CHOICE AND FORAGING

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In Experiment 1, six naive pigeons were trained on a foraging schedule characterized by different states beginning with a search state in which completion of a fixed-interval on a white key led to a choice state. In the choice state the subject could, by appropriate responding on a fixed ratio of three, either accept or reject the schedule of reinforcement that was offered (either a variable-interval five-second or a variable-interval 20-second). If the subject accepted the schedule, it entered a "handling state" in which the appropriate variable-interval schedule was presented. Completion of the variable-interval schedule produced food. The independent variable was the fixed-interval value in the search state, and the dependent variable was the rate of acceptance of the long variable-interval in the choice state. Experiment 2 was identical except that the search state required completion of a variable-interval, instead of a fixed-interval, schedule. The rate of acceptance of the long variable-interval schedule in both experiments was a direct function of the length of the search state, in accordance with both optimality theory and the delay-reduction hypothesis.

Key words: foraging, choice, optimality theory, delay-reduction hypothesis, concurrent-chains schedules, fixed-interval schedules, variable-interval schedules, key peck, pigeons

Animals from protozoans to whales search actively for food. Because each individual has a limited amount of time and energy at its disposal, one would predict that an animal's fitness should be correlated with how profitably its resources are invested. The ultimate goal of the searcher ought to be to maximize net energy gain by collecting more food in less time. Much recent theoretical work in foraging has focused on the idea that natural selection favors the most economic of alternative foraging patterns. The notion of "optimal foraging" has been applied to a number of foraging decisions that a predator may make, such as how and where to feed (Pyke, Pulliam, & Charnov, 1977). The optimal diet should have three properties: (1) as the abundance of preferred food type increases, the number of less preferred food types included will decrease (food specialization); (2) a food type is either completely included in the optimal diet or completely excluded from it—in other words, if a food type is included it should be

eaten whenever encountered, and if excluded it should never be consumed; (3) whether or not a food type should be eaten is independent of the abundance of that food type and depends only on the absolute abundance of the food types of higher rank.

Of these predicted properties of an optimal diet, the ones that have received experimental support have been the first and third (Charnov, 1976; Goss-Custard, 1977; Krebs, Erichsen, Webber, & Charnov, 1977). However, the second, all-or-none rule, has not been supported in several studies (Goss-Custard, 1977; Krebs, Erichsen, Webber, & Charnov, 1977; Lea, 1979). The change of preference appears to be gradual rather than abrupt.

Although most of the foraging studies have been carried out in the natural environment to which animals have adapted, or in laboratory studies that simulate the field situation, there have been successful simulations of foraging using operant conditioning (Collier & Rovee-Collier, 1980). These studies showed that rats became more selective between fixed-ratio schedules of reinforcement as the work required to gain access to the schedule decreased. In other words when the search cost was low, the subjects rejected the high ratio requirement and waited for the low ratio. When the search cost was sufficiently high,

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virtually all opportunities to obtain food were accepted.

In a different set of studies investigating the "matching law," the subject, usually a pigeon, distributes either its responding or its time so as to match the relative rate of reinforcement available on a particular manipulandum (Baum & Rachlin, 1969; Herrnstein, 1961, 1970; Squires & Fantino, 1971). This is very similar to what occurs in a foraging situation. Thus, foraging may be viewed as a natural analogue to time and response matching found in laboratory studies of choice.

In this context we can ask whether optimality theory can predict choice in a conditioning experiment which simulates the foraging situation. Lea (1979) designed a choice situation for pigeons, attempting to mimic the foraging situation (Figure 1). There were basically three states: (1) Search State; (2) Choice State; (3) Handling State. During the Search State, completion of a fixed-interval (FI) on a center key led to the illumination of a colored side key, either red or green. This started the Choice State. A single peck on the colored key (FR 1) initiated the Handling State. This last state led to food according to an FI schedule that had different values correlated with the dif-

ferent colors (either FI 5-sec or FI 20-sec). On the other hand, if in the Choice State three pecks occurred on the white key, or a specified interval elapsed without responses, the side key was turned off without the presentation of reinforcement. Thus, the pigeon could either continue the schedule by pecking the colored side key or reject it and advance to another trial, by not pecking or by pecking the white center key.

