EFFECTS OF SEARCH COST ON FORAGING AND FEEDING: A THREE-COMPONENT CHAIN ANALYSIS

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An experiment determined whether pigeons minimize number of key pecks per food delivery and maintain their baseline intake of food while key pecking on a three-component chain schedule. Pigeons at either 80% or 100% body weight obtained all their food during baseline and contingency sessions. During baseline sessions, pecks on the left and center keys had no consequences; each peck on the right key activated the feeder. During contingency sessions, pigeons key pecked on a three-component chain schedule simulating components of a foraging chain. In the *search component* either 3, 9 or 15 key pecks (varied parametrically across blocks of sessions) on the left key produced a stimulus on the middle key, indicating an encounter with either the low-cost prey (3 key pecks) or an equally probable high-cost prey (21 key pecks). In the *procurement component* the pigeon pecked either: (a) the left key once, thus returning to the search component, or (b) the middle key either 3 or 21 times, which activated the right response key. In the *handling component* one peck on the right key operated the feeder. The pigeons always procured the low-cost prey and minimized the number of key pecks per hopper by procuring the high-cost prey when the search-cost ratio was high (15 key pecks) but not when it was low (3 key pecks). All pigeons maintained their baselines of eating during contingency sessions by key pecking more frequently and eating more efficiently. The 80% body-weight birds produced higher overall rates of key pecking and eating. These results have implications for ecological theories of optimal foraging and for psychological theories of learned performance.

Key words: ratio schedule, chained schedule, paired baseline, foraging, performance theory, optimal behavior, deprivation, key peck, pigeon

Behavioral ecologists concerned with foraging in natural environments and psychologists concerned with responding in operant conditioning environments sometimes address similar questions about the ways in which an organism distributes its time and energy (Kamil & Sargent, 1981). Even though operant conditioners express a grow-

ing interest with foraging in the wild (see Baum, 1982; Lea, 1981, 1982; Staddon, 1980, for theoretical analyses), only a few have performed experimental analyses (e.g., Abarca & Fantino, 1982; Killeen, Smith, & Hanson, 1981; Lea, 1979). The most systematic line of research (e.g., Collier, 1982; Collier & Rovee-Collier, 1981) used both familiar and novel operant chain schedules of reinforcement to simulate components of a foraging chain such as search, procurement, handling, and consumption.

The purpose of the present experiment was threefold. First, we tested the general assumption of optimal foraging theory that pigeons maximize net energy while foraging—for example, by obtaining each hopper presentation through the fewest key pecks possible (see Krebs, 1978; Pyke, Pulliam, & Charnov, 1977; Schoener, 1971, for discussions of optimal foraging theory). Second,

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we simulated aspects of natural foraging and feeding: In nature pigeons control their own intake. Each pigeon obtained all of its food during both baseline and contingency sessions with our main group of subjects performing at 100% of their free-feeding weights. To compare their results with more traditional operant conditioning experiments in which pigeons are food deprived, we employed a second group of pigeons at 80% of their free-feeding weights. Third, we used conventional operant equipment and procedures to achieve greater control over variables typically studied in either the field or semi-naturalistic environments (e.g., Mellgren, 1982).

In the present experiment pigeons key pecked on a three-component chain schedule based upon reinforcement with food. Although the procedures of this experiment resembled those used by Collier (1982), there were notable differences: (a) Pigeons, instead of rats, performed in 3-hr sessions rather than in 24-hr sessions. (b) The three-component chain included a final handling component in addition to search and procurement components. (c) Each completion of the chain resulted in a small amount of food (a bite or two) rather than a large amount (a meal). (d) We obtained molar measures such as number of key pecks, number of hopper presentations, and number of grams eaten during both paired baseline sessions and contingency sessions (Timberlake & Allison, 1974). This experiment tested both the foraging hypothesis that pigeons would minimize the number of key pecks per food delivery and the molar performance hypothesis that pigeons would maintain their baselines of eating while foraging during contingency sessions.

METHOD

Subjects

Nine female White Carneaux pigeons about 8 years old were housed individually with water and grit freely available in their home cages. Six birds at 100% body weight performed in sessions every day, whereas the

remaining three birds performed every second or third day to ensure a return to their 80% body weights (± 10 g). All birds had previously key pecked on ratio schedules.

