

*GROUP FORAGING SENSITIVITY TO PREDICTABLE
AND UNPREDICTABLE CHANGES IN FOOD DISTRIBUTION:
PAST EXPERIENCE OR PRESENT CIRCUMSTANCES?*

KENNETH E. BELL AND WILLIAM M. BAUM

RIVIER COLLEGE AND UNIVERSITY OF CALIFORNIA–DAVIS

The ideal free distribution theory (Fretwell & Lucas, 1970) predicts that the ratio of foragers at two patches will equal the ratio of food resources obtained at the two patches. The theory assumes that foragers have “perfect knowledge” of patch profitability and that patch choice maximizes fitness. How foragers assess patch profitability has been debated extensively. One assessment strategy may be the use of past experience with a patch. Under stable environmental conditions, this strategy enhances fitness. However, in a highly unpredictable environment, past experience may provide inaccurate information about current conditions. Thus, in a nonstable environment, a strategy that allows rapid adjustment to present circumstances may be more beneficial. Evidence for this type of strategy has been found in individual choice. In the present experiments, a flock of pigeons foraged at two patches for food items and demonstrated results similar to those found in individual choice. Experiment 1 utilized predictable and unpredictable sequences of resource ratios presented across days or within a single session. Current foraging decisions depended on past experience, but that dependence diminished when the current foraging environment became more unpredictable. Experiment 2 repeated Experiment 1 with a different flock of pigeons under more controlled circumstances in an indoor coop and produced similar results.

Key words: ideal free distribution, choice, foraging, group foraging, matching law, undermatching, pigeons

The ideal free distribution (Fretwell & Lucas, 1970) predicts how foraging groups will distribute themselves among resource patches of varying profitability. For choice between two patches with continuous input, in which food items are consumed as soon as they arrive at resource patches, the ideal free model predicts that the ratio of foragers at the patches (N_1 and N_2) will equal the ratio of food resources obtained (R_1 and R_2) in the two patches. The prediction can be expressed as

$$\frac{N_1}{N_2} = \frac{R_1}{R_2}. \quad (1)$$

The theory assumes (a) that foragers have “perfect knowledge” of patch profitability, (b) that patch choice based on this knowledge will maximize intake, and (c) that all the foragers are free to enter each patch on an equal basis (Fretwell & Lucas, 1970). Supporting evidence has been found in numerous species, including dung flies (Parker, 1970), mallard ducks (Harper, 1982), three-spined sticklebacks (Milinski, 1979), cichlid fish (Godin & Keenleyside, 1984), pigeons (Baum & Kraft, 1998), and humans (Kraft &

Baum, 2001; Sokolowski, Tonneau, & Freixa i Baque, 1999).

Some researchers have noted a parallel between the ideal free distribution and the matching law of individual choice (Baum & Kraft, 1998; Gray, 1994). The matching law addresses choice in a single forager presented with multiple food sources or reinforcement alternatives. According to the matching law, the ratio of responses to two alternatives will match the ratio of the obtained rates of reinforcement at the alternatives:

$$\frac{B_1}{B_2} = \frac{R_1}{R_2}, \quad (2)$$

where B_1 and B_2 are the responses at Alternatives 1 and 2, and R_1 and R_2 are the rates of reinforcement obtained at Alternatives 1 and 2.

Choice often deviates from the strict matching of Equation 2. Deviations similar to those found in experiments on individual choice also occur in research on the ideal free distribution (Baum & Kraft, 1998; Grand, 1997; Gray, 1994). To address deviations from the matching law, Baum (1974) provided an equation known as the generalized matching law, which is expressed as

Address correspondence to William M. Baum, 1095 Market Street, Suite 217, San Francisco, California 94103 (e-mail: wbaum@sbcglobal.net).

$$\frac{B_1}{B_2} = k \left(\frac{R_1}{R_2} \right)^a, \quad (3)$$

where the exponent a indicates the organism's sensitivity to reinforcement, and k indicates bias, which reflects preference for an alternative that is independent of reinforcement (strict matching would occur when a and k both equal 1.0). Tests of the applicability of the matching relation have plotted the logarithm of response ratio as a function of the logarithm of reinforcement ratio (Baum, 1974). This transforms Equation 3 into a linear form:

$$\log \left(\frac{B_1}{B_2} \right) = a \log \left(\frac{R_1}{R_2} \right) + \log k, \quad (4)$$

which allows easy estimation of deviations from matching. The most common deviation is undermatching, which in Equation 4 reveals itself as a slope or sensitivity less than 1.0 (Baum, 1974). In individual choice, undermatching occurs because of fewer responses at the richer alternative and more responses at the leaner alternative than would be predicted by strict matching. In group foraging with resource patches of unequal profitability, undermatching can be understood as the result of fewer foragers at the more profitable patch and more foragers at the less profitable patch than would be predicted by Equation 1. A parallel to Equation 4 captures such a deviation from the ideal free distribution:

$$\log \left(\frac{N_1}{N_2} \right) = a \log \left(\frac{R_1}{R_2} \right) + \log k. \quad (5)$$

Kennedy and Gray (1993) suggested that undermatching in group foraging could result from competitive interference, unequal competitive abilities, travel requirements, or imperfect knowledge of patch profitability. Violations of the perfect knowledge assumption would result from foragers' inability to assess which patch is the most profitable. This could arise from the foragers' "perceptual limits" (Gray & Kennedy, 1994; Spencer, Kennedy, & Gray, 1995). For instance, Abrahams (1986) suggested that when an increase in the size of a foraging population leads to decreased intake rate per individual, the decrease interferes with each individual forag-

er's discrimination between resource profitabilities at the two sites.

Whatever mechanisms underlie assessment of patch profitability, accurate discrimination of patch profitability increases a forager's overall food intake. Current decisions about which patch to exploit probably depend on a weighted assessment of many environmental variables (Lefebvre, 1983; Templeton & Gir-aldeau, 1996). Presumably, one important variable in this assessment is past experience with resource patches. A number of researchers have suggested that foragers' past experience with resource patches affects their assessment of future profitability (Kamil & Yoerg, 1985; Moody, Houston, & McNamara, 1996). Organisms may use a "learning rule" based on recent relative payoffs at resource patches (Harley, 1981; Lefebvre, 1983). For example, Smith and Dawkins (1971) found that birds searched longer in areas that had previously contained high densities of food than in areas that had contained low food density.

A learning rule that capitalizes on past experience may enhance fitness in a relatively stable environment (Shettleworth, 1984). Food availability at resource patches, however, may be unstable over time. In an unstable environment, the adaptive strategy may be to track local fluctuations in resource distribution, minimizing dependence on prior profitabilities. Some studies conducted with individual foragers suggest such a tendency toward local control of foraging. Cuthill, Kacelnik, Krebs, Haccou, and Iwasa (1990) found that when the travel time required to reach resource patches varied, starlings tracked short-term changes in travel time by taking less food after shorter travel. They concluded that tracking changes in travel time, with more weight placed on recent travel requirements, is an adaptive strategy in a fluctuating environment.

