

SOCIAL FORAGING IN RATS: GROUP AND INDIVIDUAL CHOICE IN DYNAMIC ENVIRONMENTS

FORRAJEО SOCIAL EN RATAS: ELECCIÓN GRUPAL E INDIVIDUAL EN AMBIENTES DINÁMICOS

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Abstract

Group and individual choice behavior in dynamic social environments was examined in a laboratory foraging analogue. Five rats were studied across multiple sessions in a free-ranging paradigm, where food reinforcement was delivered from two patches according to variable time intervals. Five reinforcement ratios (1:1, 1:4, 1:8, 8:1, 4:1) were presented either in irregular sequence within a session (Variable condition) or across sessions (Stable). Competitiveness, defined in terms of obtained resources, was assessed by delivering food at one feeder only. The generalized matching law and ideal free distribution accounted for individual and group data well. Sensitivity of the group and individual behavior to reinforcement contingencies increased with less variability in resource availability, but also increased with greater experience. The experimental paradigm shows great promise for examining adaptive behavior in a social context.

Keywords: choice, foraging, social behavior, generalized matching law, ideal free distribution, rats

Resumen

Se examinó la conducta de elección individual y grupal en ambientes sociales dinámicos mediante una preparación de laboratorio análoga al forrajeo. Se estudiaron a cinco ratas durante múltiples sesiones bajo un paradigma de búsqueda libre (*free-ranging*), en las cuales se entregó alimento como reforzador en dos parches conforme

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a intervalos variables de tiempo. Se presentaron cinco razones de reforzamiento (1:1, 1:4, 1:8, 8:1, 4:1), ya fuese en secuencias irregulares dentro de una misma sesión (condición variable) o entre sesiones (condición estable). Se evaluó la competitividad, definida en términos de recursos obtenidos, mediante la entrega de comida en sólo un comedero. La ley generalizada de igualación y la teoría de la distribución libre ideal explicaron los datos individuales y grupales satisfactoriamente. La sensibilidad de la conducta individual y grupal a las contingencias de reforzamiento aumentó en la condición de menor variabilidad en la disponibilidad del recurso, pero también aumentó con la experiencia. El paradigma experimental muestra ser promisorio para el análisis de la conducta adaptativa en un contexto social.

Palabras clave: elección, forrajeo, conducta social, ley generalizada del efecto, distribución libre ideal, ratas

Successful foraging requires the efficient discrimination of when and where to search for food—a resource often available only in limited amounts and distributed in patches, spatially and temporally. Despite the complexity of such behavior, it is commonly assumed that foraging-related behavior can be understood from the standpoint of optimization, as behavior that maximizes net energy gain. Indeed, optimization models have proven extremely successful in accounting for foraging behavior of human and nonhuman animals, in both field and laboratory settings (see Hackenberg, 1998; Krebs & Davies, 1997; Stephens, 2008; Stephens & Krebs, 1986).

To date, the majority of optimal foraging models have been formulated to address individual behavior. In many species, however, foraging occurs in a social context, and the presence of other individuals may alter what is optimal for a single forager. In other words, the optimal outcome for an individual may depend not only on what that individual is doing, but on what others are doing as well. This adds a layer of dynamic complexity to the situation that optimization models must take into account.

One such model of social foraging is the Ideal Free Distribution (IFD), originally developed by Fretwell and Lucas (1970) to describe group foraging in environments with resources distributed in patches. The IFD is so named because it assumes that animals have complete or *ideal* knowledge of the distribution of resources in the environment, and are *free* of constraints, such as travel time or individual competitiveness for resources. Given these assumptions, the IFD predicts that the distribution of animals in each patch should be proportional to the distribution of resources in those patches:

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

where N equals the number of foragers, R equals the number of resources (prey items), and the subscripts represent the alternatives.

The fit of the behavior of groups of foragers to the IFD has been tested with multiple species in both laboratory and field settings (see Kennedy and Gray, 1993 for a review). The equation describes fairly well the cross-patch distribution of birds (e.g. Baum & Kraft, 1998; Bell & Baum, 2002; Bautista, Alonso, & Alonso, 1995; Gray, 1994; Harper, 1982), fish (Abrahams 1989; Grand, 1997; Grand & Grant, 1994, Tregenza & Thompson, 1998), invertebrates (Lamb & Ollason, 1993; Blanckenhorn, Morf & Reuter 2000), nonhuman mammals (Dreisig, 1995; Kohlmann & Risenhoover, 1997; Maguire, Ramp, & Coulson, 2006; Wahlström & Kjellander, 1995) and humans (Critchfield & Atteberry, 2003; Goldstone & Ashpole, 2004; Kraft & Baum, 2001; Kraft, Baum, & Junge, 2002; Sokolowski, Tonneau, & Baque, 1999). While the IFD has provided a reasonably good description of group foraging under a wide range of naturalistic conditions, systematic departures from the model have been found consistently; often foragers will overutilize less profitable patches, while underutilizing richer patches.

This deviation from ideal foraging appears to be driven in part by individual differences in competitiveness. Stronger competitors will dominate a single patch (although not necessarily the richer [see Milinski, 1984; Sutherland, Townsend & Patmore, 1988]), often forcing weaker competitors to spend more time in the alternative, which results in the group distribution undermatching the resource ratios (e.g. Harper, 1982, Monaghan & Metcalfe 1985). Tregenza, Hack and Thompson (1996), for example, found that in a group of 10 Cichlid fish, stronger competitors (those with higher intake rates when resources are located at a single location) performed better at lower competitor densities, but weaker competitors performed better at higher competitor densities. The authors suggest that this was due to a change in foraging strategies, from a contest between individuals at low densities to a scramble for resources at high densities. Similar results were obtained by Inman (1990) with starlings and by Grand (1997) with salmon. Together, these results suggest a complex relation between patch profitability, competitiveness and competitor density on individual distributions and intake rates.

