EFFECTS OF PREDICTABILITY AND COMPETITION ON GROUP AND INDIVIDUAL CHOICE IN A FREE-RANGING FORAGING ENVIRONMENT

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The present study examined the social foraging of rats in an open arena. The relative quantity of food varied across two food sources, or "patches." Five food quantity ratios (1:1, 1:2, 1:8, 8:1, 2:1) were presented in a series of 30-min sessions. Ratios varied randomly across 6-min components within sessions (Phase 1), or in a consistent order across sessions (Phase 2). Group and individual preferences were well described by the ideal free distribution and the generalized matching law, respectively, with evidence of undermatching at both group and individual levels. Sensitivity of individual and collective behavior to the relative quantities of food was higher in Phase 2 than in Phase 1. Competitiveness rankings, assessed before and after experimental sessions by delivering food in rapid succession from a single feeder, was positively related to sensitivity values in Phase 1, but less consistently so in Phase 2. This study illustrates a promising experimental method for investigating foraging in a social context.
Key words: choice, foraging, concurrent schedules, generalized matching law, ideal free distribution

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Adaptive decision-making requires tradeoffs between various costs (e.g., time, energy, opportunity, predation risk) and benefits (e.g., caloric gain, mating opportunities), both immediate and deferred. Optimal foraging models are quantitative characterizations of these costs and benefits (see Stephens & Krebs, 1986), and have been highly successful in characterizing various aspects of foraging in a wide range of species and settings (e.g. Biernaskie, Walker, & Gegear, 2009; Burke & Montevecchi, 2009; Doniol-Valcroze, Lesage, Giard, & Michaud, 2011; Edouard, Fleurance, Dumont, Baumont, & Duncan, 2009; Hernández & Laundré, 2005; de Knegt, Hengeveld, van Langeveld, de Boer, & Kirkman, 2007; Suraci & Dill, 2013; Wajnberg, Bernhard, Hamelin, & Boivin, 2006; also see Kennedy and Gray, 1993; Pyke, 1984; Stephens & Krebs, 1986; Stephens, Brown, & Ydenberg, 2007; Tregenza, 1995 for reviews). While the majority of models to date have focused on the behavior of individual foragers, many species forage in social contexts (e.g. Abrahams, 1989; Amano, Ushiyama,

Moriguchi, Fujita, & Higuchi, 2006; Dreisig, 1995; Grand, 1997; Harper, 1982; Humphries, Ruxton, & Metcalfe, 1999; Inman, 1990; Kohlmann & Risenhoover, 1997; Kurvers et al., 2010; Michelena, Sibbald, Erhard, & McLeod, 2008; Pulido & Diaz, 1997). A better understanding of how foraging behavior affects, and is affected by, social context is thus of great theoretical importance.

The most successful model of social foraging to date is known as the *Ideal Free Distribution* (IFD). Originally formulated by Fretwell and Lucas (1970), this model predicts the distribution of animals will match the distribution of available resources among different patches, according to the following simple rule:

$$\frac{N_1}{N_2} = \frac{R_1}{R_2}, \tag{1}$$

where $N=$ the number of foragers, $R=$ the number of resource items (reinforcers), and the subscripts represent the two alternatives. Despite the simplicity of the model, and the complexity of the social situations it encompasses, the IFD provides a good quantitative description of group behavior in a range of species, including birds (pigeons: Baum & Kraft, 1998; Bell & Baum, 2002; common cranes: Bautista, Alonso, & Alonso, 1995; sparrows: Gray, 1994; and mallards: Harper, 1982), fish (guppies: Abrahams, 1989; Coho salmon: Grand, 1997; and cichlids: Grand & Grant, 1994; Tregenza & Thompson, 1998), invertebrates (wood ants: Lamb & Ollason, 1993;

dung flies: Blanckenhorn, Morf, & Reuter, 2000; and bumblebees: Dreisig, 1995), nonhuman mammals (white-tailed deer: Kohlmann & Risenhoover, 1997; roe deer: Wahlström & Kjellander, 1995), and humans (Goldstone & Ashpole, 2004; Kraft & Baum, 2001; Kraft, Baum, & Burge, 2002; Sokolowski, Tonneau, & Baque, 1999).

The IFD is structurally similar to the matching law, formulated with respect to individual choice behavior (Baum, 1974; Herrnstein, 1970). The more recent and general form of the matching law expresses behavior and reinforcer ratios as a power function of the following form (log transformed):

$$\log\left(\frac{B_1}{B_2}\right) = s.\log\left(\frac{R_1}{R_2}\right) + \log b, \qquad (2)$$

where B_1 and B_2 are behavior (or time spent) at Patch 1 and Patch 2 respectively, and R_1 and R_2 are reinforcers obtained at Patch 1 and Patch 2, respectively. The sensitivity of behavior to reinforcement is represented by s (the slope of the resulting linear function) and b represents bias towards one patch or another (corresponds to the y-intercept of the function).

This *Generalized Matching Law* (GML) has been shown to accurately describe a wide range of choice data at the individual-subject level in a number of species (see review by Grace & Hucks, 2013). The IFD can be similarly expressed in generalized form (Bell & Baum, 2002; Fagen, 1987; Kennedy & Gray, 1993):

$$\log\left(\frac{N_1}{N_2}\right) = s.\log\left(\frac{R_1}{R_2}\right) + \log b, \qquad (3)$$

where N_1 and N_2 are the number of foragers observed at Patch 1 and 2, respectively, R_1 and R_2 are the total reinforcers (or resources) delivered at Patch 1 and Patch 2, s has been conceptualized as either the sensitivity of the group to the resource distribution (Kennedy & Gray, 1993) or the inverse of the level of interference (Sutherland, 1983; Fagen, 1987), and b is the site bias (Bell & Baum, 2002; Kennedy & Gray, 1993).

While there is structural similarity between the IFD and the GML, two models that describe the related phenomena of individual and group choice, the relationship between these levels of behavior might not be as straightforward as it appears. To begin with, while the IFD refers to the distribution of *available* resource to which the group matches its distribution, the GML states that individuals distribute their behavior according to the distribution of *obtained* resource. Differences in individual intake across the two patches can result in discrepancies between the ratio of resources available to the group and the ratio of resources obtained by individual foragers. Given that group behavior is the cumulation of individual behavior, a dissociation between matching at the two levels is possible; individual foragers may match their behavior to obtained resources without producing matching at the group level (e.g., obtaining all their reinforcement at a single patch, without switching location). Alternatively, it is also possible for group matching to arise even if no individual is matching.

