table>
Figure 3. Number of trials to criterion for each jay in each replication of each density condition.
## TABLE 3

**AVERAGE NUMBER OF PREY OBTAINED BY EACH JAY DURING CRITERION SESSIONS AT EACH DENSITY CONDITION**

<table>
<thead>
<tr>
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<th>30:20</th>
<th>25:25</th>
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<tr>
<td>Jay 31</td>
<td>26</td>
<td>24</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>Jay 34</td>
<td>29</td>
<td>26</td>
<td>23</td>
<td>21</td>
</tr>
</tbody>
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## TABLE 4

AVERAGE NUMBER OF SECONDS FOR EACH JAY TO SELECT A FORAGING AREA DURING CRITERION SESSIONS

<table>
<thead>
<tr>
<th></th>
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<th>35 : 15</th>
<th>30 : 20</th>
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</tr>
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<td>Jay 20</td>
<td>2.2</td>
<td>2.9</td>
<td>3.5</td>
<td>3.4</td>
</tr>
<tr>
<td>Jay 31</td>
<td>1.5</td>
<td>2.2</td>
<td>2.6</td>
<td>2.5</td>
</tr>
<tr>
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<td>1.5</td>
<td>1.8</td>
<td>1.8</td>
<td>3.1</td>
</tr>
</tbody>
</table>
taining different prey densities: 1) the jays prefer to forage in the area of higher prey density, other things being equal; 2) the jays develop this preference over time, requiring more time the smaller the density differences between the areas.

The first result is not unexpected. It is already known that various avian predators tend to concentrate their foraging behavior in areas of high prey density (e.g., field studies by Gibb, 1958; Goss-Custard, 1970, 1977; and laboratory experiments by Smith & Dawkin, 1971; Smith & Sweatman, 1974; Zach & Falls, 1976; Krebs, Kacelnik, & Taylor, 1978). The second result is more interesting since it implies that jays must learn about the difference in density between the two areas. Although these data are not reported in Krebs, Kacelnik, and Taylor (1978) or in Kacelnik (1979), Krebs (personal communication) reports that many of the birds in these experiments switched from sampling to exploitation gradually.

The finding that exploitation is acquired gradually is important. This contradicts many optimal foraging models which predict a discontinuous function (e.g. Emlen & Emlen, 1966; MacArthur & Pianka, 1966; Schoener, 1971). The failure to find such an all-or-none function has been reported in numerous studies on prey
selection (Willson, 1971; Reichman, 1977; Krebs, Ericksen, Webber & Charnov, 1977; Kaufman & Collier, 1981). This result has usually been explained in terms of failure to discriminate or employment of an adaptive strategy which enables the animal to monitor a changing environment (e.g., Emlen & Emlen, 1975).

Thus far, ecologists have collected little information (see above) on the ability of individual predators to discriminate between profitable and unprofitable foraging areas. And, one ecologist (Pulliam, personal communication) reports that acquisition data are often not collected at all. Much more attention needs to be given to the problem of how information required to forage in an efficient manner is acquired.

The results of this experiment do provide information on the events which precede switching during sampling and exploitation. Unlike the experiment of Kacelnik (see Kacelnik, 1979, p. 105; Krebs, Kacelnik, & Taylor, 1978, p. 31) which resulted in tits tending to switch after a run of bad luck, the present experiment resulted in jays tending to switch after finding a prey. Although there were many differences in procedure (e.g., tits were required to make one hop to complete a trial; jays were required to complete several response intervals each trial), one difference which seems especially impor-
tant was the baseline conditions used between experimental conditions.

In Kacelnik's experiment both reward rates were 7.5% during baseline conditions. The sum of the two reward rates is considerably lower than the sum of the two reward rates during experimental conditions (i.e., 15 vs 50). The low rates were used because they were found to be effective in neutralizing preference (Krebs, Kacelnik, & Taylor, 1978, p. 29). Apparently, tits did not respond equally often at the two feeders when the reward rates were similar to those used in the experimental conditions (Kacelnik, 1979, p. 95). This suggests some persistence in staying with the "most" profitable feeder unless the change in reward rate was large. Such persistence in remaining at a feeding area was also reported by Smith & Sweatman (1974) who used tits in their experiments on profitability. These results imply that tits might bring a different sampling strategy into an experiment than jays do or that the tits learn a different sampling strategy during low density neutralization than jays do during a higher density baseline.

