



## **The Role of Outcome Unit Size in the Social Foraging Strategies of Rats**

**Luis Alfaro<sup>1</sup>, Federico Sanabria<sup>2</sup>, and Rosalva Cabrera<sup>3</sup>**

**<sup>1</sup> Universidad de Guadalajara, Mexico**

**<sup>2</sup> Arizona State University, U.S.A.**

**<sup>3</sup> Universidad Nacional Autónoma de México (Fes Iztacala), Mexico**

The distribution of foraging strategies and associated activities of Wistar rats was examined with food outcomes presented in small versus large units. Groups of 4 rats foraged for food in a 4 × 3 array of covered holes, some containing 4 g of food. For some groups, food consisted of shelled sunflower seeds (small units); for other groups, food consisted of 3 pellets of chow (large units). Foraging strategies were classified as either production (seeking patches with food) or scrounging (tracking conspecifics). Production strategies were more common among groups that foraged for pellets instead of seeds. Producing food was highly correlated with contacting gates covering holes, whereas scrounging for food was highly correlated with following others in the group. The prevalence of activities associated with each foraging strategy was highly correlated with the proportion of time spent consuming food obtained from each activity (i.e., produced vs. scrounged food). Taken together, these findings suggest that, similar to other species, the finder's advantage (low with small units, high with large units) modulates social foraging strategies in rats. A simple outcome-strategy feedback mechanism appears to mediate this modulation.

*Keywords:* choice, production, rats, scrounging, social foraging, unit size

When searching for food collectively, foragers often engage in a producer-scrounger game (Barnard & Sibly, 1981). In this game, foragers choose between two mutually exclusive strategies to search for and obtain food: Producing and scrounging. Producing involves searching, exploring an area, obtaining food, and leaving it available for its intake. Scrounging involves indirectly searching, identifying other foragers that have already discovered food, and exploiting part of the leftover food (Caraco & Giraldeau, 1991; Giraldeau & Caraco, 2000; Giraldeau & Lefebvre, 1986; Coolen, Giraldeau, & Vickery, 2007).

According to social foraging theory, collective foraging strategies should reflect key aspects of the foraging outcomes (Giraldeau & Caraco, 2000; Hansen, Ward, Fürtbauer, & King, 2016). For instance, if the outcome consists of a small amount of food, a scrounger may not be able to exploit a patch found by a producer, and, thus, it may be more profitable for foragers to produce their own food. In contrast, if the outcome consists of a large amount of food, producers may not be able to exhaust a patch, and, thus, scroungers may exploit those patches without paying the cost of production.

Semi-natural research on the influence of foraging outcomes on social foraging strategy has been conducted primarily in birds (Afshar, Hall, & Giraldeau, 2015; Belmaker, Motro, Feldman, & Lotem, 2012; Katsnelson, Motro, Feldman, & Lotem, 2008). Although some work with small mammals has recently been developed under natural conditions (Harten et al., 2018), research on producer-scrounger strategies in these species is scarce. The main objective of the present study is to test whether three specific findings on social foraging strategies described below generalize to a small, communal mammalian species: the laboratory rat (*Rattus norvegicus*).

The Vickery, Giraldeau, Templeton, Kramer, and Chapman (1991) rate-maximizing model stipulates that the proportion of producers in a group is positively correlated with the advantage (in amount of food) of finding a patch over scrounging it. Most studies examining the finder's advantage have focused on the effect of the amount of food on each patch (Beauchamp & Giraldeau, 1996; Coolen, Giraldeau, & Lavoie, 2001; Giraldeau & Dubois, 2008), reporting that more food in each patch yields a smaller finder's advantage and thus fewer producers. However, food that is rapidly consumed or removed from the patch may also confer a higher finder's advantage (Hirsch, 2007). A producer may rapidly remove food that is available in larger units, leaving less food for scroungers and thus encouraging production. This is an important implication of the rate-maximizing model that has not been previously tested. The present study sought to examine whether larger units of food reduces the prevalence of scrounging behavior in rats.