Apparatus

Two Lehigh Valley Electronics three-key pigeon chambers, in which white noise and an exhaust fan masked ambient noise, were located side-by-side on a table. The panel containing the response keys and feeder was 35.2 cm wide and 34.9 cm high, measured from the mesh floor. The bird's working space extended 30.8 cm from this panel to the rear wall. The panel contained three circular openings, 2.5 cm in diameter, arranged in a horizontal row 25.4 cm above the floor. The left and right openings were centered about 9.5 cm from their respective side walls and 8.5 cm from the midpoint of the central opening. Behind each opening was a Lehigh Valley response key and an Industrial Electronics Engineers One-Plane Readout projection unit containing 12 Type 1820 28-V lamp bulbs that could be illuminated individually. A shielded houselight (Type 1819 28-V), 7 cm above the center key, was illuminated during a session. Events were controlled and data recorded by Coulbourn solid-state programming and recording equipment located in the same room.

Procedure

Each pigeon obtained all of its food during 3-hr sessions (see Hursh, 1978, 1980) while performing on a baseline procedure or a contingency procedure. The reinforcers consisted of 4-s hopper presentations. After each session, the experimenter collected spillage, determined the number of grams eaten, and refilled the hopper with fresh grain.

During 3-hr *baseline sessions*, all three response keys were illuminated. Key pecks on the left response key (yellow) and on the middle response key (white vertical line on a green surround) were recorded but had no programmed consequences. A single peck on the right response key (a black dot on a white surround) simultaneously darkened all three response keys and raised the hopper

for 4 s, after which the hopper was lowered and all three response keys were illuminated once again.

During 3-hr *contingency sessions*, a three-component chain schedule was used to simulate the search, procurement, and handling components of foraging. Figure 1 depicts the foraging chain in which each component involved a fixed-ratio schedule accompanied by particular colors or symbols on the three response keys. Only one component in the foraging chain was functional at a time and only pecks on illuminated response keys had scheduled consequences.

Fig. 1. Components of the foraging chain simulated by the contingency procedure.

The chain began with the *search component*, in which the left response key was illuminated with yellow light and the other two response keys were dark. The search-cost ratio was held constant during a contingency condition, with 3, 9 or 15 pecks on the search key resulting in termination of the search component and entry into the procurement containing either the low-cost or high-cost prey. In the *procurement component* the left response key was red, the middle response key was illuminated either with green light

or with a white vertical line on a black surround, and the right key was dark. The color or symbol on the middle response key was counterbalanced across subjects and was correlated with either a fixed ratio of 3 (the low-cost prey) or with a fixed ratio of 21 key pecks (the high-cost prey). A random probability generator ($p = .5$) determined which of the two options was presented. At this juncture the pigeon could either reject or undertake the procurement ratio. (a) A single peck on the left key, *also* counting toward the next fixed-ratio search cost, re-initiated the search component by simultaneously darkening the middle response key and changing the left keylight from red to yellow. (b) A single peck on the middle response key immediately darkened the left key and committed the pigeon to completing the procurement ratio, which required either 2 or 20 more pecks (constituting the low-cost or high-cost prey, respectively) on the center key, which in turn produced transition to the handling component. In the *handling component* the right response key was illuminated by a black dot on a white surround and the other two response keys were dark. A single key peck on the right response key darkened it and activated the hopper for 4 s, followed by return to the search component.

All nine birds performed on both the baseline and contingency procedures. There were three different contingency conditions in which the search-cost ratio in the first component was manipulated: All birds received eight consecutive sessions on each search-cost ratio (requiring 3, 9, or 15 pecks). The procurement-cost ratios in the second component (i.e., 3 and 21 key pecks) and the handling-cost ratio in the third component (1 key peck) were held constant. Although eight sessions may appear to be a small number relative to standard operant conditioning practices, both Collier and Rovee-Collier (1981) and Logan (1960, 1964) indicated that responding stabilizes rapidly during training in a closed economy, as it did in this experiment. Moreover, a small rather than large number of sessions seemed appropriate to simulate foraging in

the wild in which conditions seemingly vary on a weekly rather than a monthly basis.

The specifics of training were somewhat different for the 80% and 100% body-weight birds. Each of the three 80% body-weight birds performed on a different sequence of search-cost ratios (i.e., 3, 9, and 15; 15, 9, 3; 15, 3, and 9 key pecks) prior to eight postcontingency baseline sessions. For each of these birds there was a total of 24 contingency sessions and 8 baseline sessions. All six 100% body-weight birds received eight precontingency baseline sessions, the same sequence of search-cost ratios (i.e., 3, 9, 15, and 9 key pecks) in which two baseline sessions were interspersed between each successive search-cost ratio, and four postcontingency baseline sessions. For each of these birds there was a total of 32 contingency sessions and 18 baseline sessions.