One of the parameters Lea varied was the value of the FI during the Search State. This variation could be interpreted as manipulation of overall prey density. The purpose was to show a change in selectivity as prey density varied from low values to high values. The different preys were represented by FI 5-sec and FI 20-sec schedules in the Handling State. Lea found the effect of overall prey density predicted by optimality theory, namely an increase in the acceptance of the less-preferred prey (FI 20-sec) as the value of the FI in the Search State increased. However, this increase did not take the form of a step function. Moreover, the pigeons showed a marked bias toward rejecting the less-preferred prey (long schedule); i.e., the less-preferred prey was rejected at FI values where optimality theory predicted acceptance.

In order to see that Lea's results deviate from optimality theory in an orderly manner, we need to briefly review the correspondence of his procedure to the concurrent-chains procedure and then note some properties of choice in concurrent-chains schedules with FI schedules in the terminal links. In concurrent-chains schedules the organism responds on two concurrently available keys, each of which is illuminated by the stimulus associated with the initial link of one of the chains. Responses on each key occasionally produce the stimulus for the terminal link of the chain on that key. Responses in the presence of either of the mutually exclusive terminal-link stimuli are reinforced with food. The Foraging Schedule used by Lea (1979) may be seen as a chained schedule in which the initial link corresponds to the Search State and the terminal link to the Handling State. Unlike a concurrent-chains schedule, however, there is only one initial link and the choices occur successively. Thus, whereas in concurrent-chains schedules two options are offered simultaneously, in the foraging situation the subject chooses between

Fig. 1. Flowchart of the Foraging Schedule used by Lea (1979). The rectangles indicate the different states of the schedule; the state transition requirements are indicated by the legends. The circles indicate the keys and the letters the corresponding colors (R: red; G: green; W: white).

one option (or prey) offered now and another that may occur later.

Choice in concurrent-chains schedules with variable-interval (VI) schedules in the terminal links has been examined extensively (see Fantino, 1977, for a review). These studies have shown that choice is partly dependent upon the size of the initial links. Thus, Fantino (1969) and Squires and Fantino (1971) showed that with sufficiently long initial links, organisms are almost indifferent between the terminal links and that with sufficiently short initial links, the subject responds exclusively to the key leading to the shorter terminal link. The formulation based on these studies states that choice is determined by the degree of reduction in time to primary reinforcement correlated with entry into one terminal link relative to the degree of reduction correlated with entry into the other terminal link (Fantino, 1969, 1981). This delay-reduction hypothesis predicts the same change in preference for the less-preferred prey as a function of search time as does optimality theory.

Lea's use of FI schedules in the Handling State (terminal links) may account for the bias he found relative to the predictions of optimality theory and the delay-reduction hypothesis toward rejection of the less-preferred schedule. Several studies with concurrent-chains schedules have shown that when the terminal links are FI schedules, the relative choice proportions in the initial links do not match relative delay reduction; instead subjects respond disproportionately on the side leading to the shorter FI schedule (Duncan & Fantino, 1970; Herrnstein, 1964; Killeen, 1970).

EXPERIMENT 1

In order to assess this possibility, the present study examined choice using Lea's procedure (Foraging Schedule), with VI schedules in the Handling State. It was expected that the use of VI schedules might produce results more compatible with optimality theory and with the delay-reduction hypothesis. Also, whereas Lea used a different schedule requirement for accepting (FR 1) and rejecting (FR 3) a specific prey, the present study used the same requirement for both (FR 3). In addition, the number of sessions was increased from only five for each condition to 20 per condition, and the number of reinforcements per session

was 50 instead of 80. The positions of the keys were also different: The position of the colored key remained on the right side, but the position of the white key was left rather than central.