The nature of this relationship between the group and individual has important theoretical implications for a comprehensive understanding of foraging behavior. Accordingly, considerable attention has been given to the theoretical integration of individual and group foraging decisions (e.g. Amano et al., 2006; Bernstein, Kacelnik, & Krebs, 1988; Ruxton, Armstrong, & Humphries, 1999). Much of the work to date, however, is based either on computer simulations rather than real data (Lima & Zollner, 1996; Ollason & Lamb, 1995), or field studies where the resource ratios were not experimentally manipulated, limiting clear conclusions about the relationship between individual and group-level outcomes.

A notable exception is an experiment by Gray (1994), who studied a flock of six sparrows in a semi-naturalistic experimental context—an aviary in which the birds lived. The rate of food presentation, delivered from two distinct feeders (patches), was varied across conditions. The distribution of sparrows to food delivered at the two patches was in line with the generalized version of the IFD (Eq. 3), with consistent undermatching (mean sensitivity = 0.34). Undermatching was also obtained at the individual level, but the response patterns varied considerably from subject to subject, suggesting that the broad patterns seen at the level of the flock were not simply an aggregate outcome of individual performances.

A more recent study with a flock of pigeons in a free-ranging environment (Baum & Kraft, 1998) found similar support for Equation 3. In these

studies, food was delivered at two patches according to variable-time (VT) schedules and the number of pigeons in each location was recorded. Although preferences tended to be stronger for the rich than for the lean patch, individual choices varied from exclusive preference for the rich to exclusive preference for the lean patch. Similarly, switching varied widely between individuals, suggesting group behavior was not merely an aggregation of individual choice patterns. In light of their individual data, Baum and Kraft concluded that group matching was an emergent product of the dynamic, variable interactions present in individual matching behavior.

The relationship between individual and group choice bears importantly on one of the simplifying assumptions of the IFD, namely, that all animals are equally competitive, that is, they are *free* to move between patches, unconstrained by the presence of other foragers, and able to obtain resources at equal rates (Cresswell, 1998; Milinski & Parker, 1991). If this were the case, group behavior would be a direct product of individual-level processes. Contrary to this assumption, however, several studies have found that competitive abilities vary across subjects (e.g. Grand, 1997; Gray, 1994; Harper, 1982). In most cases, competitiveness is inferred from the relative rates of food intake in the single-patch or multiple-patch choice sessions. In the present study, we measured competitiveness directly in individual rats, both before and after blocks of choice sessions, and compared that to sensitivity and relative intake rates in the series of choice conditions. This permitted an independent assessment of competitiveness, its stability over time, and its relationship to choice patterns.

Unlike most prior research in this realm, we used rats as subjects, with apparatus adapted from a study by Farmer-Dougan and Dougan (2005). Rats are suitable for this type of research, as they are well adapted to laboratory conditions and are known to live and forage in large social colonies outside the laboratory. The procedures were derived from a recent study from our laboratory (Tan & Hackenberg, 2012), in which food was delivered according to VT schedules at two different feeder stations (patches) with a group of five rats. The distribution of rats at each patch was recorded while the ratio of food at the two patches varied within and across sessions. In the within-session variation of food ratios, unsignaled transitions

between schedule components occurred every 6 min; in the across-session variation, a single food ratio was in place for the entire 30-min session. The data were well described by the IFD and the GML, with consistent undermatching, whether the schedules were varied regularly or irregularly.

The main pattern of results was similar to that reported by Bell and Baum (2002), who also varied ratios of food delivery regularly (across sessions) and irregularly (within sessions) in a flock of 34 pigeons. They found that the collective behavior of the flock quickly adjusted to current food ratios following a change, and that sensitivities were relatively high across both condition types, though slightly higher in regular than irregular sequences. The sensitivity values reported by Bell and Baum were substantially higher than those found by Tan and Hackenberg (2012), however. It is possible that the lower sensitivity values reported by Tan and Hackenberg were due to schedule factors: Bell and Baum manipulated ratios of food *quantity*, whereas Tan and Hackenberg manipulated ratios of food *intervals*, delivered at variable times.

In the present study, we replicated the Bell and Baum (2002) method, manipulating reinforcer quantity ratios. These ratios were varied both (a) *irregularly*, in 5-min blocks within a session (Phase 1), and (b) *regularly*, in a fixed sequence, with a single ratio in effect each session (Phase 2). Unlike Bell and Baum, we studied a small number of subjects, enabling a detailed assessment of individual choice and competitiveness that was not possible in their study. Varying the predictability of the resource ratios enables a direct test of a second major assumption of the IFD, namely, that animals have perfect, or ideal, knowledge of the foraging environment. This can be approximated with prolonged exposure to regular and relatively stable contingencies.

Together with the test of competitive abilities, the present study thus addresses two main simplifying assumptions of the IFD model—(1) that animals forage *freely*, without constraints and equally subject to competitive effects, and (2) they forage *ideally*, with perfect knowledge of the habitat—in a structured laboratory analogue of a dynamic foraging environment. This ability to test the IFD and other optimization models in controlled laboratory conditions, when core assumptions can be met, is among the advantages of laboratory analyses of adaptive

behavior. We anticipated that the detailed investigation of individual behavior within this social foraging paradigm would permit a more thorough characterization of how individual-level behavioral processes combine to produce group behavior.

Method

Subjects

Ten male Long Evans rats served as subjects, five in each phase of the experiment, which were conducted separately, several months apart. Rats were approximately 4 months old at the start of the experiment, and pair-housed. Note that due to the odd number of rats per phase, one subject in each group of five was housed with a sixth rat not used in this experiment. Colony rooms were programmed on a 12 hr light/dark cycle. Food was restricted 22 hr before experimental sessions. A few minutes prior to every session, each subject was marked using nontoxic water-based paint of different colors for identification.

Equipment/Materials

Rats were tested in a large square foraging arena measuring $1.46\,m^2$, made of particleboard with 1.9 cm thick walls that were 30.5 cm high (see Fig. Fig. 1). The two corners adjacent to each feeder also had plastic extensions added to the outside of the arena, extending 47 cm from each corner and 6.4 cm above the original wall. The flooring in the arena was dark grey linoleum, with the two halves designated by a strip of electrical tape. Patches were demarcated by raised edging around each $0.11\,m^2$ area. Feeders, located in diagonally opposite ends of the arena, dispensed banana-flavored sugar pellets into a circular petri dish, 27 cm in diameter, attached to the floor by strips of Velcro. Feeders were operated externally by a Visual Basic.net program during the experimental sessions, and manually during the competitive assessments. A tone generator located at each feeder produced a 1-s tone at 1.5 kHz and 2.5 kHz with every pellet delivery at Feeder 1 and 2, respectively. In Phase 2, two webcams were positioned 73.7 cm above each patch to record events occurring within that area.