After the postcontingency baseline sessions ended, the search cost was held constant at 3 key pecks and the discriminative stimuli correlated with the procurement component were manipulated for the 100% body-weight birds. After three additional sessions with the original stimulus conditions, the stimuli correlated with the low- and high-procurement ratios were reversed for eight sessions and then reversed again for nine more sessions. After the reversal training, the discriminative stimuli correlated with the low- and high-procurement ratios were changed in an attempt to make it more difficult to discriminate between them. The stimuli were changed from a green surround versus a white vertical line (a) to a white horizontal line versus a white vertical line for six sessions, and then (b) to a small white dot on a dark surround versus a small white triangle on a dark surround for 12 sessions.

We measured the number of completions of the search-cost ratio in the first component and completions of the low- and high-procurement ratios in the second component. We also measured number of key pecks, number of hopper presentations, number of grams of grain eaten, and body weight at the beginning of each session dur-

ing both baseline and contingency sessions.

RESULTS

Table 1 presents the number of low-cost and high-cost prey that were procured and encountered during the final three sessions on each of the search-cost conditions. First, the number of low-cost and high-cost prey encountered was nearly equal regardless of search cost. Second, the total number of times the pigeon encountered an item of prey decreased systematically as a function of search-cost for all birds except Pigeon 2049-80%. Third, the 80% body-weight pigeons typically completed the search ratios more frequently than the 100% body-weight birds.

Figure 2 indicates similar patterns for all birds except Pigeon 4484. All pigeons always procured the low-cost prey. On average, eight of the nine birds procured the high-cost prey 89% of the time (range: 68% to 100%) when the search cost was 15 key pecks and only 6% of the time (range: 1% to 17%) when the search cost was 3 key pecks. Thus, the birds usually procured the high-cost prey when the search cost was high, but not when it was low.

Figure 3 illustrates the effects of reversing and changing the discriminative stimuli correlated with the low procurement cost and high procurement ratios. Five of the six pigeons rapidly learned to procure the low-cost prey and to decrease the percentage of high-cost prey procured during both the discrimination reversals and the more difficult line-tilt and shape discriminations. The behavior of Pigeon 4484 differed once again from that of the other five birds. The bird did reject the high-cost prey during sessions in which the high-cost procurement ratio was raised from 21 to 40 key pecks; however, the performance reverted as soon as the ratio was reduced from 40 to 21 key pecks.

Figure 4 shows that for all pigeons the mean number of key pecks was low during baseline sessions and high during contin-

Table 1
Number of low-cost prey (3 key pecks) and high-cost prey (21 key pecks) procured (P) and encountered (E) during the final three sessions of each experimental phase.

	Search Cost							
	3		9		15		9	
	P	E	P	E	P	E	P	E
Bird 4484-100%								
LCP	105	105	082	082	065	065	062	062
HCP	108	110	074	074	074	074	070	074
Total		215		156		139		136
Bird 6409-100%								
LCP	813	813	258	258	196	196	300	300
HCP	029	837	237	274	214	215	237	325
Total		1650		532		411		625
Bird 0827-100%								
LCP	248	249	187	187	078	078	169	169
HCP	027	231	052	204	080	096	023	175
Total		480		391		174		344
Bird 2113-100%								
LCP	288	288	123	123	104	104	175	175
HCP	010	283	120	134	108	110	128	166
Total		571		257		214		341
Bird 2103-100%								
LCP	234	234	163	163	121	121	197	197
HCP	007	254	020	200	089	128	016	192
Total		488		363		249		389
Bird 2126-100%								
LCP	204	204	104	104	083	083	190	190
HCP	018	199	086	111	081	081	074	177
Total		403		215		164		367
Bird 2049-80%								
LCP	356	356	408	408	211	211		
HCP	008	341	079	390	182	266		
Total		697		798		477		
Bird 2361-80%								
LCP	529	530	470	470	330	330		
HCP	007	501	304	502	312	330		
Total		1031		972		660		
Bird 2099-80%								
LCP	322	322	184	184	141	141		
HCP	053	317	163	173	142	148		
Total		639		357		289		

gency sessions. Seven of the nine birds showed increased overall number of key pecks as a direct function of search cost. In general, 80% body-weight birds key pecked more frequently than 100% body-weight birds during contingency sessions.