The only variable manipulated was the length of the initial link (Search State). According to the delay-reduction hypothesis, choice is dependent upon the values of the schedules in the initial link. Thus, in this study, acceptance of the less-preferred prey should increase as the value of the initial link (Search State) increases. Moreover, the delay-reduction hypothesis and optimality theory make identical predictions about the point when acceptance of the longer VI should exceed $p = .50$.

METHOD

Subjects

Six adult male White Carneaux pigeons were maintained at approximately 80% of their free-feeding weights. All the subjects were experimentally naive. The birds were fed measured amounts of food after each session to maintain weight levels. Water and grit were available in the home cages.

Apparatus

A cylindrical three-key operant conditioning chamber was used. It measured 36 cm in height and 33 cm in diameter. On one side of the wall the three translucent response keys were mounted 5 cm apart and 24 cm above the floor, each requiring a minimal force of about .13 N to be activated. Keys could be transilluminated with different colors. The right key could be either red or green, the left key could be white. The center key was dark. General chamber illumination was provided by a houselight that was mounted centrally, 32.5 cm above the floor. A solenoid-operated grain hopper was centrally located 10 cm below the keys and could provide 3-sec access to mixed grain. White noise was present. All experimental contingencies and data recording were implemented by a PDP-8E computer, under control of the Systol operant laboratory software developed in our laboratory.

Procedure

Pretraining. Since the pigeons were naive subjects, they did not peck the keys when first introduced into the apparatus. Thus, they

were exposed to several autoshaping sessions (Brown & Jenkins, 1968) and to some sessions during which the Foraging Schedule (described below) was used, with all the parameters set to minimal values. Moreover, the alternatives correlated with different colors during the Handling State in the program were the same (VI 5-sec). This pretraining lasted until each subject was pecking both keys reliably (an average of 12 sessions).

Foraging Schedule. In the procedure depicted in Figure 2, the session started with onset of the houselight and the white left key light. This initiated the Search State. After an FI schedule of reinforcement of "x" sec, the Choice State was initiated. During this state both keys were illuminated, the left key with white and the right key with either red or green. The color on the right key was selected by a computer program ($p = .5$). If the pigeon completed an FR 3 on the right key (colored), the Handling State was initiated. If, however, the pigeon either stopped responding for 30 sec or completed an FR 3 on the left key (white), the Search State was reinitiated. During the Handling State, the left key was turned off and a VI schedule was initiated. The duration of the VI schedule depended on

the alternative chosen (either VI 5-sec or VI 20-sec). Completion of this VI schedule was followed by 3-sec access to food during which neither key was lit. After reinforcement, the program was reinstated.

For Birds B55, B57, and B67 the shorter Handling State (VI 5-sec) was associated with red light on the right key and the longer one with green; for Birds B58, B59, and B68 the colors were reversed.

Sessions consisted of 50 entries to food or 55 minutes of elapsed time, whichever came first. Each bird had one session per day, six days per week.

The independent variable was the duration of the FI during the Search State. The FI values employed were: 4 sec, 10 sec, 25 sec, and 63 sec. Each of these FI values defined a condition. Each condition was maintained for 20 sessions. The order in which these conditions were studied was considered as a second factor in the design, so that three birds started with the lowest FI value (FI 4-sec) and the other three at the highest value (FI 63-sec).

Preference was assessed in terms of the probability of accepting the longer VI, whenever it was offered, over the last five sessions in each condition.

RESULTS

The preference obtained for the long VI (VI 20-sec) varied as a function of the FI value used in the Search State. This preference increased as the FI duration increased. The data in Figure 3 represent the mean values of the probability of accepting the longer VI over the last five sessions in each condition for each of the six birds. This measure of preference was obtained by dividing the number of times the subject accepted the long VI (VI 20-sec) by the number of times this alternative was presented during the Choice State.

The measure of preference for the short VI (VI 5-sec) is not included as it was always equal to 1.0 for all birds in all conditions. This means that whenever the VI 5-sec was offered during the Choice State, the subject accepted it.