Procedure

Rats were placed at approximately the center of the arena in a random order just prior to each 30-min session. Food was delivered at each patch according to independent variable-time (VT) 30-s schedules, using the following food quantity ratios: 1:1, 1:2, 1:8, 8:1, and 2:1. Thus, each feeder delivered food every 30 s, on average, with the number of pellets (1–8) determined by the assigned amount. In Phase 1, the five food ratios varied irregularly across five (unsignalled) components within a session, each component lasting 6 min. The intervals were selected randomly without replacement, such that all five occurred once per session. Six sessions were conducted in total, conducted twice per week for 3 weeks. In Phase 2, a single food ratio was in effect for an entire 30 min session, and ratios were presented in a fixed sequence: 1:1, 1:2, 1:8, 8:1, 2:1, repeated four times over 20 sessions, with a final replication of the 1:1 ratio. Thus, subjects experienced a total of 5 sessions with a 1:1 ratio and 4 sessions each of the other ratios.

During each session, food consumption per rat was recorded at the time of food delivery. Pellet consumption was not recorded when (a) broken pellets were delivered, (b) when pellets fell into unreachable locations and were not eaten, or (c) when it was unclear which rat ate the pellet. Consequently, the number of pellets recorded as consumed was usually less than pellets actually delivered (Mean difference = 7.90, SD = 8.98); such differences were unsystematic, however, and most likely of little consequence. Rat location was recorded every 30 s, using time-sampling methods. In Phase 1, location was recorded live during the session by four observers. In Phase 2, location was
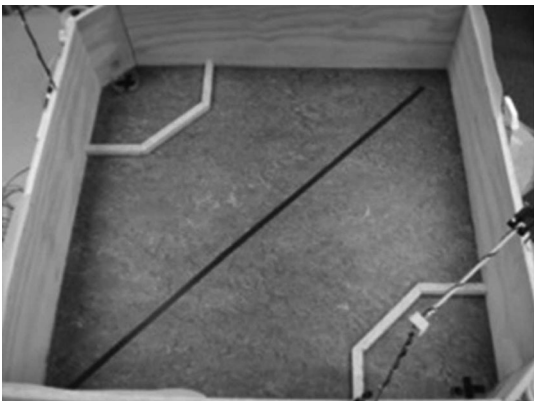

Fig. 1. Aerial view of foraging arena. Patches are located in the top left and lower right corner.

recorded from video files. A second coder checked the reliability of location coding in five randomly selected sessions. Average inter-coder reliability, calculated as the overall number of agreements divided by the number of disagreements and agreements, summed across all sessions, was equal to .92 (SD = 0.02).

Competitiveness was assessed independently in two single-feeder sessions. In Phase 1, these competitive assessment sessions were conducted 1 day apart just prior to the choice sessions. In Phase 2, one competitive assessment session was conducted immediately preceding, and another 3 months following, the choice sessions. In each of these sessions, pellets were manually delivered from a single feeder in relatively rapid succession, waiting only for consumption of the previous pellet. The preexperimental assessments in both phases lasted until 100 pellets had been delivered, and the postexperimental assessment (in Phase 2) lasted 20 min. The location of food delivery alternated across sessions. Competitiveness was quantified as the proportion of total reinforcers consumed by each rat per session.

All analyses utilized data from entire sessions. The IFD analyses were conducted using the sum of rats observed and the total number of pellets delivered at each patch for every resource ratio, and calculating the log ratio of the sums for Patch 1 and Patch 2. GML analyses were conducted using the total time samples each rat was observed at each patch, and the total number of pellets consumed by each rat at each patch for every resource ratio, and calculating

the log ratio of the sums for Patch 1 and 2. These provided log resource ratios (R1/R2) and rat ratios (N1/N2) for IFD analyses, and log intake ratios (R1/R2) and time ratios (T1/T2) for the GML analyses. Note that due to the equal number of resource ratio presentations in each phase, this method is equivalent to using the log ratio of the average rats or resources at each patch. Due to small sample sizes, nonparametric Spearman rank-order correlations were used to test relationships between variables. Note that all correlations are not significant unless reported otherwise.

Results

Group Choice

Figure 2 shows the IFD fits of log rat ratios and log resource ratios, using data summed across all time samples for each of the five resource ratios in Phase 1 (left panel) and Phase 2 (right panel). The generalized version of the IFD (Eq. 3), provided a good account of the collective behavior of the group of rats ($R^2 = 0.88$ and 0.99 for Phases 1 and 2, respectively). The group distributions considerably undermatched resource ratios, with sensitivity values of 0.37 and 0.49 for Phases 1 and 2, respectively.

Figure 3 shows average IFD sensitivity values, calculated across 30-s blocks within each 6 min component (separate panels) in Phases 1 and 2. To obtain these sensitivity values, straight lines were fitted to the log rat ratios and log resource ratios, summed for each 30-s block, for each of the five resource ratios. The slopes of these fits,
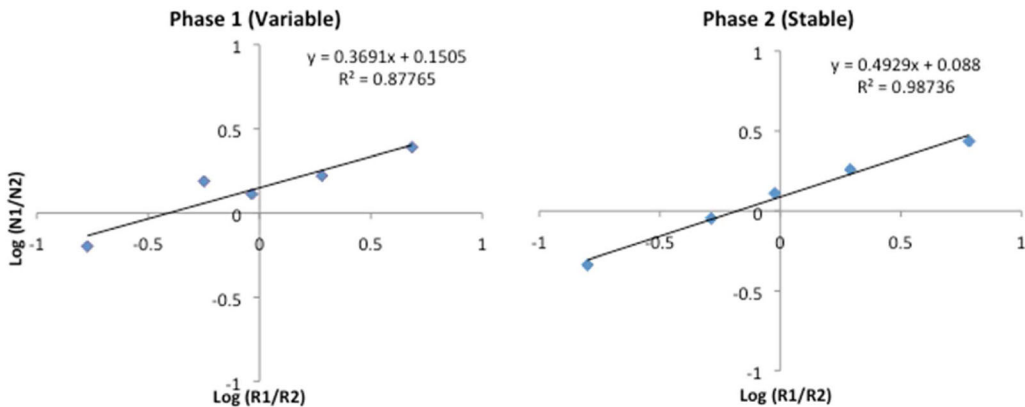