Other research conducted on individual organisms indicates that reinforcer ratios from prior sessions usually affect current behavior in a choice situation (Davison & Hunter, 1979; Hunter & Davison, 1985; Shettleworth & Plowright, 1992). Current reinforcer ratios, however, appear to influence behavior more than prior reinforcer ratios when reinforcer ratios are presented in an unpredictable or random sequence. For example, us-

ing concurrent variable-interval schedules in which individual pigeons pecked two keys to obtain food, Schofield and Davison (1997) presented reinforcer ratios in a pseudorandom sequence across daily sessions (the ratio in effect in one session was unrelated to that in effect in the prior session). The ratios used were 8:1, 4:1, 2:1, 1:2, 1:4, and 1:8. The reinforcer ratios in previous sessions had little effect on choice in comparison with the current reinforcer ratio. About 80% of the control over choice was exercised by the reinforcer ratio that occurred in the present session. They concluded that the presentation of a pseudorandom sequence of reinforcer ratios leads to enhanced control over choice by the present session and diminished control by previous sessions.

Davison and Baum (2000, 2002) took this rapid variation a step further by presenting seven different reinforcer ratios (27:1, 9:1, 3:1, 1:1, 1:3, 1:9, and 1:27) within a single day's session. Each ratio was presented for a certain number of reinforcers, no stimuli indicated which ratio was in effect, and the ratios were presented in random order. Reinforcer ratios were separated by blackouts. Davison and Baum found that under these circumstances control over choice became extremely local, shifting rapidly toward whichever alternative last provided food. The result was that preference developed rapidly for the currently richer alternative in each reinforcer ratio, with little carryover from the previous ratio.

The present study aimed to assess sensitivity to previous and current resource ratios in a flock of pigeons. Whereas Schofield and Davison (1997) used individual pigeons and pseudorandom sequences across days, this study used a flock of pigeons and examined patch choice with resource ratios that were presented in both irregular sequences and regular sequences. Like the Davison–Baum (2000, 2002) studies, it also assessed the effect of presenting resource ratios one after the other within a day's session, but, unlike the Davison–Baum studies, with no time separation between ratios. If group foraging depends on prior resource ratio, carryover should occur from one ratio to the next. The carryover would manifest as a greater number of foragers at the patch that was rich during the previous resource ratio than would be

predicted by the current ratio and a correlation between initial forager ratio and prior forager ratio. If, however, unpredictability affects group foraging, the carryover might diminish when the sequences of resource ratios are irregular. Finally, if highly unpredictable foraging situations bias foraging toward local control, then adjustment to rapidly changing resource ratios (every few minutes within a single session) should be faster than in situations in which resource ratios change less often (i.e., daily).

The present experiments used more ratios and more extreme ratios than are typical of research on the ideal free distribution, because narrow ranges of resource ratios are less likely to reveal deviations from the matching prediction (Gray, 1994) and because better estimation of sensitivity (a in Equation 5) may be had from more ratios (Kennedy & Gray, 1993).

EXPERIMENT 1

Experiment 1 was designed to assess both the degree of carryover when resource ratios were presented in a predictable (regular) and an unpredictable (irregular) fashion and the effect of rapidly changing resource distributions on forager distribution. Two conditions presented regular and irregular orders of resource ratios across several days, and four conditions presented regular and irregular sequences of resource ratios within single sessions.

If foraging depends heavily on previous experience, then (a) sensitivity (a in Equation 5) should be higher at the beginning of ratio presentations in regular sequences than in irregular sequences, and (b) correlations between the forager ratio from the final seconds of the previous resource ratio and the initial seconds of the current resource ratio should be high. If, however, an unpredictable foraging environment leads to more dependence on current resource ratios than past experience, then little carryover should occur from previous ratios in irregular sequences presented across days. Furthermore, in a highly unpredictable foraging situation, in which resource ratios change every few minutes and are in an irregular sequence, adjustment to a new resource ratio should be rapid. In comparison with presentation across days, this ad-

justment should manifest as a more rapid change in sensitivity in the initial minutes of each resource ratio and as a more rapid decrease in correlation of final forager ratio of the previous resource ratio with forager ratios of the current resource ratio.

METHOD

Subjects. Subjects were a flock of 34 pigeons (*Columba livia*) housed at the University of New Hampshire Psychology Department's outdoor pigeon coop. The pigeons had constant access to a wire mesh flyway (3 m high, 3.1 m wide, and 12.2 m long). All pigeons were fed a daily ration of food that was sufficient to maintain them but was small enough to ensure that they would participate in the experimental sessions. Pigeons had continuous access to water and grit. All pigeons had prior experience with similar patch foraging experiments (e.g., Baum & Kraft, 1998).

Apparatus. Foraging sites were two pieces of carpet (1.22 m square) with wood borders (5.1 cm by 10.2 cm) set on the floor of the flyway. The sites were separated by 1.83 m (measured center to center) and situated next to each other. Foraging at the sites was monitored by two video recorders mounted directly above. Food items were whole dried green peas obtained from a local supermarket. Any broken or unusually small peas were discarded. Food delivery occurred via plastic tubes that were mounted at the outer edge of each site (approximately 46 cm above the site). The feeding tubes exited the flyway at one side that was covered with a large tarpaulin to keep the experimenters out of the pigeons' view. Small (15 cm by 15 cm) holes were cut in the tarpaulin to enable the experimenters to monitor food consumption.

Procedure. Sessions consisted of the delivery of food items by hand through the feeding tubes. Separate experimenters delivered food items to the north and south sites. The procedure resembled Baum and Kraft's (1998) rapid presentation procedure, with one difference. To control for the possibility that the pigeons might use experimenters' auditory cues to assess patch profitability, the experimenters remained silent during the delivery of food items. The experimenter at the rich site dropped a food item, waited until it was consumed, then dropped another. The ex-

perimenter at the lean site monitored delivery on the rich site and dropped a pea as soon as the appropriate number of peas was delivered to the rich site. For instance, in a 4:1 ratio, the experimenter at the lean site delivered a pea when the experimenter on the rich site delivered the fourth pea. Average time between pea deliveries to the rich site was 2.5 s. Thus, a pea was delivered to the lean site about every 5 s in a 2:1 ratio, every 10 s in a 4:1 ratio, and every 20 s in an 8:1 ratio.

All conditions included the presentation of seven resource ratios (8:1, 1:8, 4:1, 1:4, 2:1, 1:2, and 1:1). In Condition 1, the ratios were presented in a regular sequence within a single session. Duration of the single session was 39 min. The first and last ratios of the sequence lasted 7 min, and the middle five ratios lasted 5 min. The first ratio was longer to allow 2 min for recruitment at the beginning of the session (Baum & Kraft, 1998). The last ratio was longer to guard against inclusion of data affected by the pigeons' anticipatory quitting during the last 2 min of the session (Baum & Kraft). Because the first and last 2 min of the session were excluded from the data, calculations for every resource ratio were based on presentations lasting 5 min. Condition 2 resembled Condition 1, except that ratios were presented in an irregular sequence. Condition 3 was designed for an across-session comparison, in which the sequence of regular ratios used in Condition 1 was presented, one ratio per day for 21 min, across 7 days. Conditions 4 and 5 were replications of Conditions 1 and 2. Finally, Condition 6 was an across-session comparison, like Condition 3, except that the presentation of ratios was in an irregular sequence. Table 1 summarizes ratio orders and durations used for each condition.