One difficulty with the applying the predictions of the IFD under naturalistic conditions is that it is not always possible to satisfy the simplifying assumptions of the model. For example, due to differences in sensitivity to and the discriminability of reinforcement contingencies as well as individual differences in ability to obtain resources in the presence of other competitors, resource intake rates often vary between foragers. This is where laboratory methods can be of value. In a controlled laboratory study, Gray (1994) investigated the allocation of the behavior of six house sparrows between two feeders, manipulating the ratio of resources between these patches across days. He examined agonistic interactions between individuals to establish a linear hierarchy and measure of competitiveness. Gray analyzed the responses and time allocation in relation to the IFD and the generalized matching law (GML), using the following equation:

$$\log \left(\frac{B_1}{B_2} \right) = s \cdot \log \left(\frac{R_1}{R_2} \right) + \log b \quad (2)$$

where B refers to the behavior, R refers to the reinforcement available at either alternative and s and b are fitted parameters said to reflect sensitivity and bias, respectively.

Using group response and time allocation data, rather than the typical distribution of individuals, Gray found undermatching (slopes of 0.5 or less) in the fits of the generalized IFD to feeder input ratios, similar to the typical undermatching of choice ratios to reinforcer ratios seen with individual response ratios on concurrent schedules of reinforcement. In fact, when analyzed at the individual subject level, Gray found that GML slopes did not differ significantly between birds, but when matching functions were fitted using the overall reinforcer ratios, much greater variation was seen in individual sensitivity values. Correlations between the slopes of individual GML fits and their rank in the dominance hierarchy were positive and significant. Social ranking appeared to affect foraging behavior in other ways. Dominance was also positively correlated with food intake rate, and subordinates experienced a smaller range of reinforcer ratios than dominant birds. Additional analyses found interactions between dominance ranking and patch location on intake rates: higher-ranking birds exhibited a bias towards one patch, forcing subordinate birds into the other patch.

In addition to competitiveness, another major assumption of the IFD concerns perfect knowledge of the foraging environment. By exposing animals to stable environments over relatively long periods, it is possible to approach the IFD assumption of complete knowledge of the foraging environment. Bell and Baum (2002) used the IFD framework to examine the adaptability of a flock of pigeons when the availability of resources in two different patches varied regularly and irregularly within sessions (every 6 min) or across sessions (every day). The latter set of conditions was arranged to simulate relatively stable foraging environments. The IFD described group behavior well, accounting for at least 80% of variability in the group data in all the conditions. The group choice allocations rapidly adjusted, within 5 min, to both predictable and unpredictable changes in the distribution of resources within and across sessions. Analyses of sensitivity and response allocation as a function of time within sessions showed greater reliance on present (current food ratio) than past conditions (prior food ratios) when resource presentations exhibited greater variability and unpredictability. Positive sensitivity values were obtained at the beginning of blocks in the regular and irregular-across conditions and negative sensitivity in the within-irregular conditions. In addition, correlations in response ratio across 15-s blocks were close to 1 in regular conditions but dropped rapidly to strong negative values in the irregular conditions. Generally, sensitivity of the group to resource ratios tended to be slightly greater when resource distributions were regular and predictable, although the differences were not large enough to be considered reliable.

Milinski (1984) also conducted an experiment that examined the interactions between competitiveness and IFD sensitivity with stickleback fish. He found stronger sensitivity when the availability of resources was available regularly than irregularly

(although re-analyses by Kennedy & Gray [1993] showed essentially no difference). Better competitors tended to overmatch relative to poorer competitors, and this pattern was greater under regular than irregular conditions.

The current experiment investigated group and individual foraging behavior in a laboratory experiment with rats in predictable and unpredictable environments. In this procedure, food was delivered in two patches according to variable-time (VT) schedules, in such a way that average delays to reinforcement were constant within a single reinforcement ratio, but individual delays were unpredictable. The relative rates of reinforcement between the two patches varied irregularly within a session (Variable condition) or across sessions (Stable condition).

This study aimed to replicate Bell and Baum (2002) with a different species and reinforcement schedule that was less predictable and thus more akin to a natural environment. One prior study used the IFD framework to examine rats' performance in a laboratory foraging analogue (Farmer-Dougan & Dougan, 2005), but was not explicitly concerned with resource predictability or competitiveness. We aimed to (a) provide a detailed examination of individual and group choice patterns in a dynamic social foraging environment; (b) assess the descriptive adequacy of the IFD and the GML as accounts of collective and individual behavior, respectively; and (c) further explore the relations between competitiveness, sensitivity, and foraging efficiency.

Method

Subjects

Five male Long Evans rats were subjects in this experiment. They were housed in pairs (one lived separately with another rat not in the experiment), with a 12-hr light/dark cycle. They were marked using nontoxic hairspray of varying colors. Rats were food restricted for 22 hrs prior to experimental sessions.