Fig. 2.   Log ratio of total rats in Patch 1 and Patch 2 as a function of pellets delivered at Patch 1 and Patch 2, summed across resource ratios for Phase 1 (left panel) and Phase 2 (right panel). The IFD fits are also included.
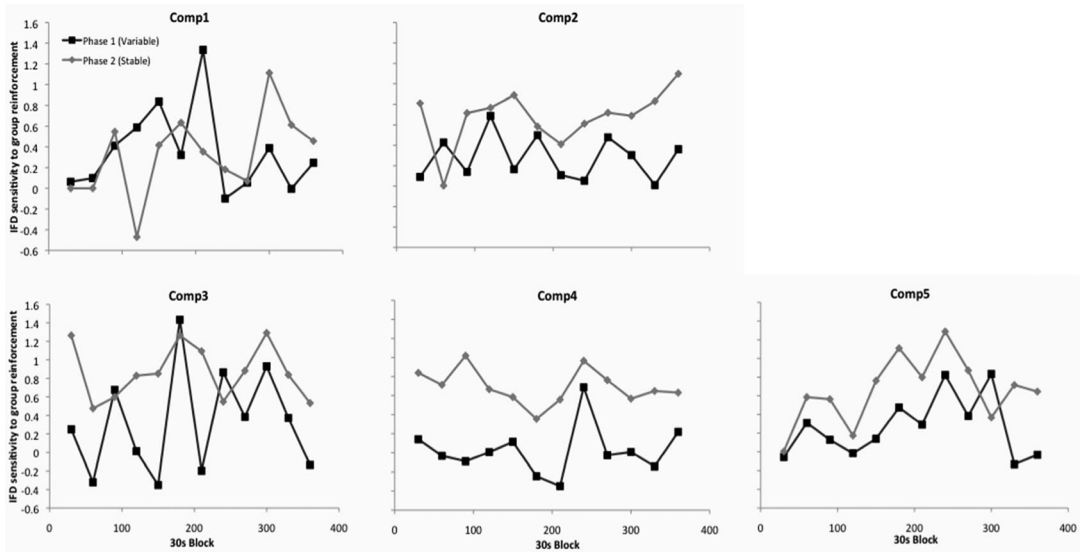
Fig. 3. Sensitivity values given by Equation 3 across 30-s blocks for each component, across all resource ratio presentations in Phases 1 (squares) and 2 (diamonds).

conducted elsewhere, are plotted as data points in Figure 3; values equal to 1 show perfect matching, while values less than 1 show undermatching and values greater than 1 show overmatching. For ease, data in Phase 2 are presented in the same manner as in Phase 1, although resource ratios remained constant across components. This provides us with an illustration of changes in the matching of rat ratios to resource ratios as a function of time. Note that data from Session 1 in Phase 1 was excluded due to a technical error that prevented the recording of resource data by 30-s samples.

Sensitivity values tended to increase and then decrease across components. In Phase 1, excluding the first component, peak sensitivity tended to shift later within a component as the session progressed, occurring at 120 s (Component 2), 180 s (Component 3), 240 s (Component 4), and 300 s (Component 5). A Spearman rank-order correlation found a positive relationship between component and time of peak sensitivity ($\rho = 0.7$). In Phase 2, sensitivity values tended to increase over the first three components, with the greatest overmatching observed in the third component. Sensitivity in Components 4 and 5 was slightly lower than in Component 3, though it did not appear to decrease systematically over time. Sensitivity in the last half of sessions tended to be greater in

Phase 2 than in Phase 1, suggesting the stability of the resource ratios in Phase 2 permitted better matching at the end of sessions than in Phase 1, where resource ratios changed every 6 min.

Individual Choice

Figures 4 and 5 show plots of log time allocation and log intake ratios for individual rats in Phases 1 and 2, respectively. The filled points represent the mean data, summed across sessions for each resource ratio, the unfilled points the individual session means. The GML (Eq. 2) provided a good fit to the data from both phases (mean $R^2 = 0.90$ and 0.99 for Phases 1 and 2, respectively, although the individual fits were poor for two rats (Blue and Purple) in Phase 1. Undermatching prevailed in both phases. In Phase 1, mean sensitivity was 0.36, with considerable between-subject variability, including negative sensitivity and strong bias for one rat (Purple). In Phase 2, mean sensitivity was 0.50 and showed less between-subject variability (range = 0.35 - 0.62) and little bias (average $b = 0.02$).