Considering the six subjects, during the schedule with FI 4-sec in the Search State, the average probability of accepting the long VI was .19. When the FI value was increased to FI 10-sec, acceptance of the VI 20-sec increased to .64. With FI 25-sec, this preference was .94

Fig. 2. Flowchart of the Foraging Schedule used in the present experiment. The rectangles indicate the different states of the schedule; the state transition requirements are indicated by the legends. The circles indicate the keys and the letters the corresponding colors (R: red; G: green; W: white).

Fig. 3. Probability of accepting the longer VI for each of the six birds as a function of the FI value used in the Search State. The solid line represents the mean. Note the logarithmic scale on the abscissa.

and with FI 63-sec, the VI 20-sec schedule was always accepted.

An Analysis of Variance showed a significant effect, $F(3,12) = 68.95$ $p < .001$, for the length of the FI in the Search State. There was no significant effect for order nor for the interaction of these variables. Thus, choice was mainly dependent on the length of the Search State.

DISCUSSION

The present results clearly show that preference for the less-preferred prey (VI 20-sec) increased systematically as the FI duration in the Search State increased. These results are in accordance with the food specialization predicted by optimality theory, although the increase in preference did not take the form of a step function (from zero to one) as predicted by optimality theory. According to optimality theory the switch from zero to one should occur at FI 7.5-sec, since for this search time the expected time to reinforcement is equal whether the subject accepts the long prey or rejects it. The delay-reduction hypothesis also predicts a switch in preference when the Search State is equal to 7.5 sec. At this duration, the average overall delay to primary reinforcement (T) from the onset of the Search State equals 20 sec. This means that at this point the long VI (VI 20-sec) represents neither a decrease nor an increase in average delay to reinforcement. With shorter Search States T is less than 20 sec and the VI 20-sec outcome should be generally rejected. With longer Search States T is more

than 20 sec and the VI 20-sec outcome should be accepted. Only with a Search time of 7.5 sec should the subject be neutral toward the VI 20-sec outcome (i.e., accept it about half of the time). We can interpolate from Figure 3 to estimate where the mean probability of acceptance crossed the .5 value on the ordinate. This estimate gives a value of exactly 7.5 sec.

EXPERIMENT 2

This experiment assessed the effects of having VI schedules during the Search State. This change made the foraging schedule more similar to the concurrent-chains procedures which have used VIs both in the initial and terminal links. Would the predictions of both optimality theory and the delay-reduction hypothesis continue to be confirmed with VIs in the Search State?

METHOD

Subjects

Six male White Carneaux pigeons were maintained at 80% of their free-feeding weights. All subjects had served in Experiment 1.

Apparatus

The apparatus was the same as that used in Experiment 1.

Procedure

The basic procedure was the same as that used in Experiment 1 except for the use of VI instead of FI schedules during the Search State. The VI values employed were: 4 sec, 10 sec, and 25 sec. Each of these values defined a condition. Each condition was maintained for 20 sessions. All six birds started at the lowest value (VI 4-sec).

The measure of preference was the probability of accepting the longer VI, whenever it was offered, over the last five sessions in each condition.

RESULTS

The preference for the long VI (VI 20-sec) varied as a function of the VI value used in the Search State. This preference increased as the duration of the VI increased. The data in Figure 4 represent the mean values of the probability of accepting the longer VI over the last five sessions in each condition for all

Fig. 4. Probability of accepting the longer VI for each of the six birds as a function of the VI value used in the Search State. The solid line represents the mean. Note the logarithmic scale on the abscissa.

six birds. This measure of preference was obtained by dividing the number of times the subject accepted the long VI (VI 20-sec) by the number of times this alternative was offered during the Choice State. The measure of preference for the short VI (VI 5-sec) is not included, as it was always equal to 1.0 for all birds in all conditions.