Equipment and Materials

Rats were tested in a square foraging arena measuring 122cm², made of particle-board with 1.9 cm thick walls that were 30.5 cm high. The two corners adjacent to each feeder also had plastic extensions added, extending 47cm from each corner and 6.4cm above the original wall. The flooring in the arena was dark grey linoleum. Individual patches were delineated by raised edging around each area, which measured 465 cm² each. Feeders, located in diagonally opposite ends of the arena, dispensed banana-flavored sugar pellets via a plastic tube that protruded downward approximately 1cm from the wall into a circular petri dish, 27cm in diameter. Note that during the experiment, the external tubing had to be removed due to destruction by the subjects, so that pellets were dispensed directly from the feeder opening. Feeders were operated externally by a VB.net program. A tone generator located at each feeder produced a 1-s tone at 1.5kHz and 2.5kHz with every pellet delivery at Feeder 1 and 2, respectively. Video footage from three different angles recorded every session.

Two webcams were positioned 73.7 cm above each patch to record events occurring within that area. A third video camera was set up from a raised position outside the apparatus to record activity in the whole experimental area.

Procedure

The experiment consisted of three main conditions, in which reinforcement ratios 1:1, 1:4, 1:8, 8:1, 4:1, were arranged unpredictably within a session (Variable condition) or remained stable throughout the whole session and varied unpredictably across sessions (Stable condition). The base schedule was a variable-time (VT) 15-s schedule, such that the ratios were VT 15 VT 15, VT 15 VT 60, and VT 15 VT 120, under reinforcer ratios of 1:1, 1:4, and 1:8, respectively. The order of reinforcement ratios was counterbalanced within each condition. Each session was 30 min in duration, immediately preceded by a 1-min adaptation period, in which the rats were placed in the apparatus in the absence of programmed contingencies and data collection. In the sessions comprising the Variable condition, the five ratios were arranged in 6-min unsignalled components.

The conditions were arranged in an ABA design, with the Variable condition constituting the A-phase and the Stable condition the B-phase. Both the Stable and first Variable conditions each lasted 10 consecutive sessions, separated by four days. The second Variable condition consisted of five sessions conducted one week after conclusion of the Stable condition.

Competitiveness was assessed in a single session following the first Variable condition, three days prior to the Stable condition. This session was of equal duration as the previous conditions, only differing in terms of the reinforcement contingencies and structure; two reinforcement schedules operated over six components of five minutes each. In the first four components, reinforcement was delivered on a VT 15-s schedule at a single patch (alternating) lasting for four components, followed by two components where no VT schedule operated, and instead 50 reinforcers were delivered successively at single patch only, contingent on the consumption of the previously delivered reinforcer. The location of the reinforcing patch alternated also during these two final components. This latter condition was similar to an FR 1 reinforcement schedule, where each successive reinforcer was delivered immediately after the consumption of the prior reinforcer, akin to the rapid presentation method used by Bell and Baum (2002).

Individual consumption of each reinforcer was manually recorded as it occurred during every session by two observers, one in each patch. It was not possible to check the reliability of the consumption data, since it was recorded in real time, and not observable from the video footage. Each rat's location was coded from the video footage using time sampling methods: rats were scored every 15 s as either inside or outside Patch 1 or Patch 2. A rat was considered inside the patch if its head and/or four feet were located within that area delineated by the raised edging of the patch. A

second coder also coded individual rat location from the video footage for seven of the sessions. Inter-coder reliability was calculated as the overall number of disagreements divided by the number of disagreements and agreements, summed across all sessions and was equal to .93 (range across sessions = .90-1.00). Discrepancies were checked by reanalysis of the video footage. Of the total 4200 data points used in the reliability check, 0.01% were errors made by the original coder.

Results

Due to a feeder malfunction that caused the delivery of multiple instead of single pellets from Feeder 2, data from six components in the initial Variable condition (the fourth and fifth components from Session 7 and all except the first component from Session 9) were excluded from analyses. Excluding the 1-min adaptation period at the beginning, data from the whole of every session were used in the analyses. For model fits, reinforcer and location data were summed within each component, and then summed across the replicates of the five different reinforcement ratios. Note that because we are plotting the ratios of rats and reinforcers in Patch 1 and 2, it does not matter whether data are summed or averaged across reinforcement ratios, as the relation is maintained.

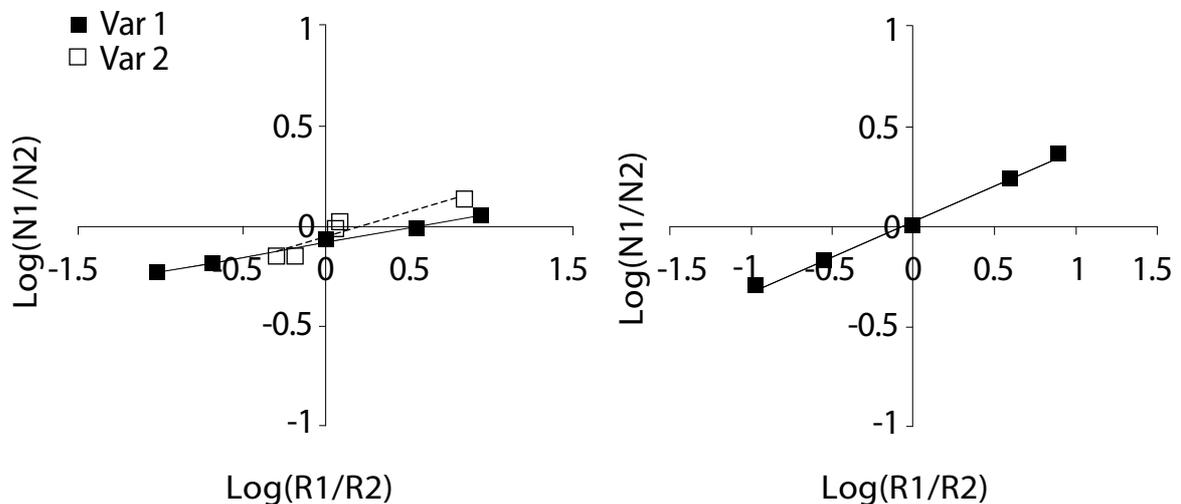


Figure 1. The log ratio of the number of rats in Patch 1 and 2 plotted as a function of reinforcer ratios in the first (Var1) and second (Var2) exposure to the Variable conditions (filled and unfilled series in left panel, respectively) and the Stable condition (right panel), summed across replicates of reinforcer ratios.