During collective foraging for food, various species of birds (e.g., spice finches, *Lonchura punctulata*) display distinct body postures when scrounging and producing (Coolen et al., 2001). Producers spend most of the time with their heads tilted towards the floor, where feeding patches may be found; scroungers spend most of the time with their heads straight, which may facilitate the detection of conspecifics exploiting an already discovered patch. These predictive postures, which we call *preceding activities*, are likely expressed differently in rats. As a secondary goal, the present study sought to identify preceding activities in rats that are predictive of producing and scrounging behavior.

Several studies suggest that animals combine previous and present information obtained in social foraging experiences, including information on outcomes, to choose among foraging strategies (Afshar & Giraldeau, 2014; Afshar et al., 2015; Beauchamp, 2000; Belmaker et al., 2012; Dubois, Morand-Ferron, & Giraldeau, 2010; Hamblin & Giraldeau, 2009; Katsnelson, Motro, Feldman, & Lotem, 2010). For instance, in house sparrows (*Passer domesticus*), Belmaker et al. (2012) reported a high correlation between the proportion of food obtained using each social foraging strategy (its *success*) and the proportion of use of each strategy. As a tertiary goal, the present study sought to verify whether such a correlation is also observed in rats.

In summary, this study evaluated three hypotheses in rats derived from findings on social foraging strategies in other species: (a) that equal amounts of food available in larger units support fewer consumers and thus yield more production than scrounging behavior (Caraco & Giraldeau, 1991; Vickery et al., 1991), (b) that foraging strategy is correlated with preceding activities, which in birds are expressed as body

postures (Coolen et al., 2001), and (c) that choice of foraging strategy is correlated with the outcome of each strategy (Afshar & Giraldeau, 2014; Belmaker et al., 2012).

## Method

### Subjects

Twenty-four male Wistar rats (*Rattus norvegicus*) were obtained from the Centro de Estudios e Investigación en Comportamiento (CEIC) of the University of Guadalajara. They did not have any training or previous experience in the apparatus and were between 5 and 6 months old at the beginning of the experiment. Throughout the experiment, each rat was housed alone. Each rat's back was colored with vegetable paint (McCormick Paints; Rockville, MD) for identification. Rats were maintained at 85% of their free-feeding weight by supplementing their food (Purina rodent lab chow 5001; Nestlé México, Ciudad de México) an hour after their experimental session ended.

### Materials and Apparatus

Figure 1 describes the 90 cm long × 120 cm wide wooden platform on which experimental sessions were conducted. This platform rested on a wooden base (20 cm tall). A wall (50 cm tall) of translucent polycarbonate delimited the perimeter of the platform. There were 12 round perforations ("holes", 9 cm in diameter) on the platform, separated from each other by at least 30 cm. Each hole was covered with a 48 g square gate (10 cm per side). Gates could slide over aluminum rails (0.5 cm wide, 20 cm long). A plastic container (2 cm deep) was placed underneath each gate. Every container had a double bottom with perforations separating the top and bottom spaces, allowing odors to spread between spaces. The bottom spaces of all containers held a mixture of ground seeds and ground pellets; the top spaces of only 4 of the 12 containers held any food. The containers that held food in their upper spaces were located at the corners of the experimental platform and were designated as *patches*.

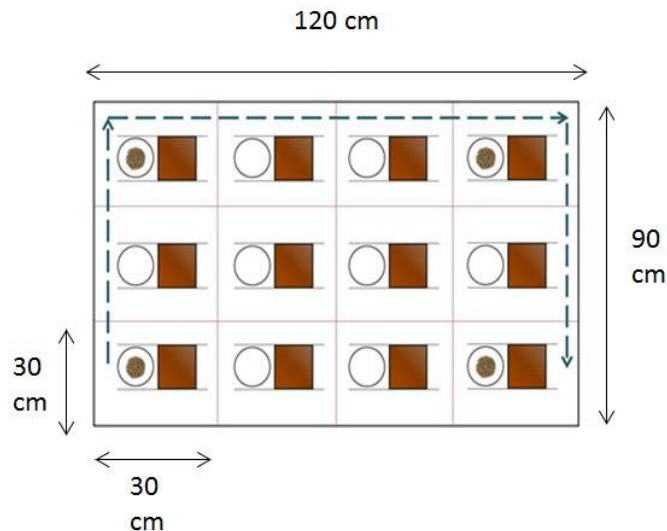


Figure 1. **Sketch of experimental platform.** The platform contained 12 holes (circles), 4 of which contained food (brown filled circles). At the beginning of each session, sliding doors (squares) covered all holes.