Individual time allocation was also analyzed in relation to group (total available) resource ratios. These data are summarized in Table 1, which shows parameter estimates for GML fits,
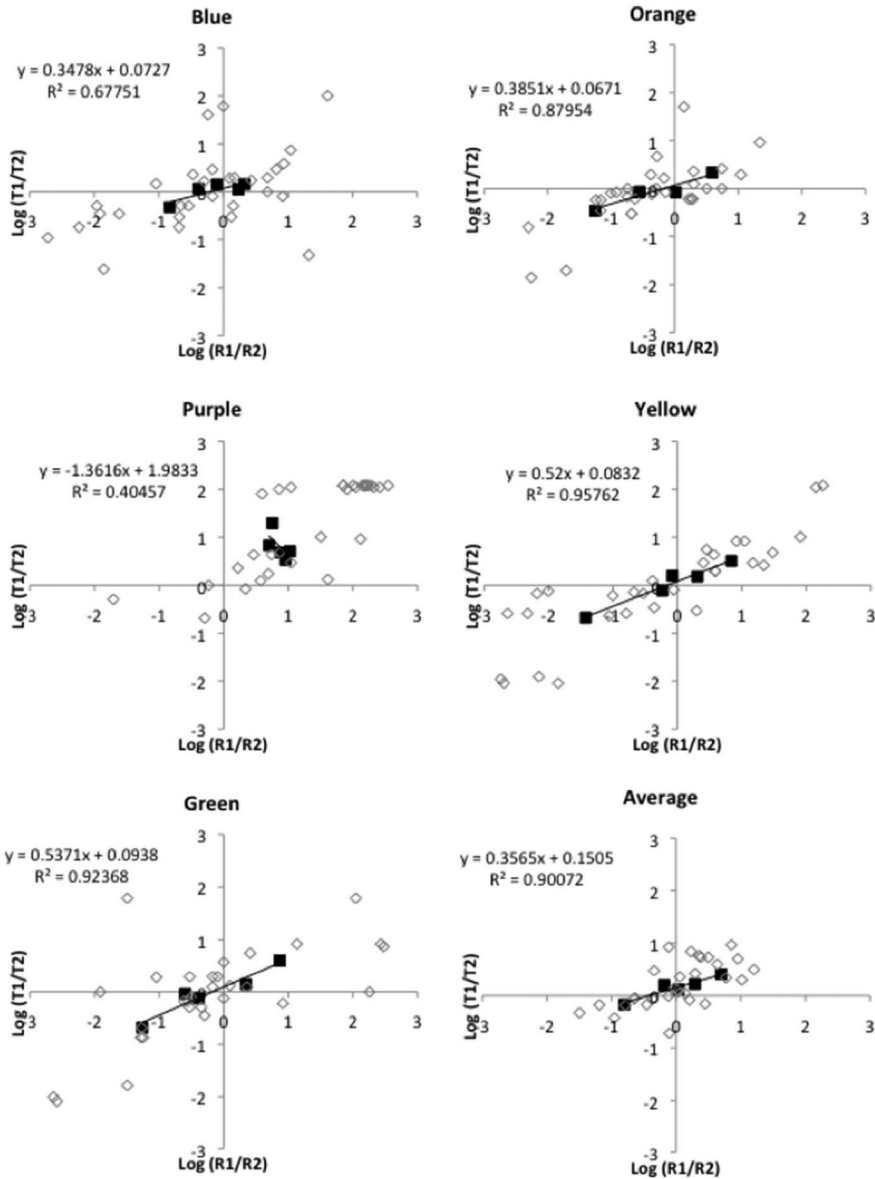
Fig. 4. Individual GML fits for Phase 1. Plots are of the ratio of time samples spent and food consumed in Patches 1 and 2, summed across replicates and components of each resource ratio (filled series) or only across components (unfilled series). The average plot shows the mean log time allocation and intake ratios calculated of each of all five subjects. Equations and R2 values for the filled series are shown.

both for individual intake ratios (left) and group resource ratios (right), aggregated over session components and resource ratios. Considering first the data from Phase 1 (top panels of Table 1), rats with moderate to high sensitivity to individual intake ratios (Green, Yellow and Orange) showed relatively greater sensitivity to group resource ratios. The remaining two rats showed either worse sensitivity to group resource ratios (Blue), or slightly less negative sensitivity (Purple).

For the majority of subjects in Phase 2 (bottom of Table 1), however, model fits were much worse using group resource data,
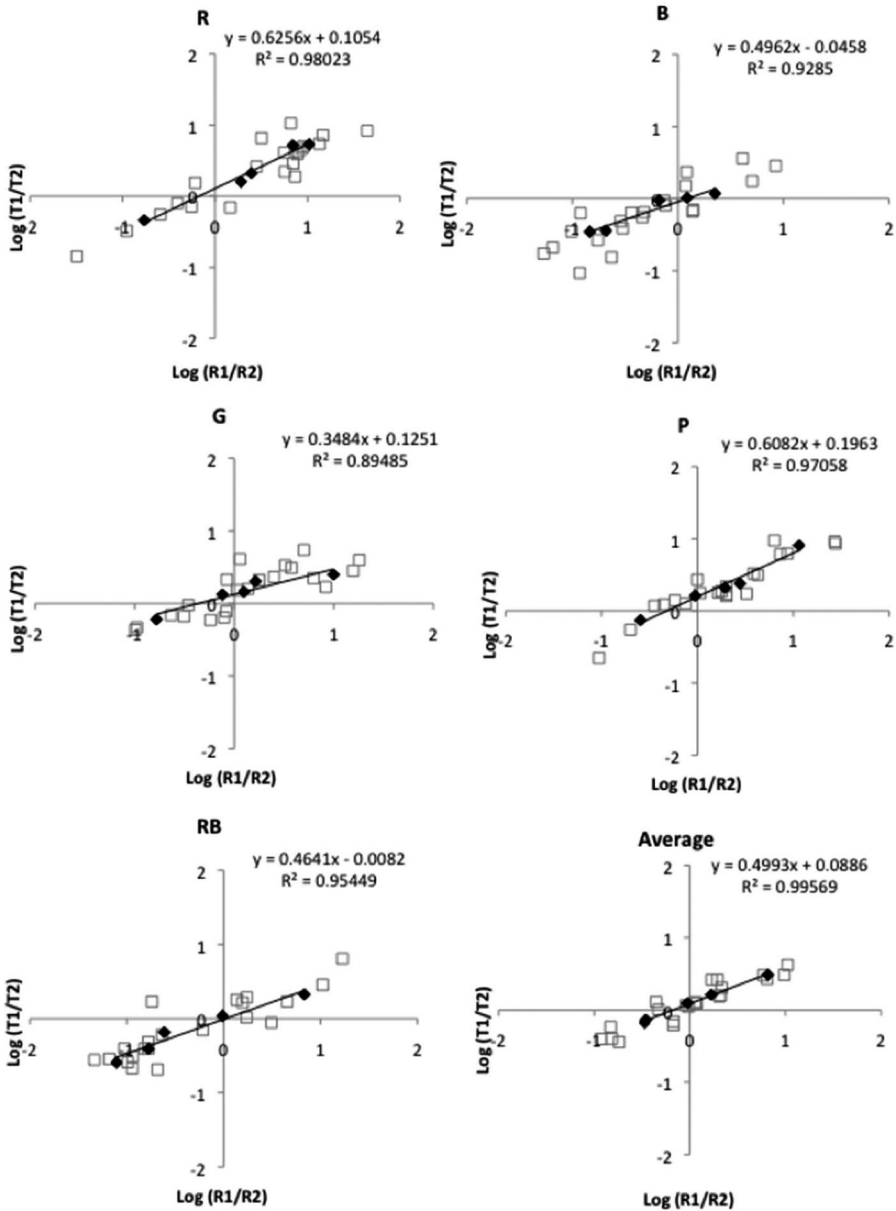
Fig. 5. Individual GML fits for Phase 2. See Figure 4 for details.

accounting for less than 15% of the total variance, and low to negative sensitivity. The single exception was Red, for which higher R^2 values and somewhat greater sensitivity to group resource ratios than individual intake ratios was seen. Bias was greater for each rat when analyzed in relation to group resource ratios.