When exposed to neutralization, tits experienced only a 7.5% reward rate, so many responses were unrewarded. Given the tit now has long runs of unrewarded responses, this sequence of events could be a statistical
fluctuation in the reward distribution but it might be that the reward distribution has changed and the response is no longer effective. Thus, the problem becomes one of how long to persist when responses no longer yield rewards. The tits must decide how many unrewarded responses should be made if energetic returns are to be maximized. The optimal solution for this sort of problem involves persisting for more trials in the face of failure when probability of reward is low than when it is high (McNamara & Houston, 1980).

In the present experiment the jays were very unlikely to be faced with a long run of unrewarded responses during baseline conditions since reward rates were 25%. Given all conditions that summed to 50%, the problem is not one of persistence. It is more likely to be a problem of deciding if the reward rates differ from 25:25. It would appear that the jays' strategy should be to forage in one area until reward is obtained and then forage in the other area until reward is obtained, since each sequence of trials serves the dual purpose in giving a possible reward and providing information on the true value of reward rate. The optimal policy is truly sequential taking into account the outcome of previous trials.

Given the different problems the tits and jays were faced with during baseline, it is likely that dif-
Different strategies used during sampling were those acquired during baseline.
CHAPTER IV
EXPERIMENT II

Often the quality of a foraging area changes as a result of the activity of the predator. The predator may significantly deplete the area it is foraging in. This could be the direct result of exploitation (e.g., eating the prey) or as a result of the predator's general activity (e.g., prey leaving the area). The consequence of depletion is that the expected rate of food intake within the foraging area declines as a function of the time spent there (Charnov, 1976). By staying too long, the predator achieves a lower expected rate of intake than could be achieved by moving to another area. In order to maximize the expected rate of intake the predator should move to another area whenever the expected rate of intake in the current area drops below the average across the environment.

Since there are few experimental studies of prey depletion (e.g., Krebs, Ryan, & Charnov, 1974), experiment II was a first attempt to determine experimentally if a predator is sensitive to the depletion of prey within a foraging area. The blue jays were faced with two foraging areas: one depleting density area, and one constant
density area whose density approximated the average value of the depleting area.

Method

Each jay was given sessions on an equal density baseline condition (30:30) until the jay chose each set of keys equally often. Then the prey density available on the left set of keys was changed to simulate a depleting area. This was done by having each block of 10 consecutive slides contain fewer and fewer moths: 6 out of the first 10 contained moths, but only 4 out of the next 10, 2 out of the next 10, and 0 out of the next 10. The prey density on the right set of keys remained unchanged in order to simulate a nondepleting area. Each block of 10 consecutive slides contained 3 moths.

Results

Figure 4 presents session by session data on the number of switches made by each jay and on the number of prey that each jay obtained. It can be seen that the number of switches decreased gradually and that individual birds decreased the number of switches at markedly different rates. The data indicate that the jays adjusted their behavior in response to prey depletion in two characteristic ways. Jays 34 and 40 showed a rapid
Figure 4. Session by session data on the number of switches (S) made by each jay and on the number of prey (T=total, D=depleting, ND=nondepleting) that each jay obtained.
decrease in the number of switches made per session and at the same time showed an increase in the number of prey obtained per session. This increase occurred largely because of an increase in the number of prey obtained from the nondepleting area. Jays 20 and 31 showed a higher rate of switching and a greater amount of variability in the number of switches made per session and showed no decrease in the number of switches until the fifteenth and twentieth sessions, respectively. Then, the number of switches decreased gradually over the next five sessions. Over the experiment the total number of prey that these jays obtained fluctuated from session to session but showed little increase. Jay 20 obtained from 17 to 20 prey per session and Jay 31 obtained from 16 to 20 prey per session. The number of prey obtained in the depleting area was approximately 12 prior to the decrease in switching and then dropped to approximately 10. At the same time the number of prey obtained in the nondepleting area increased from approximately 7 to 10.

Over the last five sessions of the experiment when the jays were making only one switch per session their foraging patterns were very similar. All jays began foraging in the depleting area, then moved to the non-depleting area. Before making the switch, individual jays obtained a fairly constant number of prey although
spending a variable number of trials (see Figure 5). The jays required less time to chose foraging areas in these last five sessions than in the first five sessions (see Table 5).

Discussion

The situation in this experiment simulated the resource depression problem described by Charnov, Orians, and Hyatt (1976). The rate at which prey could be obtained in the depleting and nondepleting foraging areas was comparable in the long run (over all the trials in the session) but differed in the short run (from one part of the session to the other) because of the distribution of patches contained prey. Since the data are not confounded by prey preferences, differences in palatability of prey, ease of capture or handling time as in the case of field studies (e.g., Goss-Custard, 1970; O'Connor & Brown, 1977), the results clearly indicate that jays can adjust their foraging pattern in response to prey depletion.