Table 1

Sensitivity and Bias values and total R² obtained in generalized IFD and GML fits to individual and group time allocation and obtained reinforcement data in the Variable and Stable conditions

IFD	Sensitivity		Bias		R ²	
Variable1	0.15***		-0.08		98.96%	
Stable	0.36		0.05		98.67%	
Variable2	0.25*		-0.05		89.69%	

GML	Individual Reinforcement			Group Reinforcement		
	Sensitivity	Bias	R ²	Sensitivity	Bias	R ²
Variable1						
34R	0.11*	-0.06	83.11%	0.11*	-0.06	80.45%
34W	0.19*	-0.12	87.95%	0.20*	-0.14	84.30%
38Y	0.20*	0.16	82.43%	0.23	0.23	72.09%
38G	0.09*	-0.35	88.43%	0.11*	-0.32	90.49%
39B	0.13	-0.15	53.58%	0.10	-0.15	52.28%
Stable						
34R	0.35	0.00	88.01%	0.28*	-0.10	85.73%
34W	0.21	-0.07	91.25%	0.41*	-0.03	84.78%
38Y	0.25	0.05	53.69%	0.06	0.06	17.17%
38G	0.36	-0.02	97.11%	0.39**	-0.02	95.37%
39B	0.48	0.15	98.88%	0.77**	0.36	95.05%
Variable 2						
34R	0.45**	0.27	98.22%	0.85*	0.72	77.80%
34W	0.27	-0.23	63.19%	0.30	-0.34	39.65%
38Y	0.02	-0.16	0.22%	-0.09	-0.15	6.08%
38G	0.27	-0.23	63.19%	0.08	0.09	4.99%
39B	0.46	-0.23	61.97%	0.82	-0.61	69.21%

The number of rats and total reinforcers delivered in Patch 1 and Patch 2 were summed within each of the five reinforcement ratios for all variability conditions to calculate ratios for the fits of the generalized IFD model. The obtained parameter fits for the model can be seen at the top of Table 1, and plots are shown in Figure 1. The distribution of rats between patches in all the conditions varied systematically with reinforcement ratios, and were well accounted for by the generalized IFD model (VAC = 99% in the first Variable and Stable conditions, and 90% in the second Variable condition). Group distributions strongly undermatched the resource distributions; slopes were markedly less than 1. Sensitivity was higher in the Stable condition ($s = 0.36$) than the two Variable conditions ($s = 0.15$ and 0.25 in the first and second Variable conditions, respectively). There were no marked biases in any of the conditions.

Values for the fitted GML parameters, using data summed across replicates of the programmed reinforcement ratios, are in the three leftmost columns of Table 1. The generalized matching law was fit to the proportion of time (calculated as number of time samples) spent in Patch 1 and Patch 2, and the number of reinforcers each individual obtained in each patch. For some rats in certain components the Stable and second Variable conditions, the number of reinforcers obtained or time samples spent in Patch 1 or Patch 2 were equal to 0, so in these conditions a constant of 0.1 was added to all data values prior to calculating reinforcement and time ratios for the GML fits (see Brown & White, 2005).

The GML provided a reasonable fit to data from the first Variable (mean individual $R^2 = 79.10\%$, $SD = 0.15$) and Stable conditions (mean individual $R^2 = 85.79$, $SD = 0.18$). Fits to the second Variable condition data were more variable than in previous conditions (mean individual $R^2 = 57.36\%$, $SD = 0.35$). Sensitivity generally was higher in the Stable condition ($M = 0.33$, $SD = 0.04$) and second Variable condition ($M = 0.29$, $SD = 0.18$) than in the initial Variable condition ($M = 0.14$, $SD = 0.05$), suggesting sensitivity increased with exposure to the procedure as well as with greater predictability in the reinforcement contingencies. Overall, slopes values approximated those obtained in the fits of the generalized IFD. Plots of the GML fits in the two Variable and Stable conditions are shown in Figures 2 and 3, respectively.

GML fits using the group obtained reinforcement ratios were calculated and are shown in the three rightmost columns in Table 1. Generally, these fits accounted for a smaller proportion of variance in individual matching behavior than the individual reinforcement ratios in all three conditions. Sensitivity values obtained with group reinforcement ratios were similar to those obtained with individual reinforcement in the first Variable condition ($M = 0.15$, $SD = 0.06$). Sensitivity to group reinforcement was greater but much more variable in both the Stable and the second Variable condition ($M = 0.38$, $SD = 0.25$ and $M = 0.39$, $SD = 0.43$, respectively). In these latter conditions, three of the rats showed sensitivity to group reinforcement that was approximately equal to or greater than that to individual reinforcement. In the second Variable condition, rats with high individual sensitivity relative to other subjects (34R, 39B), had higher sensitivity to group than individual reinforcement contingencies,

