JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR 1998, **69,** 227–245 NUMBER 3 (MAY)

GROUP CHOICE: COMPETITION, TRAVEL, AND THE IDEAL FREE DISTRIBUTION

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If a group of foragers distributes among resource patches according to the ideal free distribution, the relative number of foragers in each patch should match the relative amount of resource obtained there, unless deviations arise from factors such as incomplete information or interforager interference. In analogy to individual choice, such effects may produce undermatching—group distribution falling short of resource distribution—or overmatching—group distribution overshooting resource distribution. In the present experiments, a flock of about 30 pigeons distributed between two patches with continuous inputs of green peas. Competition was varied by changing the size or extent of the patches. When the patches were areas or troughs, some undermatching occurred. When the patches were small bowls, strong undermatching occurred. When travel was required to switch patches, undermatching decreased slightly. A visual barrier that prevented pigeons from seeing one patch from the other had no effect. Overall rate of food delivery, varied over a wide range, had no effect. It appeared that the mechanism of flock distribution depended on comparisons between patches that were successive rather than simultaneous. Although most pigeons participated in the experiments, and different pigeons participated to different extents, individual pigeons tended to be consistent in the extent of participation from session to session, suggesting the possibility that participation might reflect competitive ability. Examination of the preferences and switching of individual pigeons revealed no consistency within or across individuals. It appeared that the flock's distribution was a truly emergent phenomenon, in the sense that results at the level of the flock in no way paralleled behavior at the level of the individual.

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

The ideal free distribution is a theory that, combined with additional assumptions, permits prediction of the distribution of a group of foragers (predators or parasitoids) between two or more food sources or patches (Fretwell & Lucas, 1970; Gray, 1994; Tregenza, 1994; Tregenza, Parker, & Thompson, 1996). It expresses the idea that individuals tend to optimize energy intake by going to or staying in the patch where they achieve the highest net gain, which, if the two patches offer the same type of prey, means the highest capture rate. Because the average capture rate of an individual in a patch depends on the number of others foraging there, individuals' switching should result in all individuals obtaining the same capture rate.

For the theory to make specific predictions about group distribution in relation to resource distribution, additional assumptions must be made about the dependence of average individual capture rate (r^*) on amount or density of the resource available (A) and the number of foragers present (N). In other words, one must make assumptions about a function f of the sort

$$r^* = f(A, N). \quad (1)$$

For example, a simple function one might assume would be

$$r^* = \frac{cA}{N}, \quad (2)$$

which says that the N predators share the resource among themselves in such a way that the average is one Nth of what is available. If there were two patches, and one assumed the same functional form f for both, then the idea of equal capture rates, coupled with Equation 2, leads to

$$\frac{A_1}{N_1} = \frac{A_2}{N_2}, \quad (3)$$

where A_1 and A_2 are the availabilities at Patches 1 and 2, and N_1 and N_2 are the numbers of predators in Patches 1 and 2. When Equation 3 is rearranged, it becomes a group matching equation:

We thank Suzanne Mitchell for helpful comments and Ken Bell, Le'Ann Milinder, and Jed Schwendiman for help gathering the data.

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$$\frac{N_1}{N_2} = \frac{A_1}{A_2}, \tag{4}$$

which states that the relative numbers of predators in the two patches match the relative resource availabilities in them.

Equation 4 resembles an individual matching equation that has been the subject of much research:

$$\frac{B_1}{B_2} = \frac{r_1}{r_2}, \tag{5}$$

where B_1 and B_2 are behavior, measured in responses or time, allocated by an individual to Sources 1 and 2, and r_1 and r_2 are the rates of reinforcement (usually food) obtained from Sources 1 and 2. Equation 4 is a relation describing group choice, whereas Equation 5 is a relation describing individual choice.

In practice, ratios measured as specified in Equation 5 are fitted by a linear equation in logarithmic coordinates (Baum, 1974, 1979):

$$\log\left(\frac{B_1}{B_2}\right) = s \log\left(\frac{r_1}{r_2}\right) + \log b. \tag{6}$$

The parameters b and s, called *bias* and *sensitivity,* account for deviations from simple matching (Equation 5; b and s both equal to 1.0). Bias accounts for characteristics of the food sources that affect choice but remain invariant as the rates of obtaining food change. Sensitivity accounts for characteristics of the food sources that might change with the rates of feeding, such as discriminability of sources or cost of feeding. When such factors augment the attractiveness of a high rate of feeding over a lower one, they lead to overmatching (s greater than 1.0); when they diminish the attractiveness of a high rate relative to a lower rate, they lead to undermatching (s less than 1.0) (Baum, 1974, 1982). Both results have been found, but undermatching is more common (Baum, 1979).

An equation for group matching parallel to Equation 6 has been proposed (Fagen, 1987; Houston, McNamara, & Milinski, 1995; Kennedy & Gray, 1993):

$$\log\left(\frac{N_1}{N_2}\right) = \frac{1}{m} \log\left(\frac{A_1}{A_2}\right) + \log b. \tag{7}$$

The expression $1/m$ is substituted for s on the theory that sensitivity ought to vary inversely with the extent to which the predators in a patch interfere with one another's foraging, m representing the degree of interference (Gray, 1994; Sutherland, 1983; Tregenza, 1994; Tregenza et al., 1996). When such interference occurs, it should vary with the number of predators, affecting the average individual rate of capture obtained (Equation 1). It would increase m in Equation 7 and produce departures from the simple sharing assumption of Equation 2.

A key difference between the individual matching relation (Equations 5 and 6) and the group matching relation (Equations 4 and 7) is that the group matching relation is expressed in terms of resources *available,* whereas the individual matching relation is expressed in terms of resources *obtained*. The individual matching relation incorporates no function like Equation 1, which would relate obtained resources to available resources. In the study of operant behavior, such a function would be called a *reinforcement feedback function* and would be considered to be a property of the environment, whereas the matching relation would be considered to be a property of the organism (Baum, 1973, 1989).

The distinction between resources available and resources obtained also applies to the ideal free distribution, because the theory specifies that the group distributes in such a way that every patch provides the same average individual capture rate; that is, the obtained rate is shared, regardless of availability (Equation 1). The theory predicts a group matching relation to resources obtained:

$$\frac{N_1}{N_2} = \frac{r_1}{r_2}, \tag{8}$$

where r_1 and r_2 are the resources obtained collectively by the N_1 and N_2 predators in Patches 1 and 2.

Equation 8 differs from Equation 4 in the key respect that no assumption is made about available resources or the form of f in Equation 1 (in particular, no such assumption as Equation 2) because Equation 8 stops at the resources obtained. If the distinction between obtained and available resources is overlooked, misunderstanding may occur. For example, Tregenza (1994) correctly pointed out that the ideal free distribution necessitates no matching to resources available (Equation 4), but failed to recognize that it does necessitate matching to resources obtained (Equation 8). Even a review by Kennedy and Gray (1993) that pointed out the parallel between the individual and group matching relations failed to make the distinction. Although they wrote as if they were applying Equation 7, they were implicitly applying the generalization of Equation 8, matching to obtained resources:

$$\log\left(\frac{N_1}{N_2}\right) = s \log\left(\frac{r_1}{r_2}\right) + \log b. \qquad (9)$$

Due to this ambiguity, their discussion has been misunderstood, dismissed, or ignored (Moody & Houston, 1995; Tregenza, 1994).

Several writers have emphasized a distinction between two types of patches: (a) those in which prey arrive from time to time at a certain rate (the rate of continuous input), and the predators must wait to capture them; and (b) those in which some abundance of prey exists over the area (a standing crop), and the predators must search for the prey to capture them (Lessells, 1995; Moody & Houston, 1995; Tregenza, 1994). It is argued that in a standing crop social interaction may reduce search efficiency (e.g., by wasting time; Beddington, 1975; Free, Beddington, & Lawton, 1977), whereas when prey arrive in a continuous input, they are eaten more or less immediately, without social interaction or time wasted.

This argument depends on the incorrect assumption that when a predator sits and waits for prey it does nothing. Locomotion is only the most obvious aspect of search; the predator still must detect the prey. Because detection precludes other activity in much the same way as locomotion does, social interactions interfere with detection in much the same way as they interfere with locomotion. Although social interactions in a group of predators that are searching interfere with both locomotion and detection, social interactions in a group of predators that are waiting still interfere with detection. Both search and waiting (plus detection) may be thought of as behavior under the control of consequences (producing prey), that is, operant behavior (Dallery & Baum, 1991; Shettleworth, 1988). Among behavior analysts, waiting and detecting is known as *observing* or *vigilance* (Baum, 1975; Wyckoff, 1952).

Contrary to the argument that interference should be lower or absent in a continuous-input patch compared with a standing crop, the difference might actually go the other way around. Interference in a continuous-input patch might be higher if dominant and subordinate individuals compete over the same prey item. Although such face-to-face competition might occur occasionally in a standing crop, it might occur virtually every time a prey item arrived in a continuous input. If so, the effects of dominance relations in continuous-input patches are potentially much larger.