Figure 5 shows mean number of grams eaten and eating efficiency (i.e., number of grams per hopper presentation). The 80% body-weight birds obtained more hopper presentations, ate more grain, and ate more efficiently than did the 100% body-weight

Fig. 2. Mean percentage of low-cost prey (unfilled circles) and high-cost prey (filled circles) procured during the final three sessions of the initial exposure to each the 3, 9, and 15 key peck search-cost ratios. The error bars indicate the range.

birds during baseline sessions. Even though all pigeons obtained fewer hopper presentations during contingency sessions than during baseline sessions, pigeons at both 80% and 100% body weight approximated baseline food intake and also increased eating efficiency. There were obvious individual differences in the extent to which eating became more efficient; however, the increase was greater for the 100% body-weight birds. In addition, all 100% body-weight birds maintained their baseline weights during contingency sessions.

We examined the cumulative records for entire sessions of key pecking and eating. Those for Pigeon 2099-80% were representative of all birds. The baseline pattern of key pecking and eating was distinctive: The pigeon never pecked the left or center response keys; however, the pigeon pecked the right response key and ate for a long period of time at the beginning of the session and then again for a short period later in the session. Examination of the cumulative records

Fig. 3. Percentage of low-cost prey (unfilled circles) and high-cost prey (filled circles) procured during the discrimination reversals (V vs. G) and training on more difficult line-tilt (V vs. H) and shape discriminations (D vs. T). The fixed ratio correlated with the upper and lower symbols was 3 and 21 key pecks, respectively.

Fig. 4. Mean number of key pecks during all baseline sessions (B) and during the final three sessions of the initial exposure to each the 3, 9, and 15 key peck search-cost ratios. The error bars indicate the range.

from contingency sessions revealed that the pigeon never key pecked throughout the entire session and that the pattern of eating established in the baseline tended to be duplicated during contingency sessions (see also Lucas, 1981). In general, long bouts of key pecking and eating occurred early in the session; shorter bouts of key pecking and eating occurred later in the session.

DISCUSSION

This experiment addressed two questions: first, whether pigeons would minimize the overall number of key pecks for food delivery, and second, whether pigeons would regulate their intake during contingency sessions. The finding pertinent to the first question was that a 12 key-peck difference in the search-cost ratio dramatically affected the number of selections of the higher procurement ratio in the second component of the chain. Regardless of body weight, when the

search ratio required 15 pecks, the pigeons usually undertook the high-procurement ratio; at a search ratio of 3 pecks, they usually rejected the high-procurement ratio by returning to the search component.

The pattern of behavior characteristic of the first finding is a general one not limited to a specific experimental design. Despite the various procedural differences noted in the introduction, this finding confirmed the major results of an experiment using ratio chain schedules (Collier, 1982) and, in addition, the results of experiments using interval chain schedules (Abarca & Fantino, 1982; Lea, 1979). However, the difference between the search-cost ratios (3 vs. 15 key pecks) and procurement-cost ratios (3 vs. 21 key pecks) was much smaller in the present experiment than the range of search-cost ratios (5 vs. 200 lever presses) and procurement-cost ratios (5 vs. 100 lever presses) in Collier's experiment. This difference may be related to the smaller quantities of food pro-

Fig. 5. Mean number of grams eaten (above) and mean eating efficiency (below) during all baseline sessions (B) and the final three sessions of the initial exposure to each the 3, 9, and 15 key peck search-cost ratios. The range is indicated for each point.

duced by the pigeons' completions of the chain, as compared to Collier's rats' earning an entire meal with each chain completion.

The first finding—that the size of the fixed ratio in the search component determines the choice between engaging the procurement link or returning to the search component—may be interpreted in terms of optimal foraging theory (Orians & Pearson, 1979; Schoener, 1971). This theory assumes an animal maximizes its net energy intake and is sensitive to its average rate of intake while foraging. Moreover, according to the theory an item of food either will be included in an animal's diet, if the net energy obtained by consuming it exceeds the overall average rate of intake, or it will be excluded completely. The first finding above qualitatively supports this explanation as did the result of an experiment by Krebs, Erichsen, Webber, and Charnov (1977), who found less complete inclusion or exclusion of items

by birds tested in an open economy. The greater tendency toward "all-or-none" results in the present experiment may be related either to our use of ratio schedules or to the closed economy (Hursh, 1978, 1980).