The experimental platform was placed on the floor of a 5 m × 3 m × 3 m room. A video camera, held by an aerial harness and located 2.5 m from the floor, recorded the complete surface of the platform for each experimental session.

## Experimental Design

Rats were randomly assigned to one of the two experimental treatments, forming three groups per food condition ( $n = 4$  rats/group). For the Seeds condition, each of the 4 patches held 4 g of shelled sunflower seeds in its top space ( $84 \pm 4$  units/patch). For the Pellets condition, each patch held in its top space three 1.33 g pieces of the rodent chow used for supplementary feeding. It is important to note that, between food conditions, patches varied only in the type (seeds vs. pellets) and not the amount (4 g) of food they held. Experimental sessions were conducted once daily. Each session ended after 15 min or when all food in the platform was eaten, whichever happened first. Sessions were conducted during 6 consecutive days for each group.

## Data Collection and Analysis

The last 5 sessions of each treatment were video-recorded (i.e., the first session was dropped to avoid potential contamination by novelty effects). For each discovered patch, the following data were registered a posteriori using LINCE 1.4 (Gabin, Camerino, Anguera, & Castañer, 2012):

- 1) Opening a closed gate (*production response*),
- 2) Consuming the food of a patch whose gate was opened by another rat (*scrounging response*),
- 3) Contacting the gate without producing food (*contacting response*),
- 4) Pursuing and contacting another rat in areas away from discovered patches (*following response*),
- 5) Time spent by each rat consuming a patch it produced (*production time*), and
- 6) Time spent by each rat consuming a patch it scrounged (*scrounging time*).

Two independent observers initially coded the video-recording data using these categories. Observers then conferred and revised their coding until their agreement was 100%. To establish the effect of unit size on production and scrounging, the proportion of production responses (production responses divided by the sum of production and scrounging responses) was computed and compared across food conditions (Seeds vs. Pellets). It is important to highlight that rats could only obtain food by producing it or by scrounging for it, so the proportion of production responses is complementary to the proportion of scrounging responses. It was expected that, because pellets were available in larger units than seeds (1.33 g vs. 0.045 g), they would support fewer consumers and thus yield a higher proportion of production responses.

The proportion of production responses was not independent among members of a group: a higher proportion in one rat implied a lower proportion in the other rats in a group, and vice versa. Therefore, this measure was analyzed at the level of group. The proportion of production responses was averaged within each of three groups per food condition, and these averages were compared across conditions. Because of the small number of groups compared, a permutation test was conducted (Welch, 1990). The null distribution of differences between food conditions was constructed by pooling the data of all 6 groups and dividing it into 2 groups of 3 in every permutation possible ( $6! = 720$  combinations possible). The hypothesis that pellets yield a higher proportion of production responses was supported if the observed difference in this proportion between Pellets and Seeds was in the highest 5<sup>th</sup> percentile of the null distribution (i.e.,  $p \leq 0.05$ ).

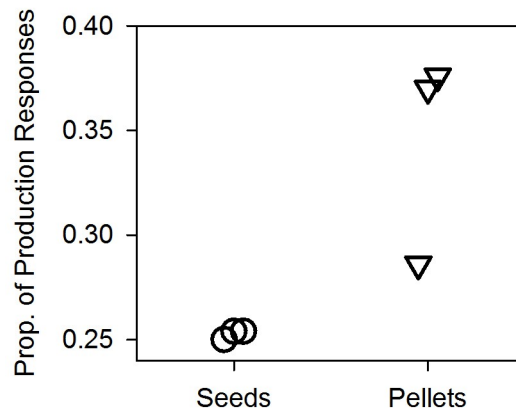
To establish if foraging strategies are correlated to preceding activities, two preceding activities were selected as potentially predictive of strategy. It was expected that *contacting* without food preceded producing and that *following* without food preceded scrounging. Note that, by definition, neither contacting nor following could result in food, so these measures were not necessarily related to producing or scrounging for food. The proportion of contacting responses (contacting responses divided by the sum of contacting and following responses) was computed for each rat and was correlated against its proportion of production responses. Correlations were conducted separately for the Seeds and Pellets

conditions. To the extent that contacting without food predicts production responses and following without food predicts scrounging responses, it was expected that the proportion of contacting responses would be significantly and positively correlated with the proportion of production responses.<sup>1</sup>