Interference may affect not only search and detection but also switching. If dominant individuals or superior competitors congregate in the richer patches, they may interfere with subordinate or inferior individuals' switching into the richer patches, forcing them to congregate in the leaner patches. The result would be too few foragers in the richer patch and too many in the leaner patch, producing a slope s in Equation 9 less than 1.0 (or a value of m in Equation 7 greater than 1.0). Such an effect might be offset by using a version of the ideal free distribution that accounts for unequal competitive weight among the foragers (Milinski & Parker, 1991). For example, Grand (1997) found that the proportion of individuals foraging in a richer patch fell short of the proportion of resources there, whereas the proportion of total competitive weight matched the proportion of resources.

Tregenza (1994) suggested that if interference is low, the distribution of a group might be more extreme than the ideal free distribution would predict, whereas if interference were high, the distribution of the group might be less extreme than predicted. By analogy to Equation 6, dealing with individual choice, these would be called overmatching (s greater than 1.0 in Equation 9) and undermatching (s less than 1.0 in Equation 9) in group choice. If predators interfere heavily with one another's detection and with one another's switching in continuous-input patches, then one might expect to find frequent undermatching in Equation 9 (or m greater than 1.0 in Equation 7). The greater the interference, the smaller the sensitivity to changes in the distribution of resources.

Kennedy and Gray (1993) found several

data sets from studies of group foraging that required a slope less than 1.0 for a least squares fit to Equation 9 (group undermatching). This would imply a value of *m* greater than 1.0. Although such a result might indicate high interference, Kennedy and Gray suggest some other possibilities, including perceptual limits to detecting differences between food sources, unequal competitive abilities among the predators, and travel requirements between patches (Gray & Kennedy, 1994; Spencer, Kennedy, & Gray, 1995).

To manipulate interference experimentally, one may vary the number of foragers, on the assumption that higher density of foragers ought to increase their interactions. Gillis and Kramer (1987), varying the size of groups of zebrafish, found that the group distribution changed from slight overmatching when density was low to more and more undermatching as density of foragers increased, in accordance with Tregenza's (1994) speculation. One may also manipulate interference by varying the size of the patches while leaving the number of foragers the same. Point sources ought to engender more competition and interference than extended sources do. The present study used bowls, troughs, and areas as patches, reasoning that competition would be highest with bowls, less for troughs, and least for areas.

The present experiments aimed both to test some of the possibilities raised by Kennedy and Gray (1993) and to gain some insight into the mechanisms by which a flock of pigeons distributes between two continuous-input patches. The different patches allowed us to determine whether sensitivity would decrease as patch size decreased. Because the perceptual limit account of undermatching predicts increased sensitivity as overall rate of prey delivery increases, both relative and overall rate of prey delivery were varied. To examine the role of switching, travel was also varied, to determine whether increased travel would lower switching frequency and increase sensitivity. To test the possibility that pigeons in one patch compare simultaneously what is happening in that patch with what is happening in the other patch, a barrier was used in one condition to prevent such visual comparison.

METHOD

Subjects

The flock of domesticated pigeons (mixed White Carneau and Silver King; *Columba livia*) contained about 30 individuals. Deaths and births caused the size of the flock to vary from 20 to 32 over the 3 years of the study, but the size was usually within a few birds of 30. They were fed a daily ration of pigeon chow after each experimental session that was large enough to maintain them but small enough to ensure a high level of participation. The flock was housed in a coop with a wire-mesh flyway attached. The flyway was 2.7 m wide, 3 m high, and 18 m long. The half closer to the coop, in which the experiments were conducted, had a solid roof.

Apparatus

Three types of patches were used: areas, troughs, and bowls. The areas consisted of pieces of indoor-outdoor carpeting (1.2 m square) surrounded on three sides by boards ("two by fours" [4 cm by 9 cm]) lying flat. In Phase A1, in which the two areas were separated by 1.2 m, requiring travel, the two boardless edges faced one another. Because the width of the flyway was insufficient to place the two separated patches across it, one had to be placed nearer the coop and one farther from the coop. The one closer to the coop was called the north patch, the one farther away was the south patch. In Phases A2 and A3, in which the areas were adjacent, a low (a two by four on edge) or high (the low barrier with a 30-cm high piece of plywood mounted on top) barrier separated those two sides. The high barrier prevented the pigeons from seeing events on one patch from the other. The adjacent areas were placed across the flyway, one being called the east patch and one the west patch. The troughs, fashioned from pieces of plastic rain gutter, were white inside and were 15 cm wide, 15 cm deep, and 1.2 m long. A bar across the top prevented pigeons from climbing into the trough while permitting them to eat from it on either side. The troughs were placed on opposite sides of the flyway, one on the east and one on the west, 1.2 m apart. The bowls were pet feeders obtained from a local supermarket; they were light blue plastic with a rounded bottom, 15 cm in inside diameter and 10 cm deep. They were placed on opposite sides of the flyway, one on the east and one on the west, 1.2 m apart. Pigeons could peck in either bowl from any direction.

The prey consisted of whole dried green peas obtained from a local supermarket and purged of any that were broken or unusually small. They were delivered by hand into each patch through a funnel on the outside of the flyway that was attached to a tube going into the flyway. Care was taken to make sure that the peas arrived in the troughs and areas at speeds low enough that they varied as much as possible in where they came to rest. In practice, the peas were highly unpredictable, because they bumped and rolled in the patches. With the area patches, shields were put up on the sides of the flyway to prevent the pigeons from seeing when an experimenter delivered a pea.

In those phases in which individual pigeons were identified, each pigeon wore a tag (5 cm by 8 cm) on its back with a number marked on it.

When sufficient manpower was available, pigeon counts were recorded on the spot, but most sessions were videotaped with standard camcorders and were coded afterwards. When two camcorders were used, the two videotapes were played back simultaneously, and sound signals were used to synchronize the playback, insuring that any pair of pigeon counts for the two patches were taken at the same moment.

Procedure

General. Experimental sessions were conducted 4 or 5 days per week, in the middle of the day, at about the same time each day, one session per day. After setting up, the experimenters left the flyway. This proved to be a sufficient signal for the pigeons to begin collecting at the patches. An experimenter stationed outside the flyway next to each patch delivered peas at variable intervals according to a printed schedule. Except for the rapid-presentation conditions, the schedules consisted of intervals generated by the method of Fleshler and Hoffman (1962) in irregular order. The intervals averaged 7.5 s (8 peas per minute), 15 s (4 peas per minute), or 30 s (2 peas per minute). In the rapid-presentation conditions, one experimenter delivered peas to the rich patch as fast as the pigeons ate them—a new one each time the previous one had been eaten—while the other experimenter delivered a pea at the lean patch at about the same time as every second or fourth pea delivered to the rich, generating a 2:1 or 4:1 ratio of rates. All sessions lasted 21 min. Preliminary sessions accustomed the pigeons to eating from the patches.

Each phase consisted of several conditions. Except when delivery rates were the same at both patches or otherwise noted, 2:1 ratios alternated sessions with 1:2 ratios, and 4:1 ratios alternated with 1:4 ratios. This was meant to prevent the flock from developing a bias toward one patch or the other. Table 1 summarizes the phases, conditions for which data were available, and the order of sessions.

Phase A1: Separated areas; low competition with travel. A study of 4 peas per minute paired with 8 peas per minute and 2 peas per minute paired with 8 peas per minute was conducted initially, and a replication was conducted about a year later (Table 1). The data were all extracted from videotapes.

Phase B1: Troughs; moderate competition with travel. Seven conditions were studied, including ones with deliveries at variable intervals and ones with rapid presentation (Table 1). Data were extracted from videotapes.

Phase C1: Bowls; high competition with travel. Four conditions were studied, three in which rich and lean patches alternated sides and one in which four sessions in a row arranged 2 peas per minute delivered to the bowl on the east and 8 peas per minute to the bowl on the west, to test whether preference increased with repeated trials the same (Table 1). Data were extracted from videotapes.

Phase A2: Adjacent areas; low competition with no travel. Three conditions were studied (Table 1). The data were all recorded on the spot, with no videotapes.

Phase A3: Adjacent areas; low competition with a visual barrier. Two conditions were studied. Rich and lean sides alternated throughout (Table 1). Data were extracted from videotapes. Four of the 11 sessions were omitted from analysis due to low participation, defined as fewer than 9 pigeons on average on the two patches combined.

In a subsequent replication, three conditions were studied. One session was conducted with 4 peas per minute delivered to both areas. In the other eight sessions, rich and

Table 1

Summary of the phases, conditions, and dates of sessions of each condition for which data were available.