Competitiveness

Results from the competitive assessment sessions varied over time. Performances in the first and second competitive assessment session in Phase 1 were weakly negatively correlated (Spearman's $\rho = -0.31$), as was performance in

Table 1

Obtained parameter fits of individual time allocation and individual and group resource data from Phase 1 (top) and Phase 2 (bottom)

Subject	Individual Intake Ratios			Group Resource Ratios		
	Sensitivity	Bias	R^2	Sensitivity	Bias	R^2
Blue	0.35	0.07	0.68	0.26	0.02	0.50
Orange	0.39	0.06	0.88	0.48	0.06	0.87
Purple	−1.36	1.98	0.40	−0.5	0.80	0.89
Yellow	0.52	0.08	0.96	0.73	0.03	0.80
Green	0.54	0.09	0.92	0.82	0.00	0.94
Mean (SD)	0.09 (0.81)	0.46 (0.85)	0.77 (0.23)	0.36 (0.53)	0.18 (0.35)	0.8 (0.18)

Subject	Individual Intake Ratios			Group Resource Ratios		
	Sensitivity	Bias	R^2	Sensitivity	Bias	R^2
Red	0.63	0.11	0.98	0.70	0.33	0.91
Blue	0.50	−0.05	0.93	0.01	−0.17	0.00
Green	0.35	0.13	0.89	−0.14	0.15	0.13
Purple	0.61	0.20	0.97	−0.07	0.34	0.01
RB	0.46	−0.01	0.95	0.00	−0.16	0.00
Mean (SD)	0.51 (0.11)	0.07 (0.1)	0.95 (0.03)	0.10 (0.34)	0.10 (0.25)	0.21 (0.39)

the pre- and postexperimental assessments in Phase 2 ($\rho = -0.41$). Because not all rats ate food pellets reliably in the first competitive assessment in Phase 1, and because the competitive assessment in Phase 2 was a more accurate representation of competitiveness during the second session, only data from the second competitive assessments in both phases are shown.

The relative consumption (proportion of total resources consumed) by each individual in the competitive assessment was positively related to relative consumption in the experimental sessions, and sensitivity to individual intake ratios in Phase 1. The left panels of Figure 6 plot the relative consumption for each rat in the experimental sessions of Phase 1 (upper panel), as well as the mean sensitivity to the intake ratios (lower panel), as a function of relative consumption of each rat in the competitiveness assessment. Spearman rank-order correlations found positive correlations between relative consumption in the competitive assessment and (a) relative consumption in the experimental sessions ($\rho = 0.7$), and (b) sensitivity to intake ratios ($\rho = 0.6$), suggesting better competitors obtained more food and were more sensitive to individual intake ratios in the experimental sessions than weaker competitors.

The right panels of Figure 6 show the relative consumption and sensitivity to individual intake

ratios from the experimental sessions plotted as a function of relative consumption in the competitive assessment for Phase 2. Results were similar to Phase 1: Both relative consumption and sensitivity increased with performance in the competitive assessment session. Positive correlations were obtained between consumption in the competitive assessment and consumption in the experimental sessions ($\rho = 0.36$) and sensitivity ($\rho = 0.60$).

Individual differences in relative consumption as a function of patch profitability was investigated by calculating the average proportion of total resources each rat obtained at each patch, divided by the average proportion of resources delivered, at ratios exceeding 1:1 (i.e. when the patches differed in relative profitability). These data from Phase 1 are summarized in the left panels of Figure 7, and those from Phase 2 in the right panels.

In Phase 1, relative consumption was related to patch quality. Competitiveness was positively correlated with relative consumption at the rich patch ($\rho = 0.80$) and weakly negatively correlated with relative consumption at the lean patch ($\rho = -0.30$). To further investigate this relationship, we conducted Spearman rank-order correlations between individual sensitivity to intake ratios and relative consumption at the rich and lean patches (data not illustrated). Relative consumption at the rich patch was positively
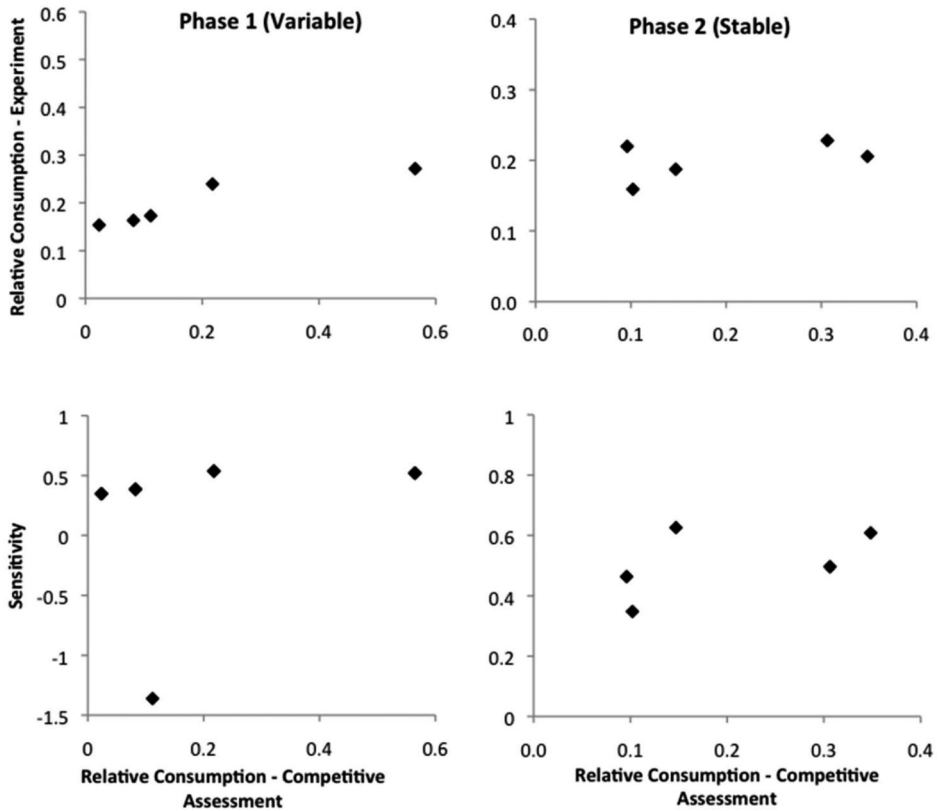
Fig. 6.   Proportion of total resources obtained by each rat during the experimental sessions (upper panels) and GML sensitivity to individual intake ratios (lower panels) plotted as a function of proportion of total food obtained during the competitive assessments for Phase 1 (left panels) and Phase 2 (right panels).

correlated with individual sensitivity ($\rho = 0.90$, $p < .05$), while relative consumption at the lean patch was negatively correlated with individual sensitivity ($\rho = -0.90$, $p < .05$). Thus, rats with higher sensitivity to individual intake rates obtained relatively more resources in the rich patch, and less in the lean. Consistent with this, a Spearman rank-order correlation revealed a strong negative relation between relative consumption at the rich and lean patch ($\rho = -0.8$; lower-left panel of Fig. 7). Stronger competitors would obtain more resources at the rich patch and fewer reinforcers at the lean patch than weaker competitors, who showed the opposite pattern.