RESULTS

Videotapes of sessions were coded to obtain pigeon counts at each patch. A pigeon was considered present at a patch if both its feet were on the carpeting. Counts were taken every 3 s and averaged over 15-s blocks. Thus, each datum was the average of five individual 3-s counts. Ratios of mean number of pigeons at one patch divided by mean number at the other patch were calculated. The logarithm of the ratio of pigeons at the

Table 1
Ratios and durations used for each condition in Experiment 1.

Condition 1 Within Regular 1	Condition 2 Within Irregular 1	Condition 3 Across Regular ^a	Condition 4 Within Regular 2	Condition 5 Within Irregular 2	Condition 6 Across Irregular ^a
8:1 7 min	1:2 7 min	8:1 Day 1	8:1 7 min	1:2 7 min	1:2 Day 1
4:1 5 min	8:1 5 min	4:1 Day 2	4:1 5 min	8:1 5 min	8:1 Day 2
2:1 5 min	1:1 5 min	2:1 Day 3	2:1 5 min	1:1 5 min	1:1 Day 3
1:1 5 min	1:8 5 min	1:1 Day 4	1:1 5 min	1:8 5 min	1:8 Day 4
1:2 5 min	4:1 5 min	1:2 Day 5	1:2 5 min	4:1 5 min	4:1 Day 5
1:4 5 min	1:4 5 min	1:4 Day 6	1:4 5 min	1:4 5 min	1:4 Day 6
1:8 7 min	2:1 7 min	1:8 Day 7	1:8 7 min	2:1 7 min	2:1 Day 7

^a Duration of each resource ratio in the across-session conditions was 21 min.

two patches (north:south) was plotted against the logarithm of the ratio of peas delivered at the two patches, in accord with Equation 5 (Kennedy, Shave, Spencer, & Gray, 1994). In particular, this form of analysis allows the separation of bias from sensitivity to resource profitability. A line was fitted by the method of least squares to estimate the parameters *k* (bias) and *a* (sensitivity).

Figure 1 shows sensitivity calculated across the seven resource ratios for each 15-s time bin of the 5 min of the ratio presentations, except for the beginning point of each curve, which represents sensitivity calculated at the beginning of the presentation. Comparison

of sensitivity derived from the first few blocks of the resource-ratio presentations allowed assessment of carryover from previous resource ratios. Although carryover might have no obvious effect in the regular conditions, it would result in negative sensitivity in the irregular conditions, because of the alternation of rich and lean sites. As shown in Figure 1, such negative sensitivities occurred in the within-irregular conditions. The initial within-irregular condition showed near-perfect matching ($a = 1.0, r^2 = .97$), but the replication showed undermatching ($a = 0.64; r^2 = .99$), indicating some carryover. The two curves converge, however, after about a minute. Fig-

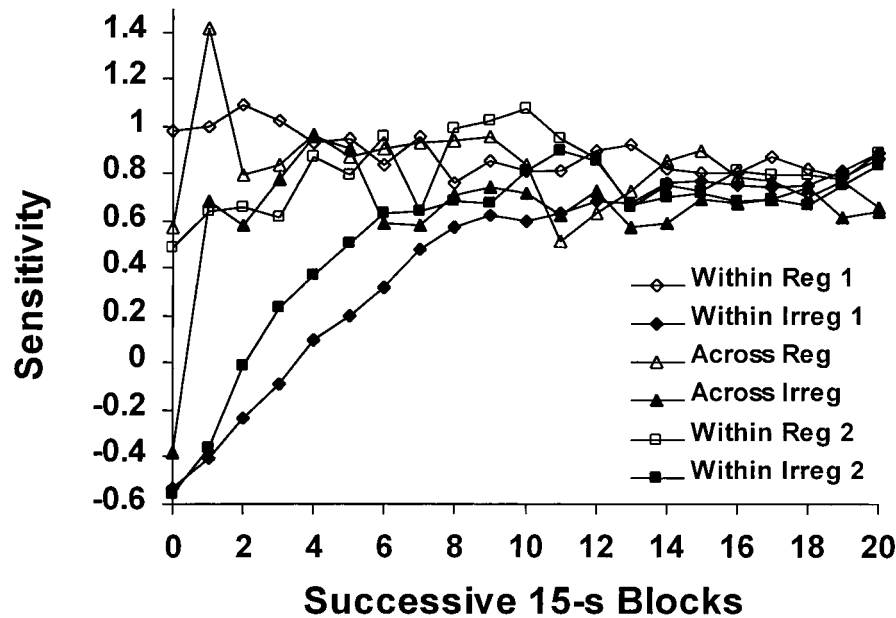


Fig. 1. Experiment 1: sensitivity (*a* in Equation 5) by 15-s block for the first 5 min of resource-ratio presentations in all conditions. Sensitivity was estimated by the method of least squares.

ure 1 also shows that initial sensitivities in the across-regular condition were higher than those in the across-irregular condition. The highest slope obtained was in the first 15-s block of the across-regular condition ($a = 1.41$, $r^2 = .88$), reflecting brief overmatching (the opposite of undermatching; sensitivity greater than 1.0). In contrast, the across-irregular condition produced undermatching ($a = 0.69$; $r^2 = .90$). Although carryover and the sensitivity differences were a virtual certainty for the within-session changes of resource ratio, the difference in sensitivities for across-session changes suggests that, in the across-regular condition, the group's foraging pattern on the prior day carried over to the next day's session.

Carryover of previous experience with a patch is beneficial only if the resource distribution is predictable (i.e., regular). Carryover would be detrimental if the resource distributions were less predictable. If unpredictability leads to increased reliance on present circumstances, then reliance on previous experience should diminish under unpredictable conditions (i.e., within-irregular presentations). Figure 1 allows examination of how rapidly the forager ratio changed in the various conditions. If control by the current resource ratio is higher in less predictable and rapidly changing foraging situations, then sensitivity should increase rapidly in the initial minutes of the within-irregular conditions to converge on the other conditions.

Figure 1 reveals that, as predicted, rapid change occurred in the within-irregular conditions. Both within-irregular conditions showed similar negative slopes at the start of the presentations ($a = -0.41$; $a = -0.36$). After 180 s, however, the within-irregular sensitivities were indistinguishable from sensitivities in the other conditions. The more rapid change in the second within-irregular condition, resulting in sensitivities similar to those from the within-regular and across-regular conditions within 90 s, suggests that the control exerted by the present session increased as the flock gained experience with rapidly changing resource distributions.