Phase	Condition (peas per minute)	Sessions
A1: Separated areas	4:8 and 8:4	8/8, 10 and 8/7, 9/95
	2:8 and 8:2	8/20, 22 and 8/18, 21/95
Replication	4:8 and 8:4	10/14, 18, 25 and 10/9, 16, 24/96
	2:8 and 8:2	11/1, 5 and 10/29, 11/4/96
B1: Troughs	2:4 and 4:2	10/25 and 10/26, 27, 28/94
	4:8 and 8:4	11/2, 4 and 11/1, 3/94
	2:8 and 8:2	11/7, 9 and 11/8, 10/94
	8:8	11/11/94
	4:4	11/14/94
	1:2 and 2:1, rapid presentation	11/17 and 11/16, 21/94
	1:4 and 4:1, rapid presentation	11/22 and 11/23/94
C1: Bowls	2:8 and 8:2	7/12, 15 and 7/11, 14/94
	2:4 and 4:2	7/20, 22 and 7/18, 21/94
	4:8 and 8:4	7/26, 28 and 7/25, 27/94
	2:8	8/2, 3, 4, 5/94
A2: Adjacent areas	8:8	3/21, 22, 23/95
	4:8 and 8:4	3/28, 30 and 3/29, 4/4/95
	2:8 and 8:2	4/11, 13 and 4/12, 18/95
A3: Areas + visual barrier	4:8 and 8:4	6/21 and 6/8/95
	2:8 and 8:2	6/12, 15, 23 and 6/14, 22/95
Replication	4:4	10/30/95
	4:8 and 8:4	11/6, 9 and 10/31, 11/7/95
	2:8 and 8:2	11/13, 16 and 11/14, 20/95

lean sites alternated (Table 1). The data were all recorded on the spot.

RESULTS

Data Analysis

For recording numbers on the spot and for coding the videotapes, pigeons were counted as follows. For the areas, a pigeon was counted as foraging if it had two feet on the carpeting; pigeons on the boards edging the areas were omitted. For the troughs and bowls, a pigeon was counted if its center was within a body length of the bowl or trough and it was oriented toward the bowl or trough (i.e., if the axis of its body formed an angle of 90° or less with the direct line to the bowl or trough). These conventions reflected our experience as to which pigeons might actually eat the next pea delivered and aimed to count only those pigeons.

Numbers from individual sessions were summarized by calculating, for each patch, the mean of the pigeon counts from the middle 15 min of the session. The first 3 min of the session were discarded because the numbers often started out far from where they stabilized; the flock appeared to adjust during the first minute or two. The last 3 min of the session were discarded because the numbers occasionally dropped near the end of the session. It is unlikely that this was due to satiation, because fewer than 250 peas were delivered, usually to 15 or more pigeons, and at least 30 peas are required to fill a pigeon's crop. More likely, some pigeons' behavior was sensitive to the fixed duration of the sessions; they may have been moving to perches in anticipation of the experimenters entering the flyway at the end of 21 min.

Figure 1 shows the course of a typical session. At the outset, there were more pigeons in the lean patch than in the rich patch, but this reversed within a minute. Toward the end of the session, the numbers dropped off (the reason for omitting the last 3 min). Two minutes before the end of the session (fifth pair of points from the end), a startle event may be seen. Occasionally, most of the flock would fly for no apparent reason, but they would

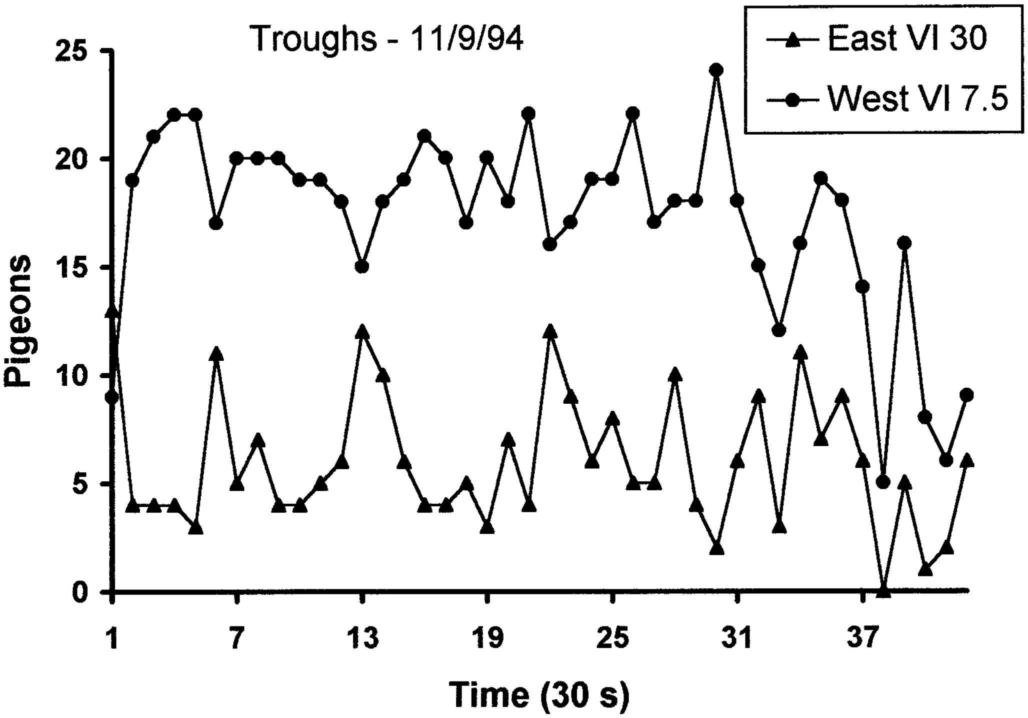

Fig. 1. A typical session. Peas were delivered at variable intervals averaging 7.5 s on the west, the rich patch, and 30 s on the east, the lean patch. The number of pigeons at each patch was recorded every 30 s. A startle event may be seen at the fifth point from the end. Adjustment at the beginning and anomalies near the end were omitted by averaging the middle 15 min.

usually return within 30 s. These events had no significant effect on the means; using medians, which would exclude such outliers, produced no systematically different results from using means. A ratio of the mean number of pigeons on one side divided by the mean number on the other side was calculated for each session.

Areas, Troughs, and Bowls

Figure 2 shows the distribution of pigeons in relation to the distribution of food for Phase A1. Each point represents one session. The broken line represents the locus of matching between pigeon ratio and resource ratio. The solid line was fitted by the method of least squares; its equation appears in the figure as a power law, which appears as a straight line (cf. Equation 9) in these logarithmic coordinates. The exponent 0.79 gives the slope of the line (s in Equation 9), and the coefficient 0.94 gives the antilogarithm of the intercept of the line, the bias (b in Equation 9). There was almost no bias, but the slope indicates some undermatching. The subsequent replication confirmed the undermatching, with a slope of 0.74 ($r^2 = .93$), but with some bias in favor of the north patch ($b = 1.41$).

Figure 3 shows the distribution of the flock in relation to the distribution of food in Phase B1 for the variable-interval conditions (top panel) and the rapid-presentation conditions (bottom panel). There was little bias in either data set ($b = 1.02$ and $b = 0.95$), and the slopes were equal ($s = 0.71$). When both data sets were combined, the slope of the fitted line equaled 0.71, the bias equaled 1.00, and r^2 equaled .95. The degree of undermatching was about the same in Figure 3 as it was in Figure 2. A t test for the difference between slopes was nonsignificant, $t(22) = 0.799$; $p > .4$. (Here and in other comparisons of slopes, t tests for independent samples were used on the theory that, even though the slopes were produced by the same flock of pigeons, the absence of any order effects

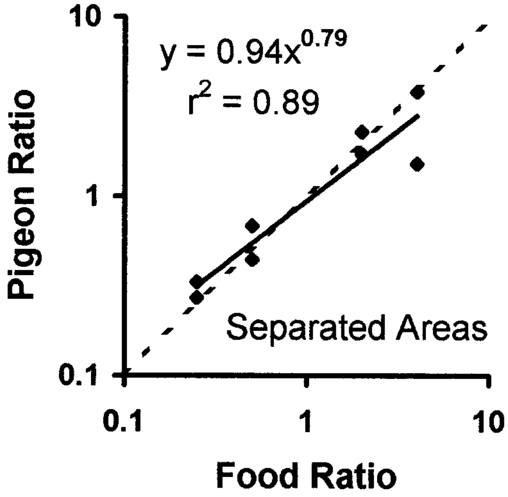

Fig. 2. Group distribution with areas separated by 1.2 m (Phase A1). The ratio of the average number of pigeons on the north patch to the average number on the south is plotted against the ratio of the rates of pea delivery for each session. The solid line was fitted by the method of least squares. In these logarithmic coordinates, its equation is equivalent to the power function shown, the exponent giving the slope (i.e., sensitivity), and the logarithm of the coefficient (i.e., bias) giving the intercept. The broken line shows the locus of perfect matching.

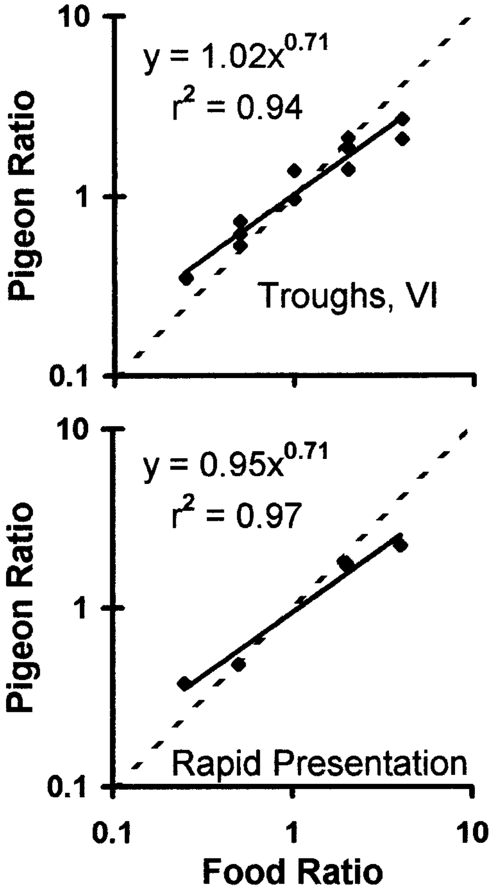

Fig. 3. Group distribution with trough patches separated by 1.2 m (Phase B1). The ratio of the average number of pigeons at the east trough to the average number at the west is plotted against the ratio of the rates of pea delivery for each session. Top: peas delivered according to variable-interval schedules. Bottom: peas delivered by rapid presentation, that is, as fast as they were eaten on the rich patch and at half or quarter that rate on the lean patch. See Figure 2 for details.

indicates that the samples may be considered independent.)