In Phase 2 (right panels of Fig. 7), the relationships between competitiveness and patch quality were mixed. Relative consumption in the competitive assessment and relative consumption were positively correlated in the lean patch (averaged across reinforcement ratios) ($\rho = 0.6$), but weakly negatively correlated in the rich patch ($\rho = -0.1$). Note that this slight negative Spearman correlation does not correspond with the positive slope shown in the figure; this is because the Spearman correlation is based on the consistency of rank order of two variables, which can differ from the relationship between the absolute values, typically used in Pearson correlations, and plotted in Figure 7. Unlike Phase 1, relative rates of resource consumption per rat in both patches were similar; a positive correlation was found between the average proportion of resources obtained in the rich and lean patch ($\rho = 0.70$; lower-right panel of Fig. 7). Additional Spearman rank-order correlations showed that sensitivity to individual intake ratios was not correlated with
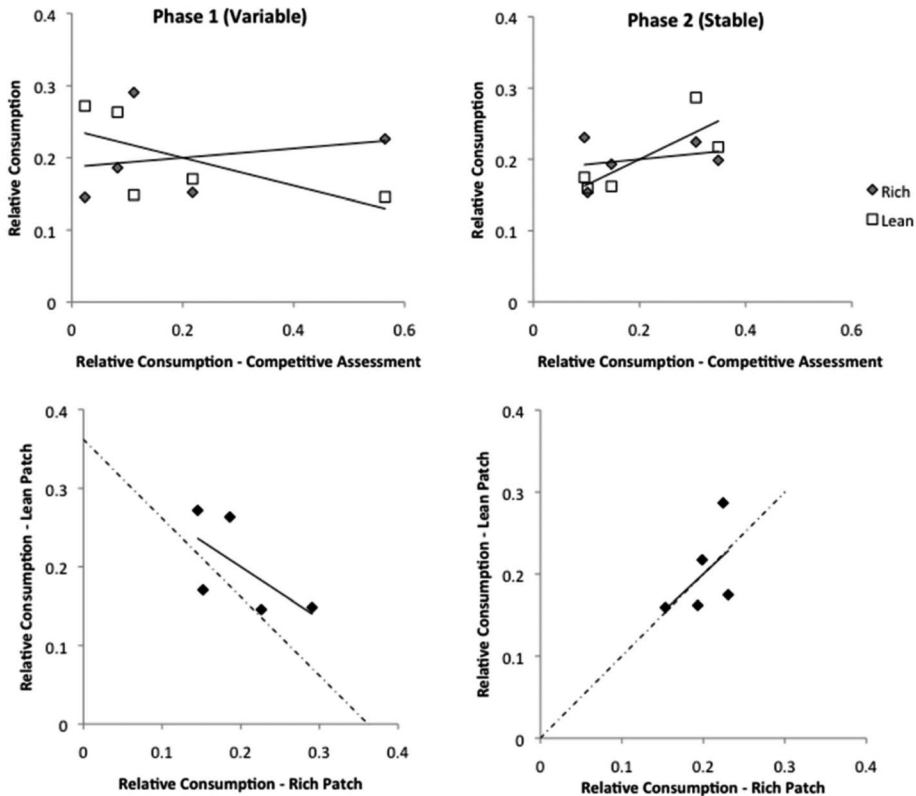
Fig. 7.   The average proportion of total food obtained by each subject in the Rich and Lean patches plotted as a function of competitive assessment performance (upper panels) and the average proportion of total food obtained by each subject in the lean patch plotted against the average proportion of total food obtained in the rich patch (lower panels) for Phase 1 (left panels) and Phase 2 (right panels).

relative consumption at the rich patch ($\rho = 0$) and only weakly correlated with relative consumption at the lean patch ($\rho = 0.3$).

Discussion

The results of this study show that the behavior of rats foraging in a social context adapts to changes in relative resource quantity when it varies unpredictably within and predictably across sessions. The distribution of rats in space and time corresponded to the relative distribution of resources in the environment as a whole, with the group and individual distributions broadly consistent with the predictions of the IFD and the GML, respectively. The results contribute to a growing body of research concerned with quantitative analyses of social foraging (Baum & Kraft, 1998; Bell & Baum, 2002, Gray, 1994; Tan & Hackenberg, 2012).

Consistent with previous research, there was clear evidence of undermatching at both the group and individual levels; more rats were observed at the leaner than the richer patch relative to the reinforcer ratio, and rats tended to spend relatively more time in the lean than in the rich patch than would be predicted by the amount of resources obtained at these patches. The sensitivity values for both the group and individuals ranged between approximately 0.4 - 0.5, falling intermediate to sensitivity values observed in previous research (Bell and Baum, 2002; Kennedy & Gray, 1993; Tan & Hackenberg, 2012), and approximately equal to others (Gray, 1994; Baum & Kraft, 1998 in the small bowl condition).

The present sensitivity values were somewhat higher than the recent Tan and Hackenberg (2012) study, though conducted with the same species and apparatus. This might reflect an

effect of the dimension along which resources were varied: relative *quantity* (present study) versus relative *rate* (Tan & Hackenberg, 2012). These differences, however, are likely not due to resource manipulations alone; previous studies in which rate and quantity have been manipulated do not show consistent differences in sensitivity to reinforcer quantity (Abrahams, 1989; Grand, 1997; Kohlmann & Risenhoover, 1997) and reinforcer rate (Baum & Kraft, 1998; Bell & Baum, 2002). Future work would profitably be directed to comparative analyses of the various reinforcer dimensions (e.g., quantity, rate, density, probability), along which resource profitability is defined for different species.