To assess the degree of carryover further, correlations were calculated between log forager ratio from the final 15 s of the prior resource-ratio presentation and log forager ratio in each 15-s block of the current

presentation; that is, across six presentations ($n = 6$), excluding the first. Figure 2 shows the correlations (Pearson's r) for all six conditions. As expected, correlations for all within conditions began high and statistically significant ($p < .05$). The correlation for the across-regular condition also began high and statistically significant ($r = .94$, $p < .05$), lending further evidence of substantial carryover from the previous day's session. The across-irregular correlation started out negative ($r = -.60$) and remained negative, indicating an immediate and continuing tendency to shift away from the previous session's performance. From the difference between the across-regular and across-irregular correlations, we may conclude that the pigeons did, in fact, use resource distribution in prior sessions when that reliably predicted present resource distribution.

Although all correlations remained high in the regular conditions, Figure 2 shows how the correlation with previous performance changed across within-irregular presentations. If control by the present resource ratio increased in highly variable conditions, we would expect to see a rapid decline in correlation in the within-irregular conditions to match the rapid increase in sensitivity (Figure 1). By the 2nd minute, the correlation for the first within-irregular condition dropped below zero. The second within-irregular correlation dropped to near zero by about 45 s. These rapid changes further support the idea that the distribution of the pigeons changed rapidly with highly variable resource ratios due to increased control by the current resource ratio and diminished control by the previous resource ratio. That the change in the second condition was faster than that in the first suggests an effect of experience; with increased exposure, the flock's distribution came to adjust faster to the current resource ratio.

Figure 3 shows fits of Equation 5 to the forager ratios from the 4th and 5th minutes, corresponding to Blocks 13 through 20 in Figure 1, of each condition's resource-ratio presentations (i.e., 14 points in each graph). All fits are excellent, with variance accounted for (r^2) ranging from .90 to .98. The slopes range from 0.64 to 0.83, showing a degree of undermatching consistent with previous research (Baum & Kraft, 1998; Kennedy & Gray,

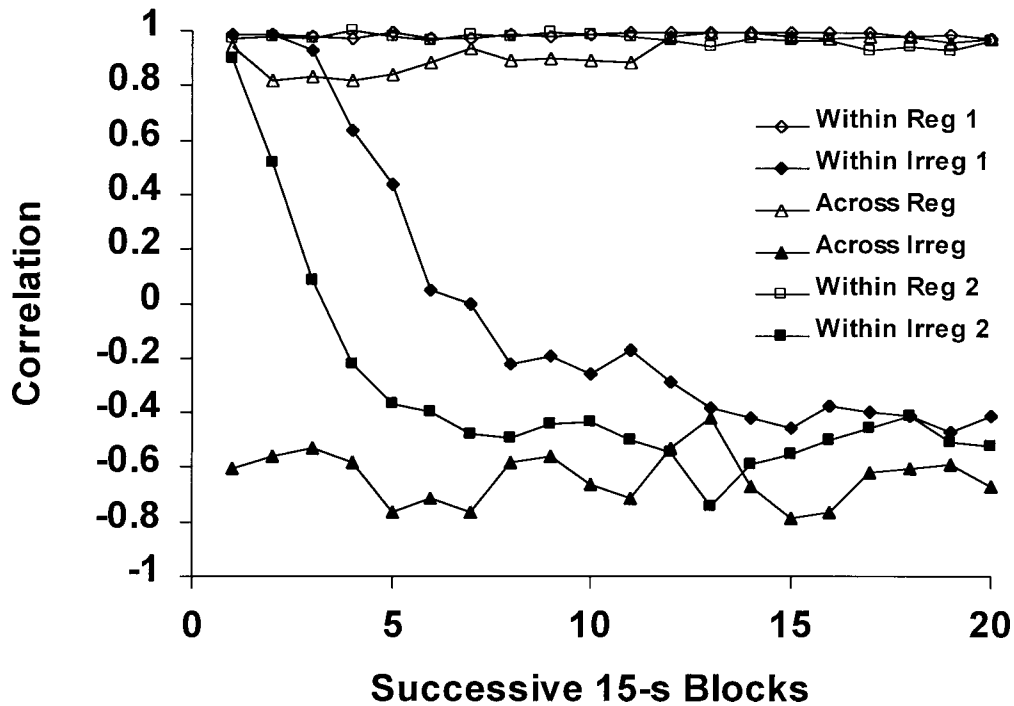


Fig. 2. Experiment 1: Pearson's r plotted as a function of successive 15-s blocks. Each point represents the correlation between the log forager ratio in the final 15 s of the previous resource-ratio presentation and the log forager ratio in each successive 15-s block of the following resource-ratio presentation.

1993). All regular conditions produced sensitivities slightly higher than comparable irregular conditions. Although consistent, these differences were too small to be considered reliable. Final sensitivities for the within-session presentations were similar to those for the across-session presentations.

DISCUSSION

Figures 1 and 2 show that the flock adjusted to changing resource ratios rapidly, even when resource ratios varied frequently and unpredictably. Whether resource ratios were maintained for 21 min and changed across days or were maintained for 5 min and changed within sessions, Figure 3 shows that after 3 min, the distributions of pigeons were similar. Because peas were delivered about every 2.0 to 2.5 s, this means that the flock adjusted on the basis of about 80 prey items (peas). For the 8:1 resource ratio, 72 peas at the rich site and 9 at the lean site would have sufficed. This might be compared with the finding of Davison and Baum (2000) with individual pigeons that adjustment was accomplished after about nine reinforcers. If the in-

dividual pigeons in the flock here each required eating or seeing several peas before the flock's distribution stabilized, that might account for the difference. Strictly with a view toward method, the experiment shows that the ideal free distribution may be studied with rapid variation of resource ratios within daily sessions (cf. Belke & Heyman, 1994; Davison & Baum, 2000).

Although the changes in sensitivity and correlation showed both carryover from previous resource ratios and high sensitivity to rapidly changing food distributions, the methods employed in Experiment 1 left room for doubt. Except for the 1:1 conditions, when a new resource ratio began, food items appeared at the rich site first. For instance, in an 8:1 ratio, seven peas were delivered to the rich site before a pea arrived at the lean site. Delivery of peas only to the rich site initially may have favored rapid adjustment. Informal observation indicated that all of the pigeons went to the rich site if seven peas in a row were delivered there first. Departure occurred only when a pea arrived at the other site. This regularity might have prevented effects of prior