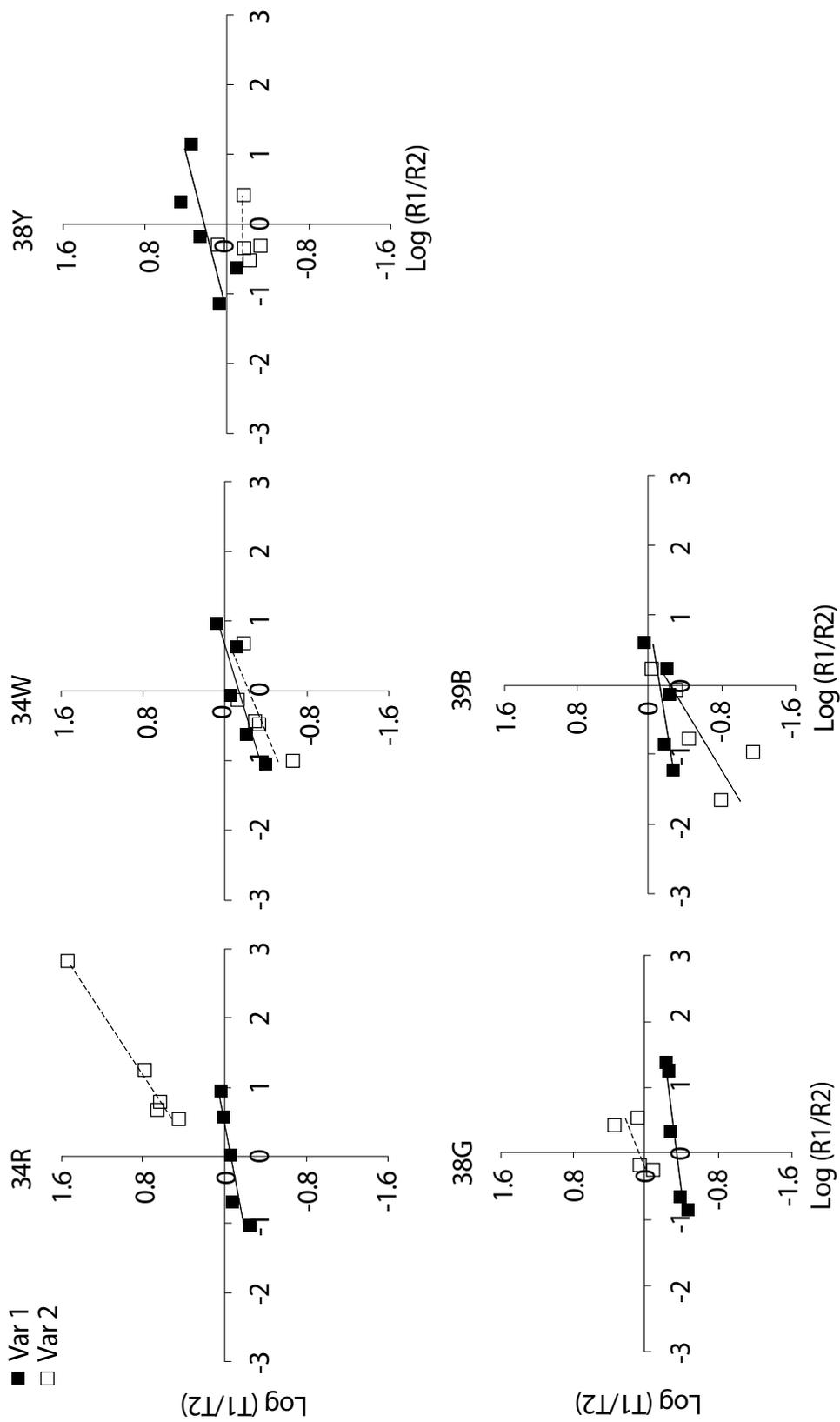


Figure 2. Average GML fits to time allocation as a function of obtained reinforcer rates for all subjects in the Variable1 (solid series) and Variable 2 (unfilled/dotted series) conditions.