Such work will require expanding the canonical models of individual and group choice, such as the IFD and the GML. Among the simplifying assumptions of the IFD is that foragers have perfect knowledge of the environment. Although perhaps unrealistic in natural settings, such perfect knowledge can be approximated in the laboratory by extended exposure to a regular and predictable environment. In the present study, sensitivity was higher and less variable when food ratios were predictable and stable (Phase 2) than when they were unpredictable and varied randomly within a session (Phase 1). This is consistent with some findings of Bell and Baum (2002). Although not statistically significant, Bell and Baum found consistently higher sensitivity (5 of 6 comparisons) in regular than irregular conditions. While we also found higher and less variable sensitivity values in the regular conditions, it is not clear whether this was due to the less predictable environment per se, or to briefer overall exposure to the contingencies: Phase 1 consisted of just 6 experimental sessions whereas Phase 2 consisted of 21 total sessions.

Patterns of IFD sensitivity within components (Fig. 3) differed from those observed by Bell and Baum (2002). In Bell and Baum's conditions with irregular, unpredictable variations in food ratios, low sensitivity values early in the component gave way to higher sensitivity values later in the component. By the end of the component, sensitivity values in the regular and irregular conditions were indistinguishable. Similarly, in Phase 1 of the present study, peak sensitivity tended to occur later rather than earlier in a component, but this was often followed by a decrease in sensitivity. In addition, there was a rightward shift in peak sensitivity values as a function of ordinal position of the component within the session, meaning that sensitivity increased both as a function of time within the component and across components in the session. That maximum sensitivity tended to occur later in components as the session progressed may seem counterintuitive, as one might expect behavior to adjust more quickly to new resource ratios upon greater experience with such changes across the session.

Within-session patterns of sensitivity in Phase 2 differed from those in Phase 1. As expected, due to stable resource ratios that lasted the whole session, sensitivity values tended to be higher than in Phase 1, especially at the end of sessions, and showed less systematic variation across time. This suggests regularity in resource distributions does influence sensitivity values, permitting better matching under stable conditions.

A second simplifying assumption of the IFD is that competitive ability is equal, and foragers are free to switch patches without regard to the presence of other animals. A mounting body of evidence challenges the strong version of this assumption, though such competition effects are complex and not well understood (see Cresswell, 1998; Grand, 1997; Sutherland, Townsend, & Patmore, 1988; Tregenza & Thompson, 1998). Gray (1994) found strong competitors showed a tendency to overmatch the resource distribution while weaker competitors undermatched: individuals able to distribute behavior more optimally between both patches also obtained higher intake rates. Similar patterns were evident in both phases of our study: positive correlations between sensitivity and competitiveness were observed. These distinct patterns of foraging behavior were at least partly the product of competition: Stronger competitors obtained more food from the rich patch, while weaker competitors obtained more food from the lean patch.

Unlike Phase 1, the mean proportion of total food obtained in the rich and lean patches during Phase 2 were positively correlated with each other, but their relation with competiveness and sensitivity was mixed; there was no clear relation between competitiveness or sensitivity and food obtained in the rich patch, and only intake rates in the lean patch were positively correlated with competitiveness. This might be due to interactions between competitiveness

and resource predictability. In highly variable environments (as in Phase 1), the costs of switching patches may not exceed the possibility of gaining more reinforcement because the discriminability of the distribution of resources is low. And because sensitivity was correlated with effectiveness, it is possible the better competitors (with higher sensitivity values) were able to identify and monopolize the rich patch. Conversely, in more stable environments (as in Phase 2), the more predictable and discriminable resource distributions might advantage the weaker competitors (with lower sensitivity values), allowing them to better identify and compete at the richer patch, so that competitive differences are only observed at the lean patch. Note that in this paradigm, multiple pellets were delivered in rapid succession, which may be difficult for a single rat to defend. This would allow a more optimal distribution of competitors that match resource distributions more proportionally, and a more even distribution of resources among foragers across patches.

The lower IFD sensitivity observed here relative to other studies might be at least partly a result of competition effects. Baum and Kraft (1998) found greater undermatching when food was dispensed into small bowls (sensitivity $= 0.38$) than both troughs (sensitivity $= 0.71$), and $1.2\,m^2$ areas (sensitivity $= 0.79$). In the current study, food was dispensed into small petri dishes that limited access to one or possibly two rats. This may have produced greater interference between foragers, enhancing competition effects, than if food was more widely distributed.

Whether due to competition or some other factors, differences in individual sensitivity suggest that order seen at the group level is not a simple product of the animals all behaving in the same way. Similar conclusions were drawn by Baum and Kraft (1998), who found that preferences and switching by individual pigeons did not correspond to that of the group, prompting the authors to regard the group-level order as an emergent phenomenon, not reducible to the behavior of individuals. In other words, the matching observed at the level of the flock was not merely the sum or average of parallel individual choices. Due to the large group size (30+ pigeons), however, it was not possible for Baum and Kraft to examine complete individual location or intake rate

data. Moreover, because only two reinforcer ratios were studied, full GML fits were not possible, limiting the analysis of individual and group choice.

In contrast, our experimental design permitted the collection of complete individual intake and location data for all ratios, subjects and experimental sessions. In the main, there was some inconsistency between individual and group distributions. Individual sensitivity values deviated from that of the IFD in some cases, and individual biases were not always towards the same location and to the same extent as that seen in the group. These findings are similar to those reported in prior social foraging research (Gray, 1994; Tan & Hackenberg, 2012), and suggest that the collective behavior of the group, while clearly composed of the behavior of individuals, is not simply an aggregate byproduct of individual choice behavior. Rather, the choice patterns of the individual and of the group reflect orderly processes at different levels of analysis; the GML and IFD provide complementary accounts of such order.

The lack of strict correspondence between group and individual choice patterns makes more sense when viewed in light of the different response profiles of individual rats. As shown in Table 1, for some rats, particularly those in Phase 1 where resource ratios varied unpredictably within a session, sensitivity was higher and GML fits better, when plotted in relation to resource ratios for the group (what others have termed *input ratios*) instead of the individual intake ratios; for other rats, particularly those in Phase 2, where food ratios were stable across a session, sensitivity was higher, and fits better, when plotted in relation to individual intake ratios instead of the group resource ratios. Perhaps in more regular and predictable environments, sensitivity to individual encounter rates is key, whereas in less regular and unpredictable environments, sensitivity to overall resource availability (including those consumed by other rats) is a crucial supplement to individual encounter rates. It seems likely that choice patterns in such dynamic social environments reflect joint control by resources *available* to the group and resources actually *encountered* by individual animals, and it is an important priority of future research to disentangle these separate but overlapping sources of control. The methods employed here, which enable detailed measurement of programmed and obtained

resources at the individual and group level, are well suited to this task.

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