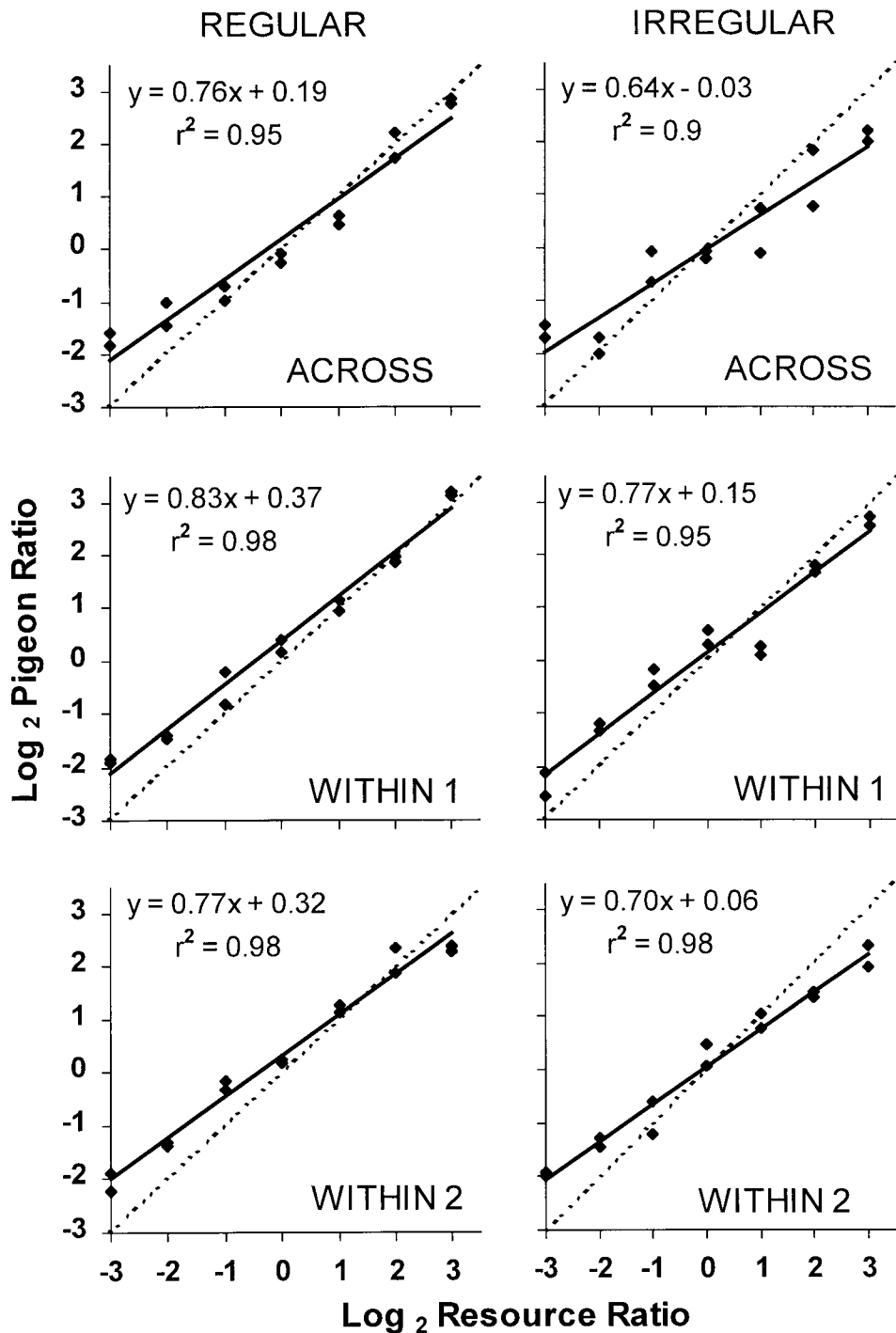


Fig. 3. Experiment 1: for the 4th and 5th minutes of resource-ratio presentations, the log ratio of the average numbers of pigeons at the two patches plotted against the log ratio of resources at the two patches. The solid lines were fitted by the method of least squares. The slope gives the sensitivity, and the coefficient equals log bias. The broken lines show the locus of perfect matching. Top left: regular resource-ratio presentations across daily sessions. Top right: irregular resource-ratio presentations across daily sessions. Middle left: regular resource-ratio presentations within sessions. Middle right: irregular resource-ratio presentations within sessions. Bottom left: replication of regular within-session presentations. Bottom right: replication of irregular within-session presentations.

Table 2
Ratios and durations used for each condition in Experiment 2.

Condition 1 Within Regular 1	Condition 2 Across Regular 2	Condition 3 Within Irregular 1	Condition 4 Across Irregular 1
8:1 5 min	8:1 Day 1	1:2 5 min	1:2 Day 1
4:1 5 min	4:1 Day 2	8:1 5 min	8:1 Day 2
2:1 5 min	2:1 Day 3	1:1 5 min	1:1 Day 3
1:1 5 min	1:1 Day 4	1:8 5 min	1:8 Day 4
1:2 5 min	1:2 Day 5	4:1 5 min	4:1 Day 5
1:4 5 min	1:4 Day 6	1:4 5 min	1:4 Day 6
1:8 5 min	1:8 Day 7	2:1 5 min	2:1 Day 7
Condition 5 Across Irregular 2	Condition 6 Within Irregular 2	Condition 7 Across Regular 2	Condition 8 Within Regular 2
Repeat Condition 4	Repeat Condition 3	Repeat Condition 2	Repeat Condition 1

experience. Because, in addition, the outdoor venue allowed wind and noise to disrupt the experiment occasionally, an additional experiment was undertaken, under more controlled conditions and with a different flock of pigeons, with the idea of both replicating Experiment 1 and seeking further for effects of previous experience.

EXPERIMENT 2

Experiment 2 was conducted in an isolated indoor coop, in which food items were delivered mechanically. In addition, instead of the food-delivery method used in Experiment 1, food items were delivered to each site simultaneously at the beginning of every resource-ratio presentation. Finally, using a different flock of pigeons offered the possibility of assessing the reliability of the results found in Experiment 1.

METHOD

Subjects. Subjects were a flock of 21 pigeons (*Columba livia*) housed at the University of New Hampshire Psychology Department's indoor pigeon coop, located in a windowless room (3 m wide, 6 m long, and 2.5 m high) lit with fluorescent lights, most of which went off during the dimly lit 12-hr dark period. All pigeons were maintained at 85% of their free-feeding weights for the duration of the study. Pigeons had constant access to water and grit. Sessions were conducted in the morning, about the same time each day. Following a

day's session, each pigeon was weighed and fed an amount of standard pigeon chow necessary to maintain its weight. All pigeons had prior experience with patch foraging experiments.

Apparatus. Foraging sites were two pieces of plywood (1.22 m square) covered with green Astroturf® carpeting. Each patch was enclosed in wooden borders (15 cm high) along its outer edges. The patches were raised on legs 15 cm to prevent the wood shavings that covered the coop floor from being blown onto them. A distance of 1.83 m (measured center to center) separated the patches, as in Experiment 1. Two video recorders mounted directly above the patches monitored foraging. Instead of the dried peas used in Experiment 1, food items used in Experiment 2 were 97-mg Noyes pigeon diet spherical tablets. Two electrically operated feeders mounted above the feeding sites delivered the pellets. Feeder operation was controlled by a microprocessor in the next room.

Procedure. Table 2 shows the order and duration of the resource ratios used in Experiment 2. These were the same as those employed in Experiment 1. Whereas sessions that contained all of the resource ratios in Experiment 1 were 39 min long, in Experiment 2 they were 35 min long; each resource ratio was presented for 5 min. During across-session conditions, resource ratios were presented daily in 21-min sessions. In Experiment 1, about 2.5 s separated prey items at the rich site, but in Experiment 2 this interval

was lengthened to 3 s. Thus, a pellet was delivered to the lean site every 6 s in a 2:1 ratio, every 12 s in a 4:1 ratio, and every 24 s in an 8:1 ratio. At the beginning of each resource-ratio presentation, two pellets were delivered to the two patches (one to each patch) simultaneously. Pellets were temporally spaced according to the resource ratio thereafter.