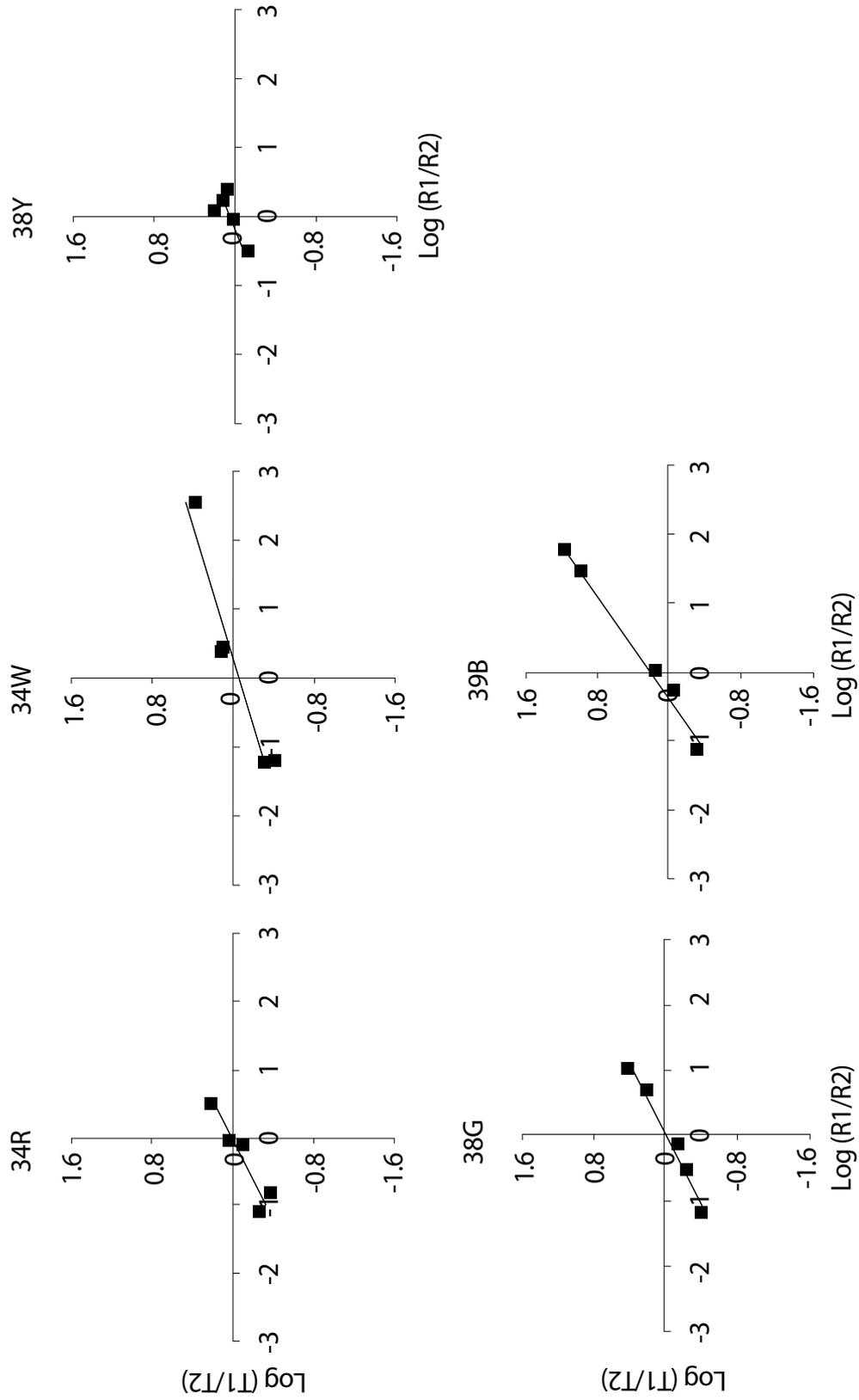


Figure 3. Average GML fits to time allocation as a function of obtained reinforcer rates for individual rats and totaled across all subjects in the Stable condition.

(around 0.8), while those with lower relative sensitivity to individual reinforcement contingencies tended to have lower sensitivity still to group contingencies (e.g. 38Y, 38G). Note, however, that this pattern was not observed in the previous Variable or Stable conditions.

Certain rats exhibited strong biases in certain conditions, but these did not persist over time. In the first Variable condition, 38Y showed a bias towards Patch 1, while 38G and 39B showed biases towards Patch 2. Only 39B continued to show a response bias in the Stable condition, however, and for the opposite patch to the first Variable condition. A strong bias for Patch 1 emerged for 34R in the second Variable condition, while all other subjects exhibited considerable biases for Patch 2.

The sensitivity values of the individual matching and the generalized IFD functions (equivalent to the aggregated distribution of time for the whole group) tended to be consistent in the initial Variable and Stable conditions, where individual matching behavior tended to be similar. However, in the second Variable condition, where there was greater variability in individual matching behavior, aggregate data showed considerably lower sensitivity than most of the individual sensitivity values.

Competitiveness

Figure 4 shows the results of the competitiveness assessment. The total proportion of reinforcers obtained by each forager in the competitiveness assessment varied between individuals, depending on patch location (left panel of Figure 4) and resource presentation (right panel of Figure 4). Some rats (34W and 34R) obtained more reinforcers in Patch 1, whereas others obtained considerably more reinforcers in Patch 2, consistent with the presence of individual location biases. Individuals also differed in their success depending on how resources were delivered in the competitiveness assessment session. When food was delivered on a VT15-s schedule and distributed unpredictably in time, rats 34W and 38Y obtained relatively more reinforcers than when pellets were delivered in rapid succession immediately after the consumption of the available pellet (rapid presentation schedule). Under these conditions, rats 34R and 38G obtained more reinforcers. The number of reinforcers obtained by rat 39B was largely unaffected by resource presentation, and this rat obtained the most reinforcement overall.

A Spearman rank-order correlation between the total proportion of reinforcers obtained in both patches over the entire competitiveness assessment session and the average proportion of reinforcers in the Stable condition was positive and significant ($\rho = 0.9$, $p < .05$), suggesting success in the single-patch conditions was positively related to success in Stable condition. Positive Spearman rank-order correlations were also obtained between the number of reinforcers obtained in the competitiveness assessment and in the Variable conditions, although these were not significant ($\rho = 0.6$ and 0.3 in the first and second Variable conditions, respectively).