Figure 4 shows the distribution of the flock in relation to the distribution of food for Phase C1. There was little bias (b = 1.15), but considerable undermatching (s = 0.38). A subsequent replication confirmed these results (b = 1.03, s = 0.33, and r^2 = .90). The statistical significance of the lower slope in Figure 4 compared with the slopes in Figures 2 and 3 was verified by t tests; the values of p were less than .0005: $t(20)$ = 4.849 for areas versus bowls; $t(30)$ = 6.775 for troughs versus bowls.

Figure 5 shows pigeon ratio plotted against overall rate of pea delivery. The pigeon ratios are the same as in Figures 3 and 4. The overall rates of pea delivery were calculated for the conditions with variable-interval schedules from the scheduled rates (e.g., if peas were delivered at intervals averaging 30 s on one side and 7.5 s on the other, the overall rate was 10 per minute), but were measured from the videotapes for the rapid-presentation conditions. Each line connects two or more conditions in which the food ratio was the same. The figure includes all conditions for the bowls and troughs (Figures 3 and 4) for which such comparisons could be made. Few of the lines show any appreciable slope. The longest lines, for troughs with rapid presentation included, going out to about 25 peas per minute, show a slope close to zero. There appears to be no relation between pigeon ratio and overall rate of delivering food.

Although overall food rate had no effect on pigeon ratios, it had an effect on the within-session variability in the pigeon numbers. Figure 6 shows variance (n = 30) among 30-s samples in the middle 15 min of sessions

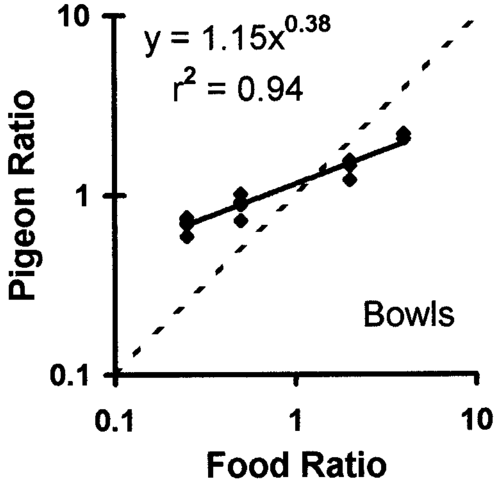

Fig. 4. Group distribution with bowl patches separated by 1.2 m (Phase C1). The ratio of the average number of pigeons at the east patch to the average number at the west is plotted against the ratio of the rates of pea delivery for each session. See Figure 2 for details.

with troughs (Phase B1) plotted as a function of overall rate of delivering peas, as in Figure 5. Each point represents one session. There was a strong downward trend in variance as rate of feeding increased. The different symbols indicate the results from rich and lean patches in the various 2:1 and 4:1 conditions. Because there appeared to be no systematic difference between rich and lean patches or between 2:1 and 4:1 conditions, the decrease in variability may be attributed entirely to the increase in overall density of food. The 2:1 conditions for bowls revealed a similar downward trend in variance, although the range of overall delivery rates was only 6 to 12 peas per minute.

Figure 7 shows the distribution of pigeons in relation to the distribution of resources for Phase A2. As in Figures 2, 3, and 4, each point represents one session, the coordinates are logarithmic, the broken line represents perfect matching, the solid line was fitted by the method of least squares, and its equation appears as a power function, which corresponds to the solid line in these logarithmic coordinates. There was little bias (b = 0.92), but considerable undermatching (s = 0.61). The line fitted the data well (r^2 = .93). Comparison with the results of Phase A1 (Figure 2 and the replication) suggests that requiring 1.2 m of travel in Phase A1 may have increased the sensitivity (s in Equation 9) of the flock's distribution. When the difference in slopes was tested for significance with a t test, however, the difference was nonsignificant, $t(15) = 1.490$; $p = .08$ (comparing with Fig-

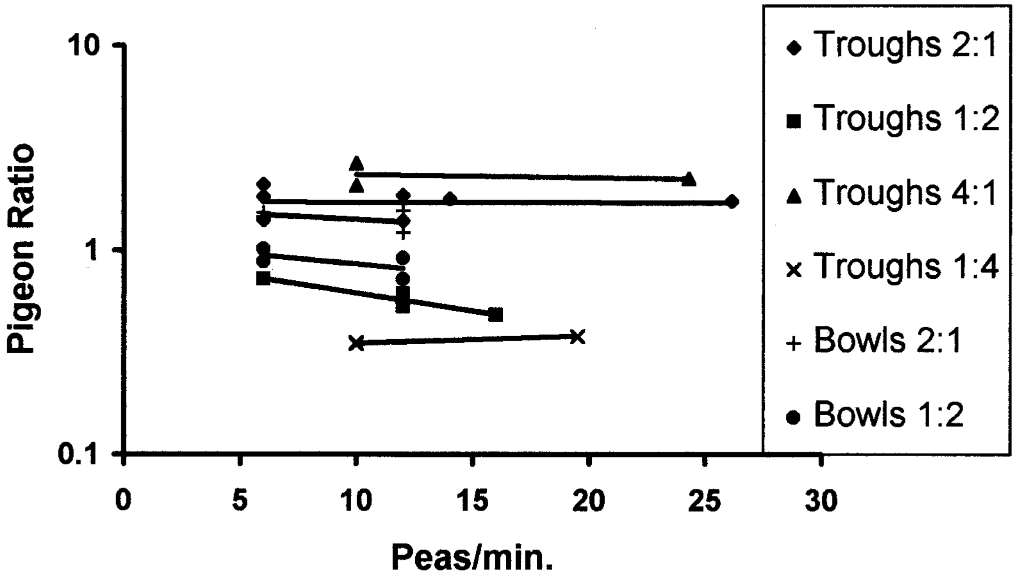

Fig. 5. Pigeon ratios from Figures 3 and 4 (troughs and bowls) plotted against overall rates of pea delivery. Where necessary (because some plots contained more than two points), lines were fitted by the method of least squares. Note logarithmic y axis.

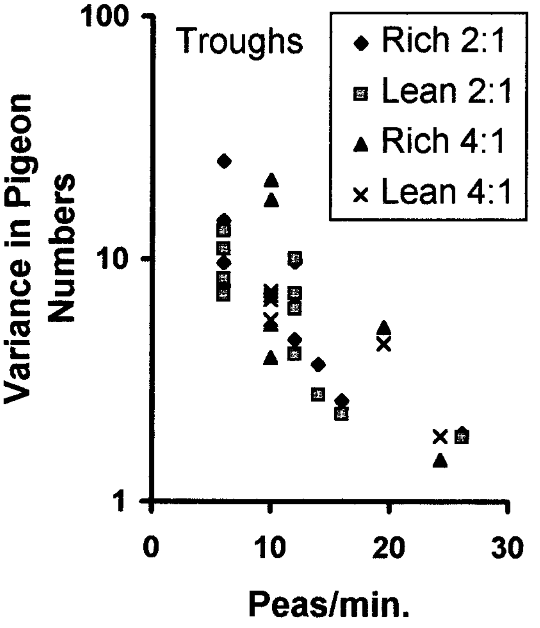

Fig. 6. Variance in number of pigeons at a patch plotted against overall rate of pea delivery for the sessions with troughs shown in Figure 3. Each point represents the variance in 30 pigeon counts at one patch in one session during the middle 15 min of the session.

ure 2); *t*(17) = 1.397; *p* = .09 (comparing with the replication).

Figure 8 shows the flock's distribution in relation to the distribution of resources for Phase A3. Because the results from the two conditions with the visual barrier were similar, they were pooled. The first condition ($n = 7$) showed negligible bias ($b = 0.99$), moderate undermatching ($s = 0.61$), and a good fit ($r^2 = .94$). The later replication ($n = 9$) showed little bias ($b = 1.16$), a similar degree of undermatching ($s = 0.50$), and a close fit ($r^2 = .97$). The regression line in Figure 8 shows a degree of undermatching ($s = 0.56$) close to that in Figure 7; adding the visual barrier had no detectable effect on the flock's distribution. Because there was no significant difference between the results of Phases A2 and A3 (Figures 7 and 8), those data were pooled and tested for a difference of slope with Phase A1, the first condition (Figure 2) and the replication pooled. The slopes were 0.58 for adjacent areas and 0.76 for areas with travel. This *t* test showed the difference to be statistically significant, *t*(41) = 2.412; *p* = .01.