In Condition 1, resource ratios were presented within the session in regular order. Condition 2 was an across-session regular comparison. In Condition 3, within-session presentations were made in irregular order. Condition 4 was an across-session irregular comparison. Conditions 5, 6, 7, and 8 replicated Conditions 4, 3, 2, and 1, respectively. A 1:1 21-min session was presented between conditions to serve as a reset condition. This procedural change was designed to prevent carryover from the last ratio of a previous condition from biasing the first ratio of the current condition.

RESULTS AND DISCUSSION

As in Experiment 1, videotapes of experimental sessions were coded to obtain pigeon counts at each site. Counts were taken every 3 s and were averaged over 15-s blocks for the first 5 min of each ratio presentation. To compare across conditions, the parameters a and k of Equation 5 were obtained in the same manner as in Experiment 1.

Like Figure 1, Figure 4 shows slopes plotted as a function of successive 15-s blocks, except for the first point on each curve, which shows sensitivity calculated for the beginning of the resource-ratio presentations. As in Figure 1, carryover would produce positive initial sensitivities in the regular conditions and negative initial sensitivities in the irregular conditions. As in Experiment 1, the negative sensitivities at zero on the x axis show some carryover in the within-irregular conditions. In contrast with Experiment 1, however, sensitivities in other conditions begin near zero. The only exception is the first within-regular condition, which was also the first condition of the experiment. The second within-regular condition began near zero. These near-zero sensitivities suggest the absence of carryover. For the within-session presentations, the apparent lack of carryover resulted from the reset sessions between conditions; if the forager ratio at the beginning of the session is ig-

nored, the expected sensitivities appear (0.50 for the first within-regular condition and 0.63 for the second). For the across-session presentations, for which no reset sessions occurred between sessions, the near-zero initial sensitivities indicate an absence of carryover, as if the resource ratio of the prior session came to be irrelevant. In keeping with such an idea of "learned irrelevance," sensitivity in the first 15-s block of the first across-regular condition ($a = 0.35$, $r^2 = .53$) was higher than in the second across-regular condition ($a = 0.17$, $r^2 = .36$). Although sensitivity in the first 15-s block of the first across-irregular condition was positive ($a = 0.22$, $r^2 = .38$), contrary to an expectation based on carryover, the same sensitivity in the second across-irregular condition was close to zero ($a = 0.08$, $r^2 = .18$). Thus, repeated exposure to conditions in which resource distribution was less predictable may have led to decreased control by previous experience in favor of more control by current circumstances. Sensitivity rose across time in all conditions, stabilizing at about 0.5 after 3 min.

If repeated exposure to unpredictable foraging conditions resulted in decreased carryover and increased influence of current circumstances, then sensitivity also should increase faster in the initial minutes of a resource-ratio presentation. Examination of the top and bottom graphs in Figure 4 reveals that, with the exception of the across-regular conditions, sensitivity increased faster in the second presentation of the condition. This agrees with the speed-up in growth of sensitivity observed for the within-irregular conditions in Experiment 1: a faster increase in the replication than in the initial condition (Figure 1). The speedier adjustment suggests that exposure to highly variable foraging situations decreased the influence of the previous resource ratio in favor of the current resource ratio.

To assess carryover further, an analysis similar to that shown in Figure 2 was conducted. Figure 5 shows the forager ratios from the final 15 s of the previous resource ratio correlated with the forager ratios in successive 15-s blocks of the next resource ratio. As in Figure 2, the correlations begin and remain high for all the regular conditions, begin high and decrease to become negative for the within-irregular conditions, and begin and re-

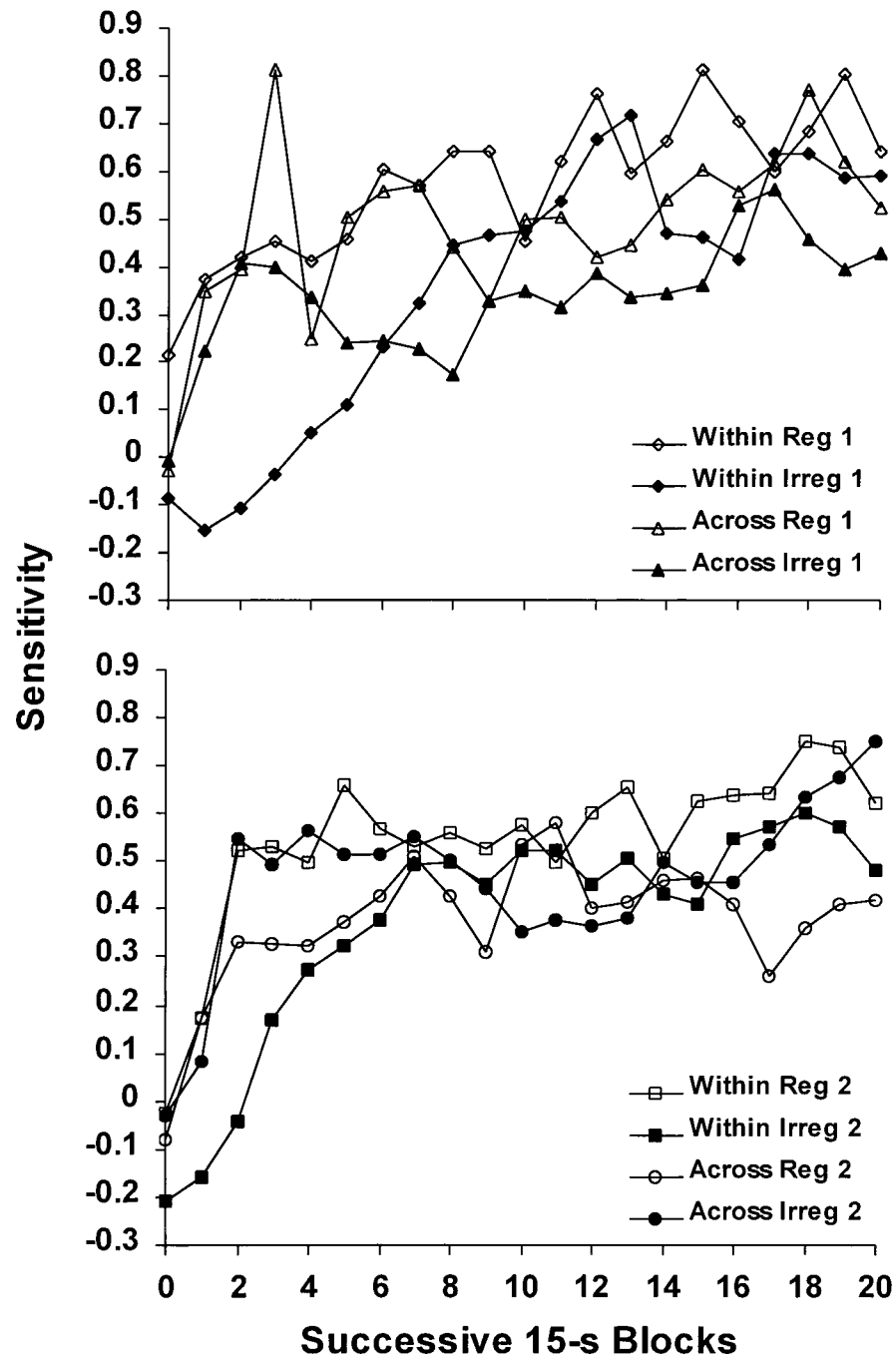


Fig. 4. Experiment 2: sensitivity (a in Equation 5) by 15-s block for the first 5 min of resource-ratio presentations in all conditions. Sensitivity was estimated by the method of least squares. Top: results for the initial presentation of each condition. Bottom: results for the replications.