Spearman rank-order correlations also were calculated between the total proportion of reinforcers obtained across both patches over the entire competitiveness as-

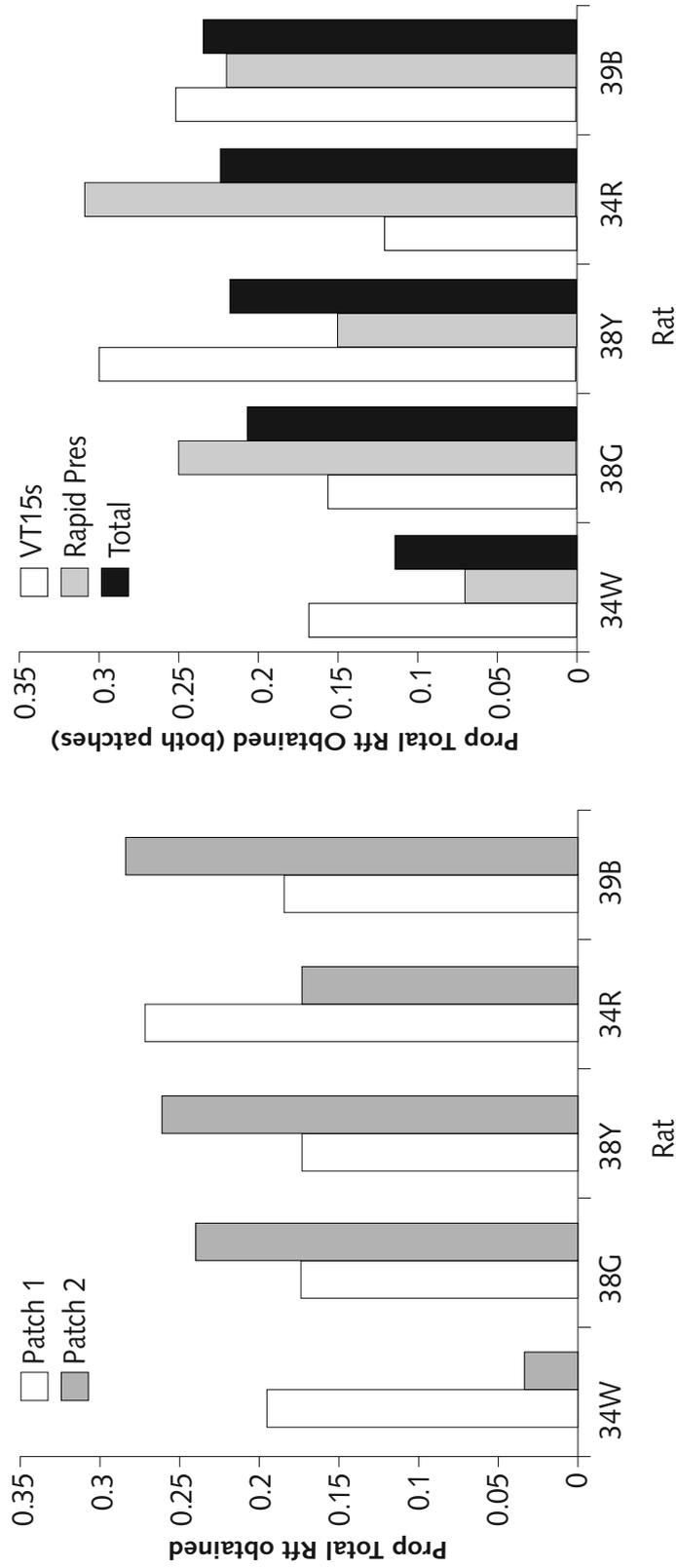


Figure 4. Total proportion of food obtained by each rat by reinforcer location (left panel); Patch 1 shown in unfilled bars, Patch 2 in filled bars) and reinforcer presentation schedule (right panel); VT15s schedule shown in unfilled bars, rapid presentation schedule shown in light grey bars, and summed across both schedules shown in dark grey bars).

assessment and the obtained sensitivity values in the experimental conditions. Competitiveness was positively correlated with sensitivity in the Stable and second Variable conditions ($\rho = 0.7$, and $\rho = 0.67$, respectively), but showed only a weak negative correlation with sensitivity in the initial Variable condition ($\rho = -0.1$).

Discussion

In this foraging paradigm, the distribution of time and individuals between two patches was in rough proportion to the overall ratio of obtained resources available in those patches. Group and individual behavior was well accounted for by the generalized IFD and the GML models. The overall pattern of results was similar to that of previous studies (Baum & Kraft, 1998; Bell & Baum, 2002; Gray, 1994), though most prior studies have not measured individual behavior with sufficient precision to evaluate both the IFD and GML with respect to the same data set. The one prior study that did examine both individual and group behavior within the context of a single experiment (Gray, 1994) found results broadly comparable to the present results—more specifically, undermatching (slope values less than 1.0) at both the individual and group level.

Compared to prior studies in both the laboratory and the field (see Kennedy & Gray, 1993 for a review), rats in the present experiment showed lower sensitivity values (most sloped < 0.40) in terms of the IFD and GML. One possible reason is most likely due to using VT schedules to deliver reinforcement and the manipulation of average delay in the reinforcement ratios. Unlike most previous research, in which reinforcement parameters have been more regular, the random interreinforcer intervals may have made the reinforcement contingencies more difficult to discriminate, especially in the Variable condition, where reinforcement ratios changed every six minutes. Subsequent research should further explore the impact of resource discriminability on choice patterns, including other dimensions of reinforcement, including magnitude and probability.

Consistent with Gray (1994), matching was best accounted for by individual reinforcement contingencies, rather than that of the group; in the majority of cases, GML fits using group reinforcement ratios accounted for less variance in time allocation data than fits using individual reinforcement ratios. The exceptions to this were the two best competitors (39B and 34R) in the later Stable and second Variable conditions. These rats also showed greater sensitivity to group reinforcement rates in these conditions.