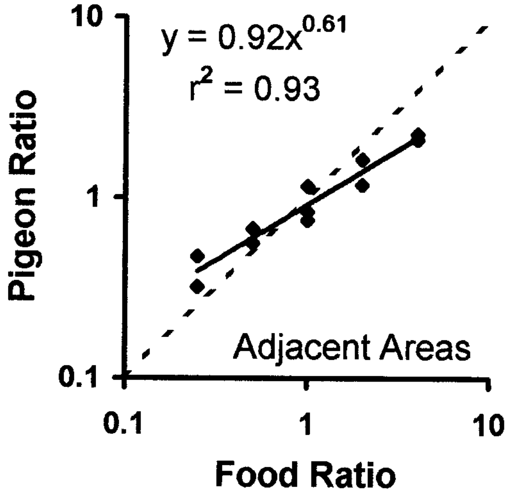

Fig. 7. Group distribution with adjacent areas (Phase A2). The ratio of the average number of pigeons at the east patch to the average number at the west is plotted against the ratio of the rates of pea delivery for each session. See Figure 2 for details.

Noncorrespondence Between Group Results and Individual Performances

Group choice could arise simply from individual pigeons' choices, if each individual behaved as the group behaved. Then the group performance would just be an aggregate or average of the similar individual per-

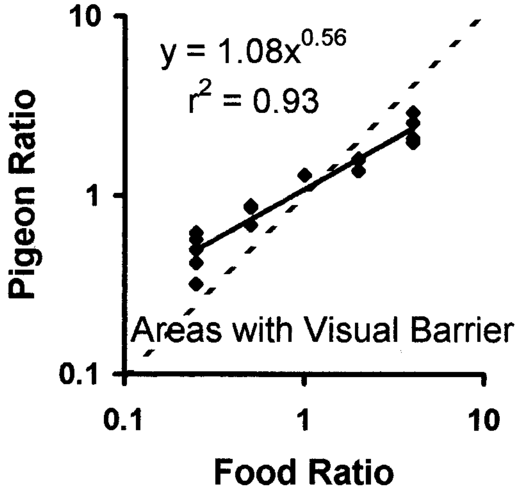

Fig. 8. Group distribution with adjacent areas separated by a visual barrier (Phase A3). The ratio of the average number of pigeons at the east patch to the average number at the west is plotted against the ratio of the rates of pea delivery for each session. See Figure 2 for details.

formances. We assessed this possibility for the phases in which we gathered data on the individual pigeons.

For Phases A1 and A3, the conditions with areas separated by distance or a visual barrier, the identities of the individual pigeons on each patch were recorded every 30 s. For Phase A1, this included four sessions of 2:1 resource ratios and four sessions of 4:1 resource ratios. For Phase A3, this included two sessions of 2:1 resource ratios and five sessions of 4:1 resource ratios. Conditions were grouped by resource ratio regardless of whether the rich site was north or south for Phase A1 or east or west for Phase A3. For the middle 15 min of each session, three measures were calculated for every bird for which there were enough sightings: preference, probability of switching, and participation. Preference was calculated from the proportion of times the pigeon was sighted on the rich patch out of the total number of times it was sighted on the rich and lean patches combined; 0.5 was subtracted from the proportion, so that preference varied between −0.5 (exclusive preference for the lean patch) and 0.5 (exclusive preference for the rich patch), with indifference at 0.0. Proportions, rather than ratios, were used so that exclusive preferences could be included. Preference was calculated only if a pigeon was sighted at least twice. Probability of switching was calculated by dividing the number of times that the pigeon was sighted on a different patch from the one on which it had previously been sighted by the total number of times it was sighted minus one (i.e., by the maximum number of switches possible). For example, if the bird was seen on the lean patch once and then three times on the rich patch, the probability of switching was .333, because only one switch occurred, whereas in four sightings three switches could have occurred. For this measure to be calculated, a pigeon had to be sighted at least twice in the session. No switch was counted if the pigeon left a patch and returned to the same patch. Participation was calculated from the total number of times the pigeon was sighted, a number that varied from 0 to 30. Because the overall participation of the flock varied across sessions, participation was reexpressed in relative terms using standardized *z* scores for each session.

Figure 9 shows preference plotted against standardized participation, for each of the four conditions (separation and barrier, 2:1 and 4:1 resource ratios), one point per pigeon per session. Although more strong preferences occurred for the rich patch than for the lean patch, in all four conditions the entire range of preferences occurred, from exclusive preference for the rich patch (0.5) to exclusive preference for the lean patch (−0.5). Regression lines appear in the graphs to illustrate that there was only a weak tendency for more high-participation birds to be found in the rich patch. The tendency was highest in the separated areas with a 4:1 resource ratio, but was absent altogether in the separated areas with a 2:1 resource ratio.

Figure 10 shows the probability of switching plotted against standardized participation, one point per pigeon per session. Probability of switching varied over a wide range, from 0 to about .8. (The instances of probability equal to 1.0 resulted from sessions in which a pigeon was sighted twice, once in each patch.) The regression lines indicate there was some tendency for switching to decrease with increased participation, although the relation was weak, and, among the points showing no switching (probability of 0), participation ranged widely, from lowest to highest.

Figure 11 shows probability of switching plotted against preference, for the same data as in Figures 9 and 10. Because strong preference must imply a low probability of switching, preferences near −0.5 or 0.5 cannot pair with high probabilities of switching. The broken lines in each graph indicate the triangular area within which the points are generally expected to fall; a point may fall outside the area only due to small sample size. Figure 11 reveals the wide range of variation in the performances of individual pigeons. Although the conditions with 4:1 resource ratios show many pigeons with strong preference for the rich patch, by no means were all or most of the pigeons distributing their behavior in the same way.

Figure 12 evaluates the degree to which individual pigeons behaved consistently from one session to the next. Each point represents 1 pigeon's performance in two sessions: The measure of one session (Session $i + 1$) is plotted against the measure of the previous

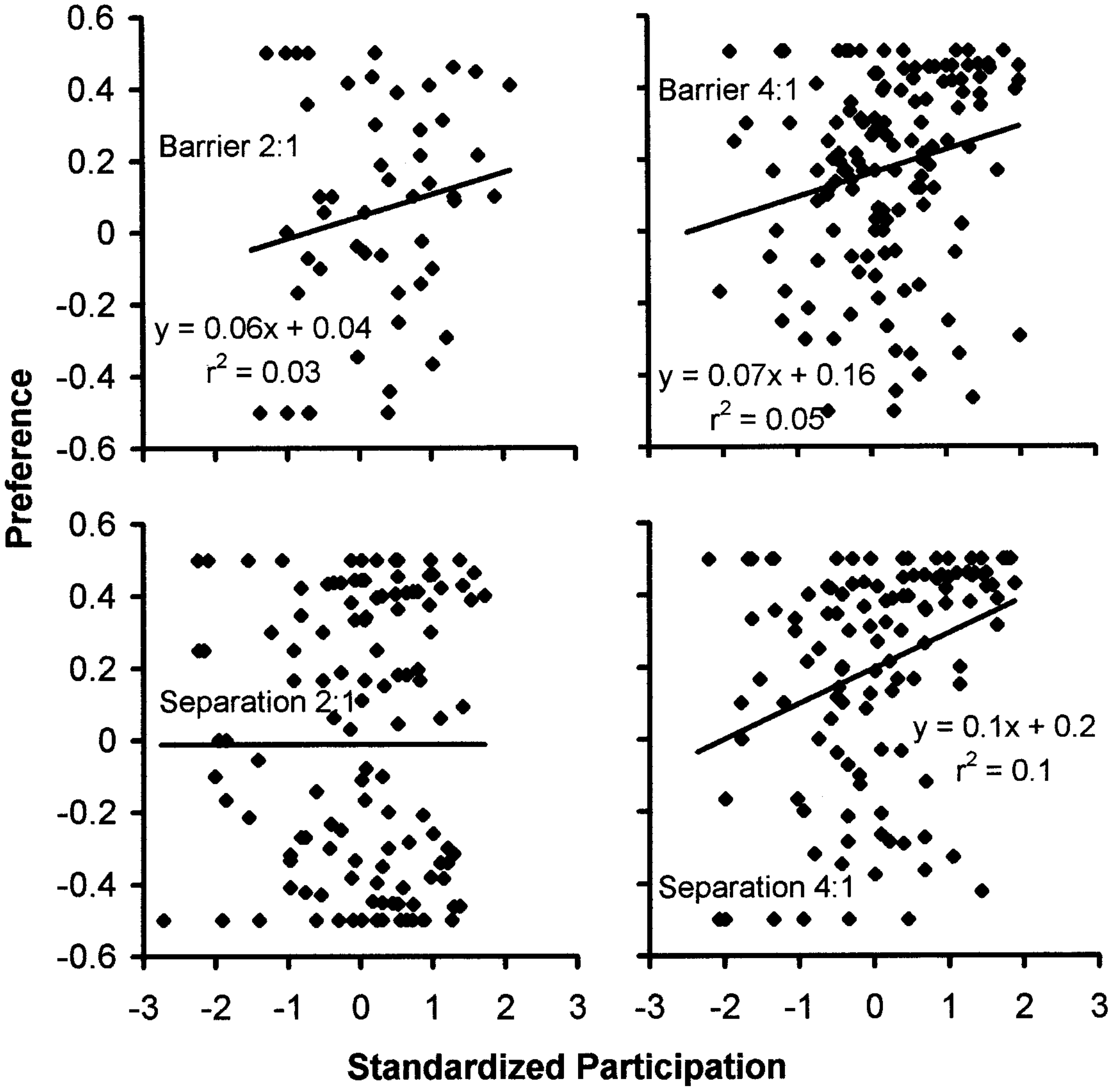

Fig. 9. Individual preference, measured as the proportion of sightings on the rich patch minus 0.5, plotted against the standardized *z* score of participation (number of sightings) for 2:1 and 4:1 resource ratios in areas separated by a visual barrier (Phase A3; top row, "barrier") or separated by 1.2 m of travel (Phase A1; bottom row, "separation"). A preference of 0.5 or −0.5 indicates a pigeon was sighted only on the rich or the lean patch. Each point represents the performance of 1 pigeon in one session. Lines were fitted by the method of least squares. The equation of each line is given in the graph, along with the proportion of variance accounted for (r^2), except for "Separation 2:1," for which slope, intercept, and r^2 were all close to zero.