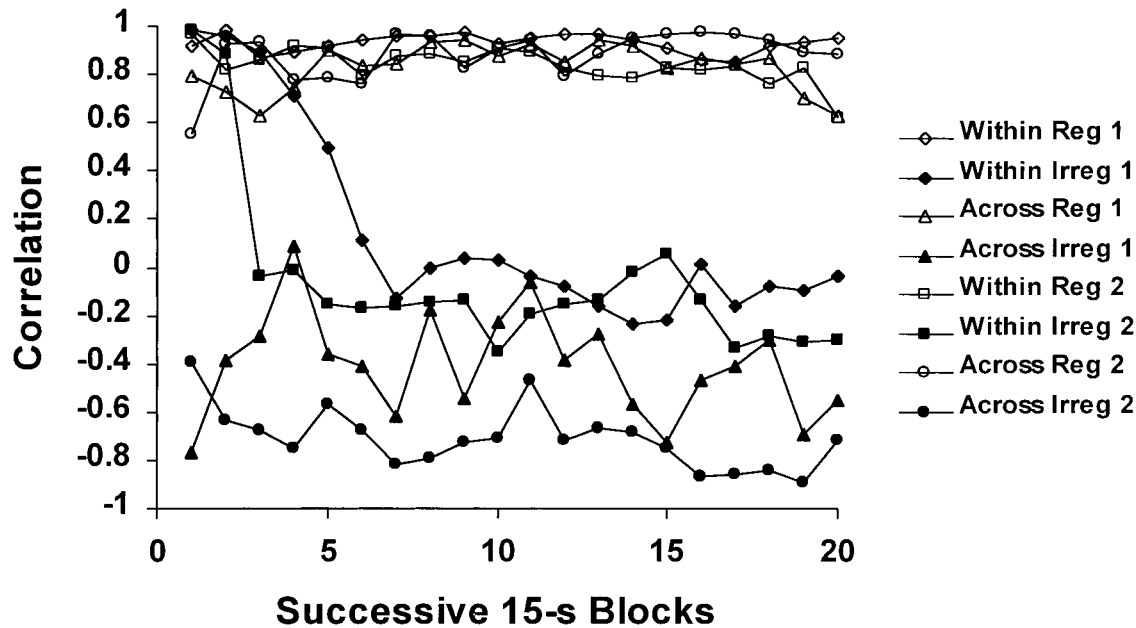


Fig. 5. Experiment 2: Pearson's r plotted as a function of successive 15-s blocks. Each point represents the correlation between the log forager ratio in the final 15 s of the previous resource-ratio presentation and the log forager ratio in each successive 15-s block of the following resource-ratio presentation.

main generally negative for the across-irregular conditions. The falls in correlation for the within-irregular conditions took place rapidly, falling below zero in less than 2 min. As in Figure 2, if experience increased control over distribution of pigeons by the present resource ratio, we would expect to see a slower decline in correlation in the first within-irregular condition than in the replication. Comparison of the two curves in Figure 5 reveals that the expected difference occurred in Experiment 2, as it did in Experiment 1. Although both across-irregular conditions showed negative correlations, the replication showed stronger and more stable correlations. The correlations from the replication resembled the correlations from the across-irregular condition in Figure 2, possibly reflecting the greater foraging experience of the flock used in Experiment 1.

Figure 6 shows log (Base 2) forager ratios from the 4th and 5th minutes of the resource-ratio presentations plotted against log (Base 2) resource ratio. The least squares regression lines represent Equation 5. Comparison with Figure 3 reveals that stable sensitivity tended to be lower in Experiment 2, ranging from 0.40 to 0.68. Although variance account-

ed for was uniformly high in Figure 3, three of the r^2 values in Figure 6 fell short of .90. Nevertheless, we may draw the same general conclusion that the sensitivities in all conditions converged after 3 min of exposure to the resource ratios.

GENERAL DISCUSSION

The main result was that even in a highly unstable environment flocks of pigeons distributed themselves between two resource patches within minutes and after remarkably few occurrences of food items per individual. By the end of 3 min (about 60 to 90 prey items), the flocks arrived at about the same sensitivity, regardless of frequency of change (across vs. within session) or regularity of presentation. Figures 1 and 4 reveal substantial overlap across conditions after 3 min. Figures 3 and 6, which summarize sensitivity for the last 2 min of the initial 5 min, reveal that, although sensitivity varied, the variation across conditions was unsystematic. It always came to about 0.75 (average for Experiment 1) or 0.54 (average for Experiment 2). Why sensitivity was lower in Experiment 2 than in Experiment 1 remains to be understood, be-