Variability affected group and individual sensitivity to reinforcement contingencies. Sensitivity in the Stable condition was higher than that in both Variable conditions, although the difference in sensitivity with the later condition was considerably smaller. This is consistent with the effect of unpredictability on sensitivity values found by Bell and Baum (2002), who found that a flock of pigeons quickly adjusted their distribution to variable resource ratios, though sensitivity remained higher under pre-

dictable conditions. Our findings add to this, suggesting that rats show a similar rapid adaptation of choices in a dynamic environment. The greater sensitivity seen in the second Variable condition relative to the first Variable condition suggests experience improved matching performance. It is possible that the increase in sensitivity observed in the initial Variable and Stable conditions is also due to learning, though the fact that this trend does not continue in the later conditions suggests increased experience is not the sole explanation for the difference in sensitivity between the first two conditions. Thus, the increase in IFD and GML slopes seen in the initial change in reinforcer predictability is likely due to an increased sensitivity to the reinforcement contingencies resulting from the decrease in variability as well as greater experience in the procedure.

Individual choice behavior using individual intake rates resembled that at the group level, albeit somewhat more variable due to individual differences in sensitivity. Variability in individual sensitivity appeared to increase with exposure to the procedure; it is possible that greater experience affected performance differently across individuals (e.g., by increasing sensitivity to contingencies or the development of adaptive foraging behaviors for some, but not others), without disrupting the matching behaviour of the group. The slope of the IFD was generally similar to the individual GML slopes, and was comparable to the average of all the individuals for all three conditions. Interestingly, the patterns observed with the overall slope value were different to the results of Gray (1994), who found considerably lower slope values for group than individual measures of foraging sensitivity.

The relation between individual and group behavior is relevant to the concept of emergence, raised by Baum and Kraft (1998). Despite clear order at the group level, well described by the IFD, Baum and Kraft found no comparable degree of order at the individual level, prompting them to consider the group-level process an emergent phenomenon irreducible to lower-level processes. We found no such disconnect between individual and group behavior: Both varied systematically with the contingencies, and there were clear parallels between most of the individuals and the group. The differences between the present results and those of Baum and Kraft may be due at least in part to the somewhat different methods employed. Our highly structured environment and relatively small group of subjects enabled tracking the time allocations of individual rats, permitting fits of individual data to the GML. This was not feasible in the Baum and Kraft study, which used a more free-ranging environment with a flock of 30+ pigeons. As a result, they were forced to rely on less direct measures of individual behavior with which to relate to the group measures. Whatever might be responsible for the differences, the present experimental paradigm, which permits simultaneous analyses of individual and group behavior, is well suited to empirically address the correspondence between orderly activities at multiple levels of analysis.

In the competitiveness assessment, some rats performed better (acquired a greater proportion of available resource) at particular patches, or under different reinforcer

presentation conditions (whether on a VT 15-s schedule, or rapid presentation). In the experimental conditions, some individuals (39B, 34R) obtained more reinforcers by exploiting a particular patch in Stable conditions with greater direct competition, whereas other individuals (e.g., 38Y) obtained more reinforcers when variability was high, and with less intense direct competition. This is supported by greater positive correlations between number of reinforcers obtained in the competitiveness assessment and the Stable condition, than the Variable conditions. Thus, stronger competitors did better when resource availability was more predictable and less variable, more similar to conditions in the competitiveness assessment, which allowed a few rats to obtain most or all of the reinforcers at a single patch (similar to the despotic interactions described by Harper, 1982; Monaghan & Metcalfe, 1985). Conversely, in unpredictable conditions, where more switching and distributed responding would be more profitable, these 'dominant' competitors exhibited less of an advantage.

Analyses of individual sensitivity as a function of competitiveness showed that better competitors tended to also show stronger sensitivity. This was true in the Stable condition when resource availability was predictable, similar to Gray (1994), but also in the second Variable condition, when resource availability varied unpredictably within sessions. The present competitiveness findings are largely in line with previous research with nonhumans and humans, using stable reinforcement ratios (with the exception of Milinski, 1984) where there has been a tendency for strong competitors to overmatch relative to poorer competitors (Critchfield & Atteberry, 2003; Gray, 1994, Harper, 1982; Inman, 1990; Milinski, 1984).

The schedules of food delivery employed in the present study, in which pellets were only delivered singularly and at irregular intervals, might have resulted in more direct competition between individuals. Perhaps schedules that result in less direct competition would produce different patterns in individual success. For example, if multiple pellets were delivered at more than one location simultaneously and unpredictably, dominating a single patch would not necessarily lead to maximum reinforcement and other foraging strategies, such as switching patches frequently, might result in greater reinforcement. It has been demonstrated in previous studies that competitiveness and foraging behavior differ when temporal variability in resources (Humphries, Ruxton, Metcalfe, 1999; Milinski, 1984) and patch size varies (Monaghan & Metcalfe, 1985). In the present research, it was not feasible to analyze competitive success as a function of forager density, so it is unclear how stronger and weaker competitors fared at each patch as a function of competing individuals present.

The measure of competitiveness utilized in the current study was relatively crude. The resulting analyses did not take into account the amount of time different rats spent actively foraging when calculating competitive success. Consequently, incorporating the presence of other competitors and total time spent actively foraging into our measure would increase its predictive and explanatory utility. Additionally, measures of competitiveness may only predict foraging success to the extent that conditions in assessment are similar to those in testing. The present results showed differences

in intake rate as a function of schedules of reinforcement in our competitiveness assessment, suggesting it is important to consider this when designing methods for assessing competitiveness outside of an experimental context.

In conclusion, the present experiment found that rats' choices in a laboratory social foraging analogue bore an orderly relation to obtained resource ratios in ways that were well described by the IFD and GML. The results join with those of other studies examining social foraging across a range of different species and settings, and provide a powerful set of methodological and quantitative tools for examining adaptive behavior in a social context.

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