session (Session *i*). Usually the two sessions were on consecutive days, but sometimes several days intervened, particularly for the 2:1 resource ratio with the visual barrier. Because Session $i + 1$ was always the next session in the sequence, if, for example, there were five sessions, a bird that participated in all five sessions would generate four points, a bird that participated in four sessions would generate two or three points (depending on whether the missing datum was in the middle or at one end of the sequence), and a bird that participated in only two sessions would generate a point only if the two sessions followed one another in the sequence.

If a pigeon's behavior were consistent from session to session on a measure, its points in one of the graphs in Figure 12 would fall in

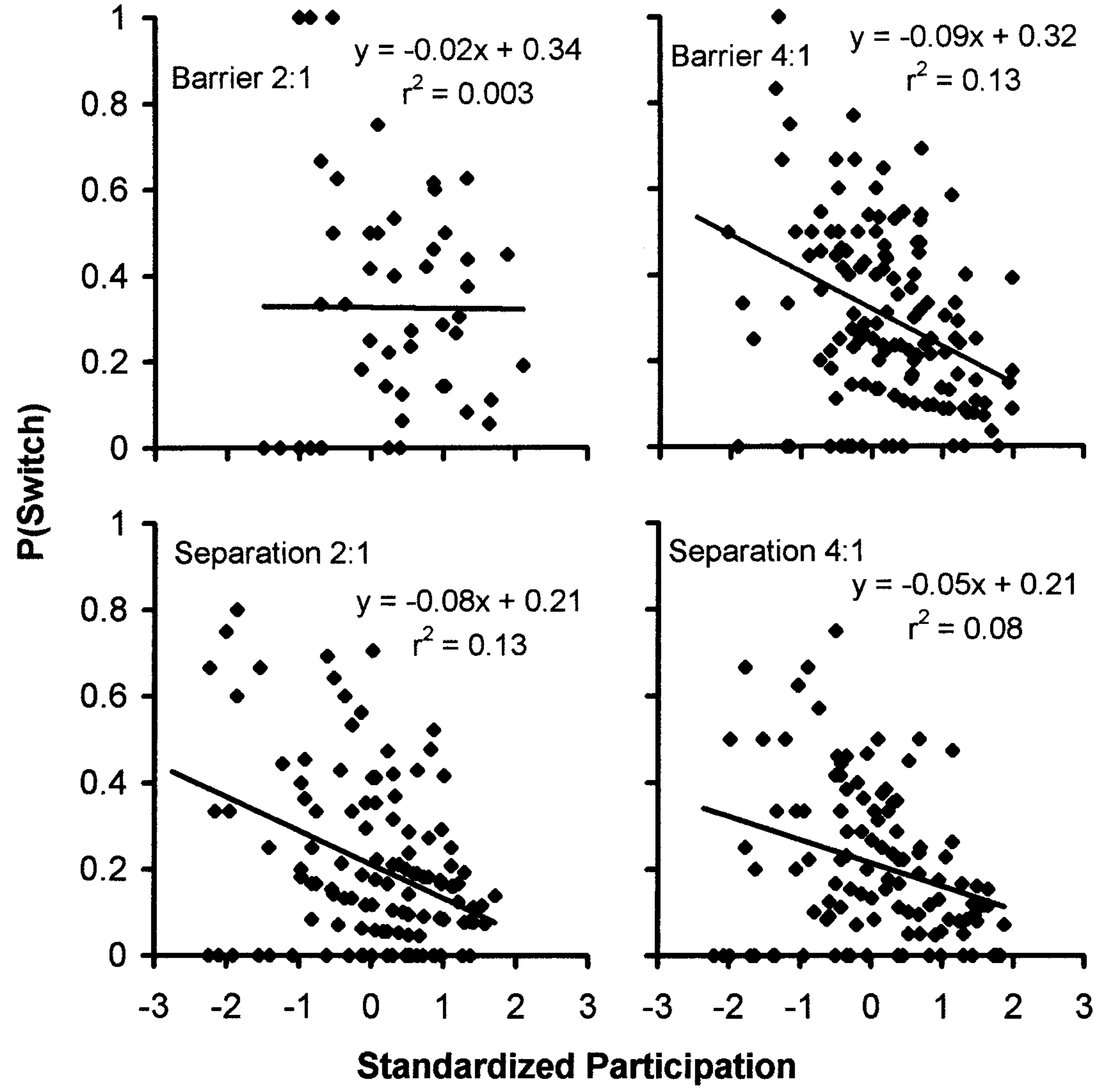

Fig. 10. Individual probability of switching patches plotted against standardized *z* score of participation for 2:1 and 4:1 resource ratios in areas separated by a visual barrier (Phase A3; top row, "barrier") or separated by 1.2 m of travel (Phase A1; bottom row, "separation"). Each point represents the performance of 1 pigeon in one session. Lines were fitted by the method of least squares. The equation of each line appears in the graph, along with the proportion of variance accounted for (r^2).

a cluster. Because Figures 9, 10, and 11 show that the measures varied greatly from pigeon to pigeon, if each pigeon were consistent with itself, the graphs in Figure 12 would show positive correlations. (It is theoretically possible for a positive correlation to arise if individual birds' data increased monotonically across sessions, but no such sequencing occurred in fact.) Regression lines appear in the graphs, but equations are included only for those for which the proportion of variance accounted for (r^2) exceeded .2. The third column of graphs shows that individual pigeons tended to be consistent in their degree of participation; for three of the conditions the relationship was substantial, and even for the fourth (2:1 resource ratio with the visual barrier), there was a stronger positive relation (r^2 = .12) than in any other graph. No such consistency appeared for