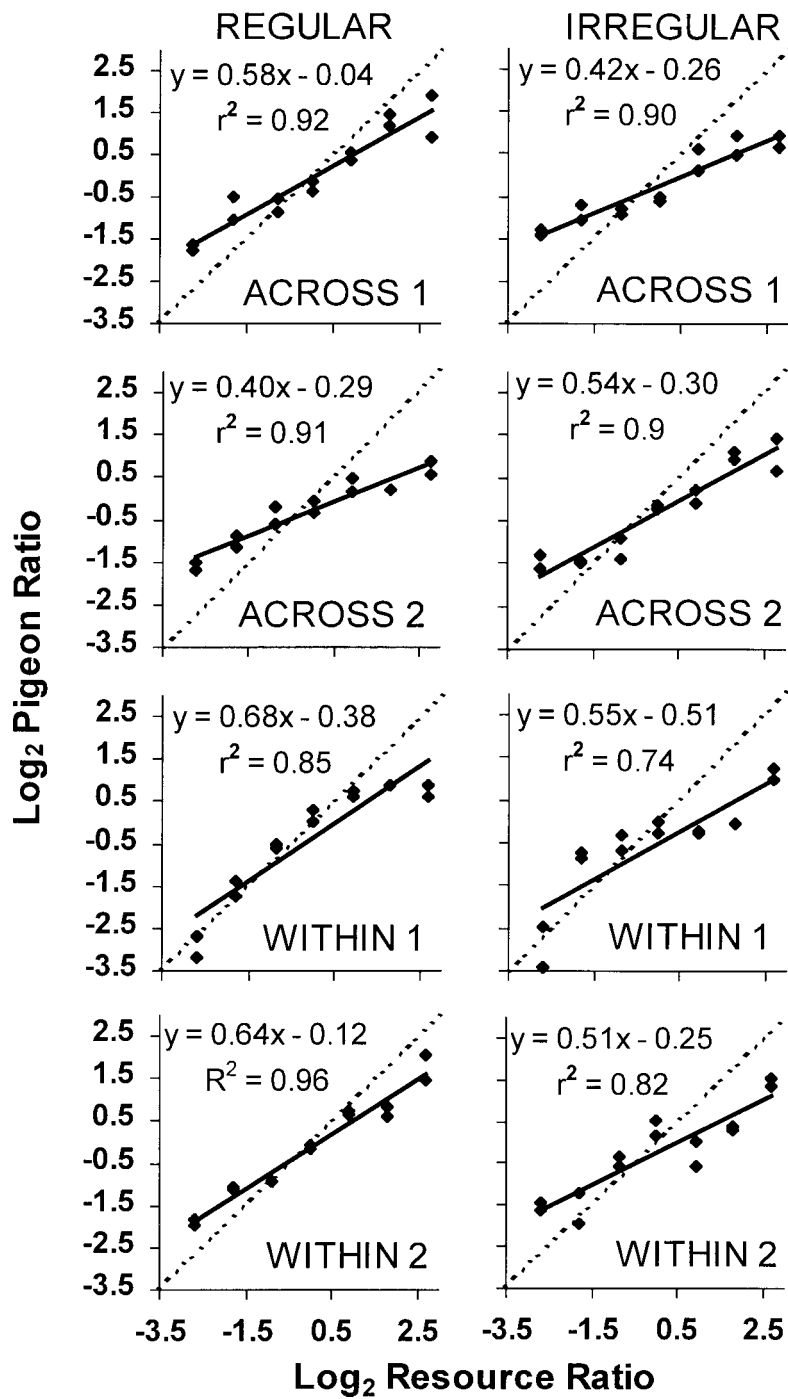


Fig. 6. Experiment 2: for the 4th and 5th minutes of resource-ratio presentations, the log ratio of the average numbers of pigeons at the two patches plotted against the log ratio of resources at the two patches. The solid lines were fitted by the method of least squares. The slope gives the sensitivity, and the coefficient equals log bias. The broken lines show the locus of perfect matching. Top left: regular resource-ratio presentations across daily sessions. Top right: irregular resource-ratio presentations across daily sessions. Second row left: replication of regular across-session presentations. Second row right: replication of irregular across-session presentations. Third row left: regular resource-ratio presentations within sessions. Third row right: irregular resource-ratio presentations within sessions. Bottom left: replication of regular within-session presentations. Bottom right: replication of irregular within-session presentations.

cause the differences between the two were numerous. Likely candidates could be the differences in flock experience, flock size, between-condition exposures to a 1:1 resource ratio, and feeding regimen. Future research might distinguish among these. That average difference aside, the results support the idea that a flock may adjust rapidly to changing resource ratios and that studies of the ideal free distribution with pigeons may be conducted with the more efficient method of varying resource distributions within daily sessions. These conclusions may be compared to those of Davison and Baum (2000) with respect to choice in individual pigeons.

The experiments described here were conducted to determine the relative dependence of group foraging on previous foraging experiences and on current patch profitability. In the regular presentations, we expected that previous experience would result in significant carryover from one resource ratio to the next, and Figures 2 and 5 show that it did. In the irregular presentations, for which resource ratios were less predictable, Figures 2 and 5 show no carryover in the across-irregular conditions and rapid dissipation of carryover in the within-irregular conditions. In a sense, however, one could argue that the irregular conditions might show effects of past experience, because of the regular alternation of rich and lean sites (Tables 1 and 2). Negative correlations at the beginning of a session (Figures 2 and 5) might show that the flock discriminated the alternation by switching from the previously rich to the previously lean (now to-be-rich) patch. Evidence in favor of this idea appeared in the increasingly negative and stable correlations from the first across-irregular condition to the replication in Figure 5 and in the speedier drop in correlation in the within-irregular replications in both experiments (Figures 2 and 5). Such changes are consistent with the idea that the flocks' experience with the irregular presentations not only increased their reliance on present resource ratio but also allowed some response to the more global pattern of rich-lean alternation.

The patterns of carryover ought to affect estimates of sensitivity (the parameter a in Equation 5), and they did. Sensitivity in the regular presentations and in the across-irregular presentations was positive in the first 15

s, whereas sensitivity in the within-irregular presentations started out negative (Figures 1 and 4). Sensitivity grew, however, in all conditions, and did so rapidly even in the within-irregular presentations.

In sum, the present results suggest that foragers rely on prior information from exposure to feeding sites that differ in resource profitability, but that this reliance may be quickly overridden by current resource profitabilities. This conclusion is supported by the findings from both experiments that regular presentation resulted in positive sensitivity at the beginning of resource-ratio presentations, that irregular presentation resulted in negative sensitivity at the beginning of resource-ratio presentations, that forager ratio at the end of one resource ratio was often highly correlated with forager ratio at the beginning of the next, and that sensitivity and correlation shifted rapidly in the within-irregular conditions. The degree of carryover, however, depended on how variable the foraging environment was. In the more stable environments (across-session presentations), carryover was high if presentation was regular, but when presentation was irregular, carryover was suppressed in favor of dependence on current profitabilities. This agrees with the finding of Schofield and Davison (1997), for individual pigeons, that choice was more controlled by present reinforcement schedules when resource ratios were presented in an irregular (pseudorandom) sequence. The present finding of rapid adjustment in the within-irregular conditions agrees with the finding of Davison and Baum (2000), for individual pigeons, that when reinforcer ratios change frequently and irregularly, choice comes to depend largely on local conditions of food occurrence.

The present study may provide evidence for adaptive response to global aspects of foraging environments. The two flocks of pigeons had never been exposed to the highly variable foraging conditions of the within-session presentations. Both flocks demonstrated an increase in speed of adjustment from the initial condition to the replication (Figures 1, 2, 4, and 5). That is, adjustment to the current resource ratio was enhanced in a within-irregular condition following previous exposure to that type of condition. Considering that resource availability in nature may be

highly unpredictable, the optimal strategy for foraging organisms should be to rely on a combination of past experience with present foraging success, and to adjust rapidly when feeding sites lose their predictability. The findings in this study confirm this pattern of behavior.

Further research using the ideal free distribution to predict forager distribution might make use of the effect of prior exposure to different distributions of resources. Further, the rapid adjustment to variable resource distributions suggests that experimental sessions can be relatively short in duration. Like the present studies, previous experiments found that equilibrium distributions can occur rapidly and remain stable throughout sessions. For instance, Harper (1982) found that ducks on a pond distributed within 2 min. Even though previous research has found that equilibrium distributions can occur rapidly, most of the studies have used stable resource ratios in effect over lengthy time periods. Few studies have used periods of 7 min or less to analyze group foraging (Godin & Keenleyside, 1984). The present findings indicate that equilibrium distributions can occur in nonstable resource ratios over very short periods.

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