Considering the six subjects, during the schedule with VI 4-sec in the Search State, the average probability of accepting the long VI was .35; with VI 10-sec, the preference for the VI 20-sec increased to .91; and with VI 25-sec, the preference was .99. An Analysis of Variance showed a significant effect, $F(2,15) = 16.94$ $p < .001$, for the duration of the VI in the Search State.

DISCUSSION

As in Experiment 1, the present results clearly show that the preference for a less-preferred prey varied as a function of the VI value used in the Search State. The preference for the short VI (VI 5-sec) was always equal to 1.0 for all birds in all conditions. These results are in accordance with optimality theory and the delay-reduction hypothesis.

Although the switch of preference for the long VI in the Handling State—from below .5 to above .5—occurred between VI 4-sec and VI 10-sec as required by optimality theory and the delay-reduction hypothesis, the line connecting the mean data in Figure 4 shows that the .5

value was crossed at an (interpolated) VI value of 5.0 sec, a value somewhat smaller than the 7.5 sec required by those theories and found in Experiment 1. Comparison of Figures 3 and 4 shows that there was an increase in preference for the less-preferred prey with all the VI values employed during the Search State when compared to the same values employed in Experiment 1.

GENERAL DISCUSSION

Although Lea (1979) reported a change in preference for the long prey as the FI values in the Search State increased, preferences for the short prey in his study were more extreme than those required by optimality theory. We extended Lea's results by arranging VI instead of FI schedules in the Handling State. Although we obtained the same general pattern of results as did Lea, our results were more consistent with those required by optimality theory. This difference is compatible with research on concurrent-chains schedules, wherein the use of FI schedules in the terminal links produced disproportionate preference for the shorter FI (Duncan & Fantino, 1970; Herrnstein, 1964. Killeen, 1970) relative to similar comparisons with VI schedules. However, it should be pointed out that the test of going from FI to VI Handling Schedules (a within-subject comparison) was not carried out.

Two other procedural differences between Lea's study and the present one should perhaps be noted. First, whereas Lea studied five sessions per condition, we studied 20. This may not have been a major source of difference, however, since our data suggest that the trend for each condition was already evident by the 5th session. Considering the first five sessions, during the schedule with FI 4-sec in the Search State, the average probability of accepting the long VI was .25; with FI 10-sec, the preference for the VI 20-sec increased to .71; with FI 25-sec, equal to .96; and with FI 63-sec, equal to .98. Second, in the present experiments it was equally difficult to accept or reject a prey in the Choice State (FR 3), whereas in Lea's study it was easier to accept a prey (FR 1) than to reject it (FR 3). Nevertheless, Lea obtained a greater rejection for the long prey in all conditions. Thus it is likely that with equal FR schedules Lea would have obtained even larger deviations from optimality theory.

The difference between the results of Experiment 1 and 2 (i.e., the greater rate of acceptance found with VI schedules in the Search State) has implications for choice in more typical concurrent-chains schedules. Specifically, if FI schedules were used in the initial links, greater preference should occur for the preferred alternatives than in comparable concurrent-chains schedules using VI schedules in the initial links. This effect awaits investigation.

The present results are not only in accordance with optimality theory but also with the delay-reduction hypothesis, in that choice was determined by the degree of reduction in the expected time to primary reinforcement. With the shortest Search State (4-sec), only the short VI schedule was correlated with a reduction in time to reinforcement. For most birds, preference in this case was strongly for the short VI, i.e., the long VI was seldom accepted. With the longest Search State (FI 63-sec or VI 25-sec), both VI schedules were correlated with a reduction in time to reinforcement. In this case subjects accepted both VI schedules whenever available. Thus, the results show that aspects of foraging behavior may be explained by the same principles as operant choice.

In conclusion, the present results support the notion of optimality in foraging behavior and they suggest a principle of operant conditioning (the delay-reduction hypothesis) consistent with this behavior. These results, those from Lea (1979), and other results from laboratory studies (cf. Fantino & Logan, 1971) encourage the use of technology developed in the operant laboratory in the study of foraging behavior.

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