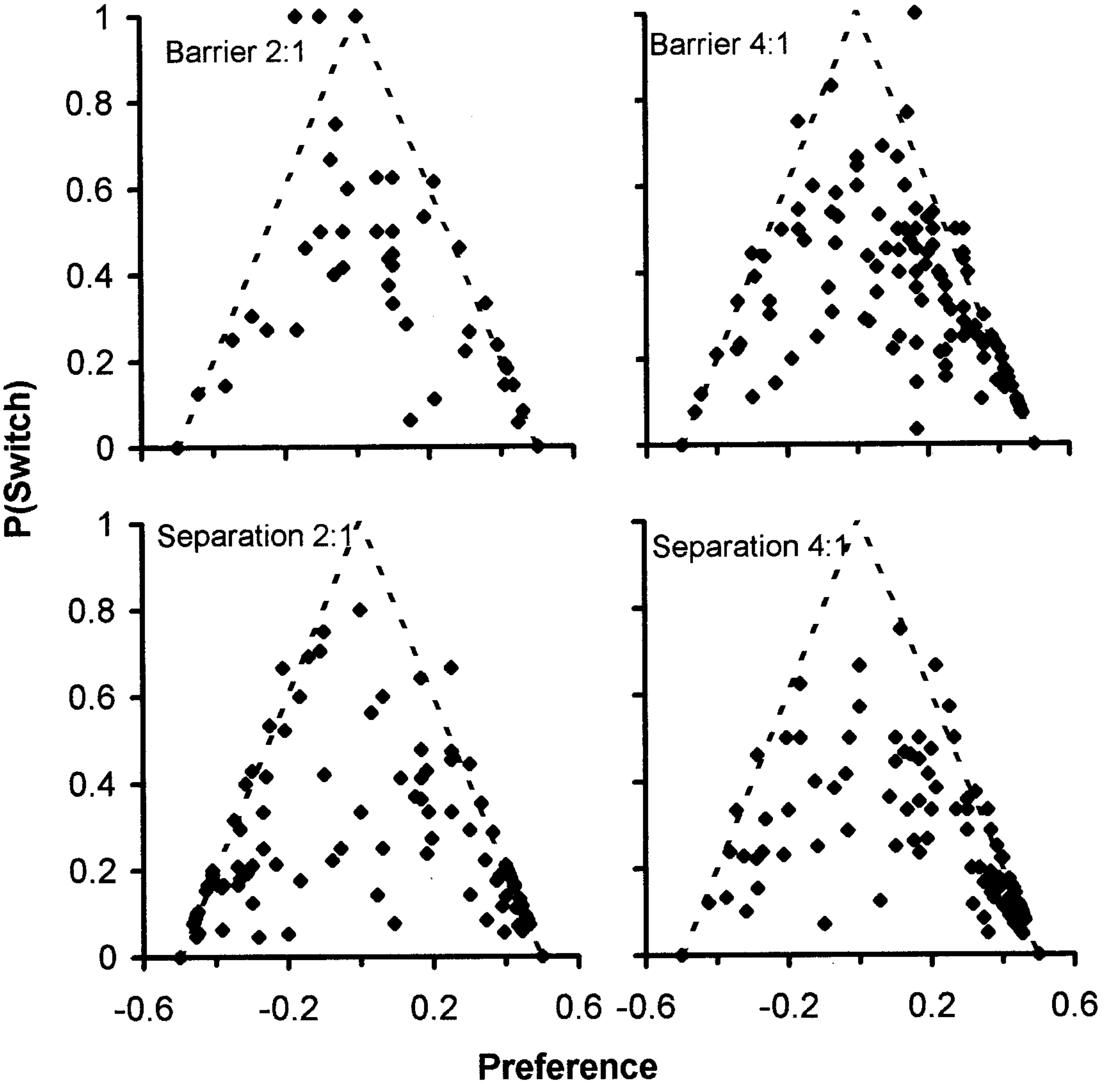

Fig. 11. Individual probability of switching patches plotted against preference, measured as the proportion of sightings on the rich patch minus 0.5, for 2:1 and 4:1 resource ratios in areas separated by a visual barrier (Phase A3; top row, "barrier") or separated by 1.2 m of travel (Phase A1; bottom row, "separation"). A preference of 0.5 or −0.5 indicates a pigeon was sighted only on the rich or the lean patch. Each point represents the performance of 1 pigeon in one session. The broken lines indicate the constraint that switching must decrease as preference for either patch increases.

preference or probability of switching; some of the relations were negative, and none of the positive relations was strong (r^2 ranging from .004 to .11).

DISCUSSION

The results support the ideas that competition varied inversely with the size of the patches and that competition had the predicted effect of lowering the flock's sensitivity to resource distribution. Sensitivity with the bowl patches ($s = 0.38$; Figure 4) fell substantially lower than sensitivity with troughs ($s = 0.71$; Figure 3) or with areas ($s = 0.79$; Figure 2). Although the difference between troughs and areas fell short of statistical significance, the difference was in the expected direction: Sensitivity with areas was slightly greater than with troughs.

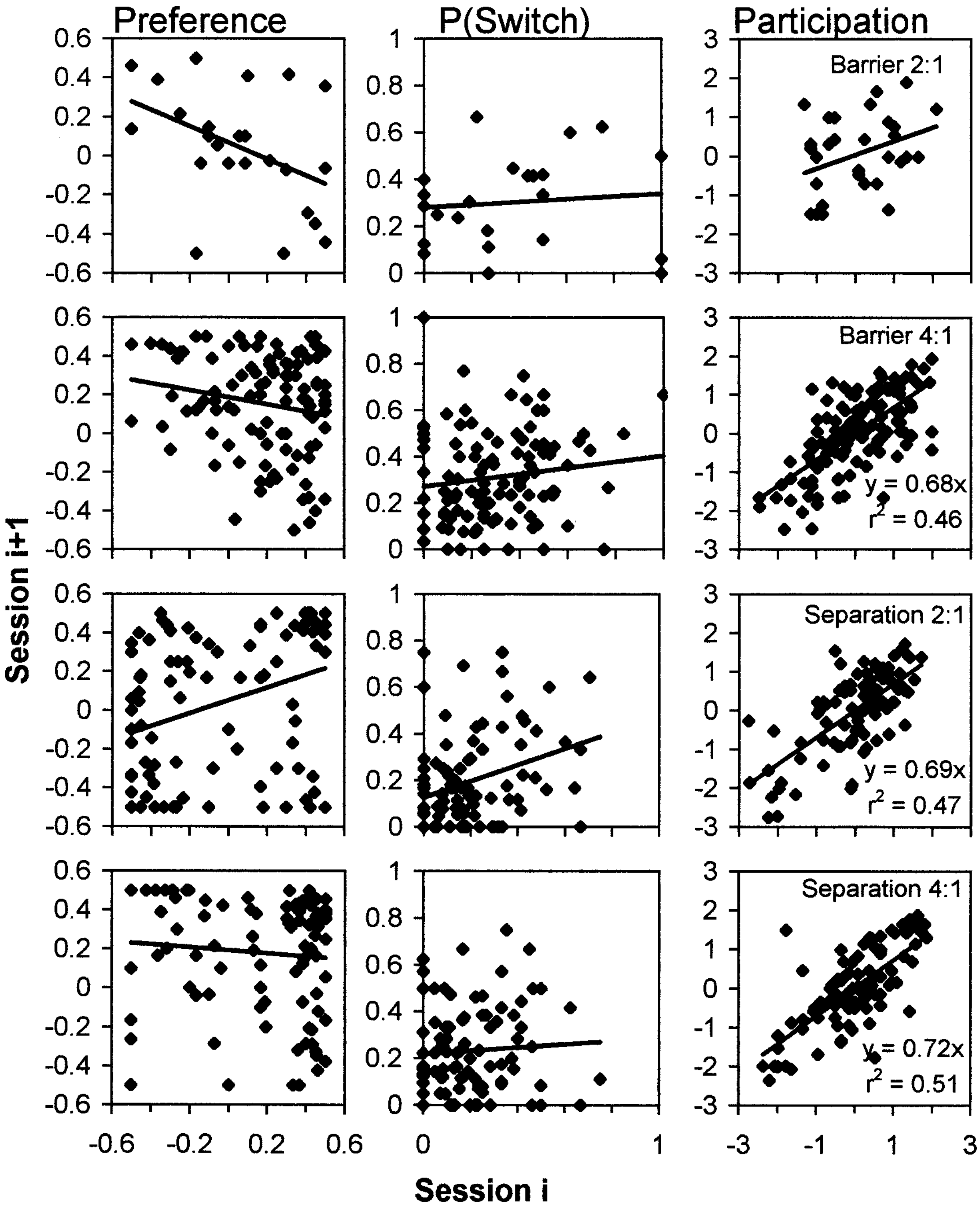

Fig. 12. Individual pigeons' data represented as phase-space diagrams. For each measure, its value in one session ($i + 1$) is plotted against its value in the preceding session (i). Measures and conditions as in Figures 9, 10, and 11; each column represents one measure, and each row represents one condition. Each point represents the performances of 1 pigeon in two sessions. Lines were fitted by the method of least squares. Equations appear only for the lines for which the proportion of variance accounted for (r^2) exceeded .2. A line with a positive slope indicates that individual pigeons tended to be consistent from session to session. Individuals were highly consistent only in their relative levels of participation.

Separating the areas by a distance of 1.2 m, requiring travel, produced a small increase in sensitivity. The slopes determined with travel ($s = 0.79$ in Figure 2 and $s = 0.74$ in the replication) exceeded those determined with adjacent patches ($s = 0.61$ in Figure 7 and $s = 0.56$ in Figure 8). That comparison proved to be statistically significant, even though the size of the difference was small.

The increased sensitivity due to travel may result from a decreased frequency of switching. Figure 10 reveals that the overall level of switching was lower when the patches were separated than when they were adjacent. The difference may be seen in the intercepts of the regression lines; those for the adjacent patches (barrier conditions) were 0.32 and 0.34, whereas those for the separated patches were only 0.21. Because all the slopes were similar and negative, these intercepts reflect overall average differences in probability of switching. A lower frequency of switching when travel is required for switching resembles the results found for individual pigeons' distribution of behavior in experiments on operant choice (Baum, 1982). In both types of experiment, decreased switching is associated with increased sensitivity to resource distribution. Further research on the relation between switching and sensitivity might be helpful, particularly in light of theoretical treatments that rely on assumptions about switching (Houston et al., 1995).

That the sensitivities in Figures 2, 7, and 8 fall short of 1.0 indicates that the typical result, even when competition is minimized by using sites that comprise a substantial area, is undermatching (s less than 1.0 in Equation 9). Relative to the matching prediction of the ideal free distribution (Equation 8), too many pigeons stayed on the lean patch and too few stayed on the rich patch. Although the exact mechanism by which the flock distributes itself remains to be understood, the results rule out some possibilities while suggesting others. First, the absence of any effect of overall food density (shown in Figure 5) contradicts the theory of Kennedy and Gray (1993; Gray & Kennedy, 1994; Spencer et al., 1995). Their suggestion that the flock might undermatch because the difference in food rates between the two patches might fall under a perceptual limit appears to be ruled out by the results in Figure 5. As overall rate increased with a constant ratio of rates, the difference between rates increased. If the difference between rates were the key factor, then the pigeon ratios in Figure 5 should have grown more extreme as the overall rate increased. Ratios less than 1.0 should have decreased; ratios greater than 1.0 should have increased. Instead, the absence of such changes in Figure 5 suggests that the flock's distribution was determined strictly by the ratio of the input rates to the two patches.