In the field a predator faced with declining prey population has essentially three options: 1) The predator can move elsewhere to hunt for its preferred prey (These movements could be local or long-distanced depending on how far reaching the prey depletion is). 2) The predator can change its diet by turning to some other prey not pre-
Figure 5. Number of prey obtained and number of trials made in the depleting area by each jay before switching.
Fig. 5.
TABLE 5

AVERAGE NUMBER OF SECONDS FOR EACH JAY TO CHOOSE A FORAGING AREA OVER THE FIRST AND LAST FIVE SESSIONS

<table>
<thead>
<tr>
<th></th>
<th>First Five</th>
<th>Last Five</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jay 20</td>
<td>10.9</td>
<td>6.3</td>
</tr>
<tr>
<td>Jay 31</td>
<td>9.5</td>
<td>6.8</td>
</tr>
<tr>
<td>Jay 34</td>
<td>4.9</td>
<td>2.6</td>
</tr>
<tr>
<td>Jay 40</td>
<td>4.1</td>
<td>2.7</td>
</tr>
</tbody>
</table>
viously taken for some reason (e.g., prey is of low palatability or requires greater capture and/or handling effort). 3) The predator could exploit its current prey type more extensively by taking prey it previously ignored for some reason (e.g., small size). In the present experiment only the first option was available. And, the jays did indeed adjust their foraging pattern.

Acquisition data indicate that the jays rapidly learned to begin each session by foraging in the depleting area which was initially of higher density than the non-depleting area. Learning where to search appears to involve both returning to a specific area and remaining in that area after finding prey items (Croze, 1970). Alcock (1973) has experimentally demonstrated that red-winged blackbirds first search locations where food has been found in previous sessions before searching other locations. Croze (1970) has discovered that after finding a bait wild crows altered their searching pattern by concentrating their searching in the area of the find. Such behavior has also been reported for thrushes (Smith, 1972) and for captive ovenbirds (Zach & Falls, 1976).

Whenever faced with a clumped prey population the predator can enhance the likelihood of further captures by remaining in the vicinity of a capture. For the jays the prey distribution in the depleting foraging area was
essentially a clumped distribution. And, given that the clump "ran out" as prey were captured, the jay was faced with deciding when to leave. Two approaches have been taken in modelling such a problem. One is to construct a simplified model of what predators have been observed to do. A notable example is the suggestion by Gibb (1962) that titmice hunting for insect larvae hidden in pine cones learn how many larvae to expect in different localities; and slacken their search when the expected number of larvae have been taken from the cones. The other approach is to assume that the predator is an optimal forager and to derive the optimal strategy. Charnov (1973, 1976) shows that a predator which is searching optimally, in the sense of maximizing its net rate of energy, will leave a patch when the net rate of energy intake in the patch drops to the overall average rate for the habitat.

Data from this experiment do not support a fixed number strategy in the strict sense of taking the same number of prey and leaving immediately after that number has been taken. Once the nth prey had been obtained the jays persisted for an additional trial. If the trial was an unrewarded trial, then the jay switched foraging areas. If the trial was rewarded, then the jay persisted until an unrewarded trial occurred and then switched foraging
areas.

Prior to the present study the only experiment on prey depletion that investigated the type of strategy used was Krebs, Ryan, and Charnov (1974) who studied the black-capped chickadees search for mealworms on artificial pine cones. They found that the giving up time, defined as the interval between the time that last prey was captured and the time the forager left the patch, was nearly constant for all patches despite the fact that the amount of food varied between patches. In low density patches there were 1 to 6 prey and in high density patches there were 3 to 12 prey. In the present experiment the amount of prey in a foraging area was always constant. In this situation it was found that jays appeared to leave the area on the basis of a number expectation. It appears that the amount of variance in the spatial distribution of prey is critically important in determining the optimal strategy (see Green, 1980; and Iwasa, Higashi, & Yamamura, 1981 for mathematical models).