There is an alternative, and perhaps preferable, account in terms of operant principles of conditioned reinforcement. This approach indicates that behavior at the choice point is controlled by the relative conditioned reinforcing strength of the discriminative stimuli on the left and center response keys. The first finding is difficult to explain in terms of a contiguity theory of conditioned reinforcement because the discriminative stimulus for the return to the search component controlling choice behavior is far removed from the primary reinforcer in comparison to the discriminative stimulus for procuring the high-cost prey. However, this result is consistent with a temporal delay-reduction hypothesis (Fantino, 1977; see also Fantino & Logan,

1979). Although the effectiveness of conditioned reinforcers in a chain usually decreases with each additional link, Duncan and Fantino (1972) showed that temporal variables can override the effects of segmentation, and their delay-reduction hypothesis predicts the trend of this finding (cf. Abarca & Fantino, 1982). Moreover, this first finding is consistent with a temporal delay-reduction hypothesis even though the direction of the effect is reversed in comparison to traditional procedures in which the schedule in the second component determines the strength of conditioned reinforcement and hence responding in the first component.

In the first session following implementation of a new search-cost ratio and following a discrimination reversal, there were rapid changes in the control exerted by the discriminative stimuli. This result is problematical for any theory of conditioned reinforcement that assumes that the strength of a conditioned reinforcing stimulus accrues slowly. In addition, if an analysis of "the psychological distance to reward" (Fantino, 1977) is applied to experiments using ratio schedules rather than the more common interval schedules, it is functionally indistinguishable from the psychological law of less work (Hull, 1943; see also Solomon, 1948). Such an explanation is seldom, if ever, offered for conditioned reinforcement even though it is related to Tolman's (1932) report that rats prefer spatially and temporally shorter routes through a maze.

One interpretation of this law is that pigeons will minimize number of key pecks per hopper presentation (see also Hodos & Trumbule, 1967). Figure 6 depicts theoretical search-cost functions in which the pigeon minimizes pecks per hopper at the lowest point. The first finding is consistent with this least-effort explanation because our pigeons usually minimized key pecks per hopper by procuring 0% of the high-cost prey at a search-cost ratio of 3 key pecks and by procuring 100% of the high-cost prey at a search-cost ratio of 15 key pecks. At a search-cost ratio of 9 key pecks the pigeon necessarily minimized the number of key

Fig. 6. Number of key pecks per hopper presentation as a function of percentage high-cost prey procured for each the 3, 9, and 15 key peck search-cost ratios on the assumption that the pigeon always procures the low-cost (3 key peck) prey. The pigeon minimizes pecks per hopper at the lowest point on each theoretical search-cost function.

pecks per hopper regardless of the percentage of high-cost prey procured, an ambiguous situation contributing to the greater variability of results observed in this condition.

Both optimal foraging theory and conditioned reinforcement theory address the first question—whether pigeons minimize number of key pecks per reward. Thus, they explain moment-to-moment choices whether to procure the high-cost prey each time it is encountered. However, neither these nor matching-law formulations address the second question—whether pigeons regulate their intake. The second finding, that key pecking and eating efficiency increased and food intake remained constant despite fewer hopper presentations during contingency sessions, is amenable to analysis by molar theories of learned performance. For example, Hogan and Roper (1978) concluded that an animal responds to increases in ratio size over a limited range by increasing key pecking and thereby maintaining baseline intake. In contrast, Allison, Miller, and Wozny

(1979) concluded that increases in the size of simple fixed ratios increased key pecking and decreased intake relative to baseline levels.

Deprivation appeared to affect the type of feeding patterns whereby our pigeons achieved their baseline levels of eating. All birds increased key pecking and eating efficiency during contingency sessions relative to baseline levels, a finding consistent with the hypothesis that social feeders compete by increasing rate of consumption when resources in a patch are scarce (Geist, 1974). However, the increase in eating efficiency was greater for the 100% than for the 80% body-weight birds. Thus, it appears that the 80% body-weight birds depended more on the "foraging strategy" of increased key pecking, whereas the 100% birds depended more on the "feeding strategy" of increased eating efficiency.

The procedures used in this experiment permit use of conventional operant conditioning equipment to achieve greater control than semi-naturalistic procedures such as those in which rats run loose in the laboratory (e.g., Mellgren, 1982). We conclude that the methods of operant conditioning and the theoretical framework of learned performance equilibrium provide a comprehensive and rigorous testing ground for ecological hypotheses about foraging behavior. We hasten to add that eating efficiency is a variable that should be incorporated both into models of optimal foraging and into molar models of instrumental performance (e.g., Staddon, 1979; Timberlake, 1980).

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