Second, the absence of any effect of the visual barrier (Phase A2 vs. Phase A3; Figure 7 vs. Figure 8) indicates that, whatever the mechanism of distribution, it is unaffected by inability to look directly at the other alternative. Templeton and Giraldeau (1996) found that starlings' foraging choices were affected by the ability to observe another starling foraging (Krebs & Inman, 1992). No mechanism that includes such visual comparison could qualify here. Instead, the distribution must arise from some sort of comparison of events that occur while foragers are actually in the patches. If, for example, relative rate of feeding at the patches were the variable controlling distribution, individual pigeons would have to assess it by visiting both patches while switching back and forth between them.

A study of a flock of 6 sparrows by Gray (1994) showed undermatching between group choice and overall relative reinforcement and similar undermatching between individual choice and individual relative reinforcement, but a diversity of results for the 6 individuals' choices in relation to overall relative reinforcement. In the present study, no information was available about the individuals' feeding. Except perhaps for the rapid-presentation conditions, however, it seems unlikely that any of the pigeons ate many peas. For example, if 210 peas (10 per minute for 21 min) were delivered to 15 to 20 pigeons, the average number eaten would be only about 10 to 15 peas. If any pigeons ate more, others must have eaten fewer still; some may have eaten none at all. It remains possible that individual pigeons' choices reflected their eating, but it seems unlikely. The diversity of preferences in Figures 9 and 11 and the lack of consistency shown in Figure 12 (left column) militate against that sort of regularity at the level of the individual. Perhaps smaller numbers of birds and higher rates of feeding allowed individual relations to emerge in Gray's study.

The present results suggest that, whatever the mechanism of the flock's distribution, it produces outcomes at the level of the flock that are in no way mirrored by the behavior of the individuals. The inconsistencies of the individual performances in the key variables of preference and probability of switching (shown in Figures 9, 10, and 11) rule out the most obvious explanation of the flock's distribution: that it was simply an aggregate or average of parallel individual choice relations. It is likely that some yet-to-be-discovered uniformity exists in the individual performances, but that regularity, whatever it may be, generates rather than resembles the group performance. This noncorrespondence between the aggregate and the individual, usually indicating that a complex aggregate performance arises from simple individual rules, characterizes the aggregate phenomenon as *emergent.* The flock's distribution is emergent in the sense that it cannot be thought of as the aggregate of many individual distributions, all more or less the same. Instead, it probably emerged from dynamic interactions among the individuals. For example, the probabilities of switching were high enough to confirm what informal observation suggested: The situation was always extremely fluid and that the identities of the pigeons making up the group at a patch were constantly changing, even if the size of the group changed little.

Whatever the rules that govern the behavior of the individuals, they differ from the regularities at the level of the group, but they work in aggregate so as to produce the performance of the group. The decreasing variability in numbers shown in Figure 6 suggests some possibilities of the rules governing individuals. In general, it indicates that the food acted as an attractor, drawing and keeping the foragers near. The lower the rate of food, the more foragers drifted away, and the higher the rate of food, the more the foragers tended to cluster at the source. This might provide a basis for a dynamic model of group foraging (e.g., Hannon & Ruth, 1994). Bernstein, Kacelnik, and Krebs (1988) offered some speculations about the form of the individual rules.

The undermatching and the individual variation observed might have occurred in part because the pigeons were of unequal competitive ability or *competitive weight* (Grand, 1997; Gray, 1994; Milinski & Parker, 1991). If the assumption that all foragers feed equally were violated—that is, if some pigeons were able to gain more than others—and if the better competitors preferred the richer patch, then the relative number of pigeons at the rich patch would fall below that predicted by matching (Equation 8). Another type of matching could occur, however: matching to relative total competitive weight (Milinski & Parker, 1991). If one could assign weights to all the individuals, it might turn out that the ratio of total competitive weight in the patches matched the ratio of food in the patches. In an experiment with juvenile salmon, Grand (1997) assessed competitive weight by introducing a large quantity of food to the group in a single area and recording how much of the food was captured by each individual. The proportion captured by an individual salmon defined its competitive weight. Grand found that, when food was presented at two locations with a rate ratio of 2:1, although the ratio of fish fell short of 2:1, the ratio of total competitive weight approximated 2:1.

Although we had no assessment of competitive weight parallel to Grand's, it seems possible that a pigeon that participated more in foraging might also have higher competitive ability. Perhaps level of participation might serve as an indicator of competitive weight. This line of speculation was suggested because level of participation was the only variable that revealed high consistency within individuals (Figure 12). Because it also showed a weak positive relation to preference (Figure 9), it seemed possible that if total competitive weight assessed this way were compared across patches, the ratio of this variable might more closely match the food ratio than did the pigeon ratio. For those conditions in which we had the data on individual pigeons (Phases A1 and A3) we calculated each pigeon's relative participation in each session (eight sessions of Phase A1 and seven sessions of Phase A3). Using these numbers, we calculated the average total competitive weight for each patch during the middle 15 min of the session. The ratios of these averages were used in place of the pigeon ratios in regression analyses that paralleled those in Figures 2 and 8. For both conditions, the slope of the regression line and the goodness of fit increased. For Phase A1 (separated areas), the slope increased from 0.79 to 0.90, and r^2 increased from .89 to .93. For Phase A3 (areas with a visual barrier), the slope increased from 0.61 to 0.69, and r^2 increased from .94 to .96. The approximation to matching with separated areas suggests that relative participation might indicate competitive weight in pigeons, but the continued undermatching with the visual barrier suggests that other factors might also be at work.

Effects of variable competitive ability suggest the possibility that individual pigeons might have interfered with one another. Different researchers have argued for different uses for the word *interference,* some suggesting that it should apply only to social effects among predators in a standing crop and others applying it to continuous input and even to the sharing of resources implied in Equation 2 (Lessells, 1995; Milinski & Parker, 1991; Tregenza, 1994). The strong undermatching with bowls as patches (Figure 4) in comparison with troughs (Figure 3) and areas (Figure 2) suggests a possible role for interference when the choices are between continuous inputs. The small area around the bowls probably forced some pigeons to switch from the richer patch to the leaner one. The excellent fit of the line ($r^2 = .94$) shows that the effect was highly reliable. The slope of 0.38, substantially greater than zero, indicates that the interference failed to overwhelm the effect of resource distribution completely.

The type of interference implied by Figures 2, 3, and 4 might be distinguished from interference among predators searching in the same patch, thought to be the outcome of predators avoiding one another, thereby curtailing search, or wasting time in aggressive encounters (Beddington, 1975; Free et al., 1977; Hassell & Varley, 1969; Milinski & Parker, 1991; Tregenza et al., 1996). The interference that keeps foragers on the lean patch when they might otherwise switch to the richer patch might be called *switching interference,* whereas the interference that occurs among predators in the same patch might be called *searching interference,* because its effect is to lower the rate or efficiency of search. Both should probably be distinguished from *resource sharing,* the division of resources that occurs among a group of predators in the same patch (Equation 2). Such a three-way distinction has the virtue that the different effects may be tied to different quantitative aspects of the situation. Switching interference is reflected in the degree of undermatching, the degree to which the ratio of foragers falls short of the ratio of resources. If switching interference were tied to the parameter m, it might justify the substitution of $1/m$ (Equation 7) for the slope s (Equation 9). Resource sharing refers to the validity of the simplest interpretation of Equation 2: that each forager obtains an equal share of the resources available in the patch. Diversity in competitive weight and the extent to which competitive weight must be factored into the account of forager distribution indicate the extent of resource sharing (Grand, 1997). In continuous-input patches, unequal resource sharing and competitive weight might be linked to interference with prey detection, whereas in standing crops, one must consider interference with search. Because searching interference applies particularly to the time and efficiency lost when multiple predators exploit prey dispersed over an area (Free et al., 1977; Hassell & Varley, 1969; Milinski & Parker, 1991), it would find expression in the functional form of Equation 1. A number of possible functional forms have been proposed (e.g., Beddington, 1975; Moody & Houston, 1995; Sutherland & Parker, 1992; Tregenza et al., 1996). Future research will decide among the various possibilities.

In summary, the generalized group matching equation proved useful for analyzing the effects of competition and travel. On the whole, the results support the idea that competition dampens group distribution, reflected in undermatching. The undermatching probably results from interference on switching, rather than any form of interference within the patches. Travel appeared to have only a small effect on flock distribution; it slightly decreased undermatching, but the effect was only clear when the results of conditions were combined. A visual barrier appeared to have no effect on the flock's distribution, suggesting that any comparison between patches occurs sequentially rather than simultaneously. The results from observing individual pigeons within the flock revealed no consistency, either across birds or from session to session within birds, in preference or probability of switching, suggesting that the orderliness of data for the flock as a whole may be a truly emergent phenomenon. Only the tendency to participate in the experiments revealed any consistency; although participation varied widely from pigeon to pigeon, consistency was high within pigeons. As an estimate of competitive weight, participation had the expected effect of decreasing the amount of undermatching but failed to increase the slope all the way to matching, suggesting that other factors may operate as well.

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Received October 20, 1997
Final acceptance January 27, 1998