In order to determine the prey distribution, the jay must assess the variability. Green (1980) has mathematically demonstrated that assessment of patch quality is especially important in the case where patches tend to have no prey at all or many prey and that assessment of patch quality does no good when the number of prey varies
very little. If the distribution of successive encounters with food items is hump shaped, as in the case of Gill and Wolf (1977), the encounter process does not behave as a Poisson process; thus, the marginal value theorem (Charnov, 1973; 1976) is an inappropriate model for such cases. Rather than using a continuous variable to model the accumulated food intake, a discrete variable should be used (e.g. Oaten, 1977).
The ultimate biological answer to why animals move about as they do is that the resources necessary for the survival and reproduction of the genotype are not all found at the same place, and that those individuals who are capable of surviving and reproducing in the wild must be capable of getting from one place to another and of apportioning their in various places in accordance with the spatiotemporal distribution of resources and their own biological requirements. The question is, how do they accomplish these feats? How do they manage to come as close as they do to optimal strategies?

Given a predator that searches for prey which are distributed in discrete patches, the problem becomes when to leave one patch and move to another. Charnov (1976) has constructed a model for the patch persistence problem. He assumes that the predator visits many patches and depletes each patch as it forages. The optimal forager should leave each patch when the rate of food intake from the current patch drops to the average rate of food intake across the environment. Oaten (1977) has criticized this model stating that the laws of large numbers which justify
many deterministic models in biology, will not cause the accumulated consequences of the deterministic optimal procedure (based on average information) and the stochastic procedure (based on specific information) to converge. One can expect the two to be different since the uncertainty concerning the true state of nature can be an important factor in the stochastic case. So, the optimal procedure must take account not only of what the state seems to be (e.g., the conditional expected capture rate) but also of what it might seem to be in light of further information (e.g., if there is one more capture).

Initially the predator has no information about the quality of a patch. The major problem here is how to determine the optimal time for leaving the patch by estimating the number of prey remaining given the number already taken. Since searching for prey serves as a census for the number of prey that exists in the patch, when a predator finds a prey its estimate for the number of prey originally present in the patch increases. Nevertheless, the estimate decreases by one after the prey is taken. The balance between these two tendencies changes with the distribution of prey. Recently Iwasa, Higashi, and Yamamura (1981) developed a mathematical model which demonstrates these changes: under a regular distribution (i.e., binomial) the tendency to decrease the
estimate is greater, so the estimate goes down at the moment of capture. When the distribution is contagious (i.e., negative binomial) the tendency to increase is so great that the estimate jumps up each time a capture is made. And, whenever the distribution is random (i.e., Poisson) the two tendencies cancel each other, so the estimate of the remaining prey decreases exponentially with time regardless of the number of prey captured.

Since the functional form of the estimate changes with the distribution of prey, the corresponding strategy changes too. For example, when the distribution is regular the estimate is a function of the number of prey found. Thus, the predator should leave the patch when a fixed number of prey have been found. When the distribution is contagious, the estimate is a function of both the number of prey found and the time interval between successive captures. And, since the typical contagious distribution has many empty patches and a few highly concentrated nonempty patches, the time since last capture is the best estimate of when patch has been depleted. Finally, whenever the distribution is random, the estimate is a function of time only. So, in this case, the optimal strategy is a fixed time strategy.

Such an emphasis on the distribution of prey is especially important in light of the present studies.
Their results indicate that the optimal strategy for leaving a foraging area may vary in the manner suggested by Iwasa, Higashi, and Yamamura (1981). A satisfactory explanation of the different behaviors observed must deal with the spatial distribution of prey items as experienced by the predator being studied and must include a careful account of the individual predators while foraging.

The procedure developed for the present studies provides one technique for investigating a predator's response to prey distributions. The results from the constant density experiment were very orderly. Although there was considerable variation between birds in the length of time it took to reach criterion, there are three very positive features. 1) Each jay was remarkably invariant in terms of how long it took to adjust to each density condition across replications of the experiment. 2) The basic effect reported by Krebs, Kacelnik, and Taylor (1978), and to be expected from the psychological literature on probability matching (e.g., Uhl, 1963), was clearly obtained. The smaller the differences in density between the two areas, the longer it took the jays to adjust their behavior. This result increases our confidence in the validity of the technique. 3) The jays were responsive to small density differences. This suggests that this technique provides a sensitive way of
measuring the preferences of the jays for prey which vary along different dimensions such as crypticity.

The results from the depleting density experiment were also very consistent even though the jays varied in the length of time it took to reach stabilization. The results make two important points. 1) The jays do respond to prey depletion. The fact that the jays adjusted their behavior to short term prey depletion appears to indicate the technique is a sensitive way of measuring responses to changes in the spatial distribution of prey. 2) The jays appear to use a hunting by expectation rule. This result increases my confidence in asserting that the rule the predator uses depends on the distribution of prey. This technique provides excellent control over the presentation of prey distributions and can therefore be used to determine the jays' rules for deciding when to leave a foraging area.
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