Once a positive correlation between production and contacting responses was demonstrated, two composite measures were defined to establish whether choice of foraging strategy is correlated with the outcome of each strategy. Producing and contacting were categorized as *production activities*; scrounging and following were categorized as *scrounging activities*. The proportion of production activities (production activities divided by the sum of production and scrounging activities) was computed for each rat, and it was correlated against the relative payoff of production (production time divided by the sum of production and scrounging time). Correlations were conducted separately for the Seeds and Pellets conditions. To the extent that choice of strategy is related to the relative payoff of each strategy, it was expected that the proportion of production activities and the relative payoff of production would be significantly and positively correlated.

## Results

Figure 2 shows the proportion of production responses of each group in each food condition. As anticipated, a higher proportion of production responses was observed in the Pellets condition than in the Seeds condition (mean difference = 0.09,  $p = 0.05$ ). This finding suggests that, compared to the smaller (per unit) seeds outcome, the larger pellet outcomes favored production more than scrounging.



**Figure 2. Mean proportion of production responses in each of 3 groups (4 rats per group) in two food conditions (small seeds vs. large pellets).**

<sup>1</sup>The non-independence of behavioral measures among rats within the same group does not constrain the correlation between these measures. To illustrate this point, for each of four correlations conducted in this study, one measure was shuffled among the 4 rats within each of the 6 groups, yielding  $4! = 24$  permutations of the shuffled measure. For simplicity, we repeated the same permutation in each group within the same food condition (e.g., if a measure of Rats 1 and 2 in one group were swapped, it was swapped for Rats 1 and 2 in all groups). The median of these correlations ranged between -.034 and .005; the standard deviation ranged between .382 and .529. This shows that high positive correlations between measures were not artifacts of the non-independence of these measures among rats within the same group.

Figure 3 plots the proportion of production responses of individual rats as a function of their proportion of contacting responses. These proportions were positively correlated in both Seeds ( $r = .95, p < 0.01$ ) and Pellets ( $r = .77, p < 0.01$ ) conditions. It thus appears that contacting and following were anticipatory of producing and scrounging.

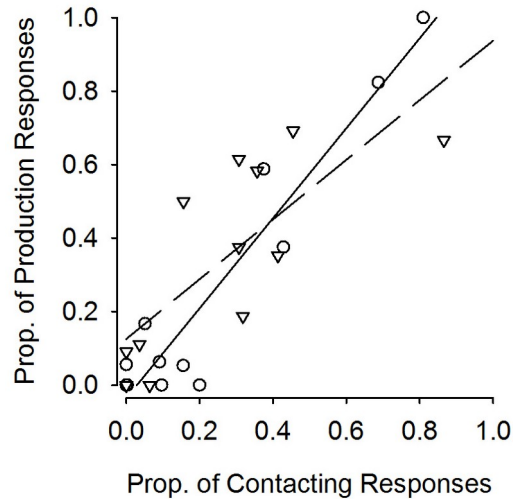


Figure 3. **Proportion of production responses plotted against proportion of contacting responses for each individual rat in each of two food conditions (Seeds in circles, Pellets in triangles).** Lines are linear regressions within each food condition (Seeds is continuous, Pellets is dashed).

Figure 4 plots the proportion of production activities (which includes production and contacting responses) of individual rats as a function of the relative payoff of production. These two measures were positively correlated in both Seeds ( $r = .96, p < 0.01$ ) and Pellets ( $r = .85, p < 0.01$ ) conditions. It thus appears that the choice of foraging strategy was associated with the relative payoff of each strategy.

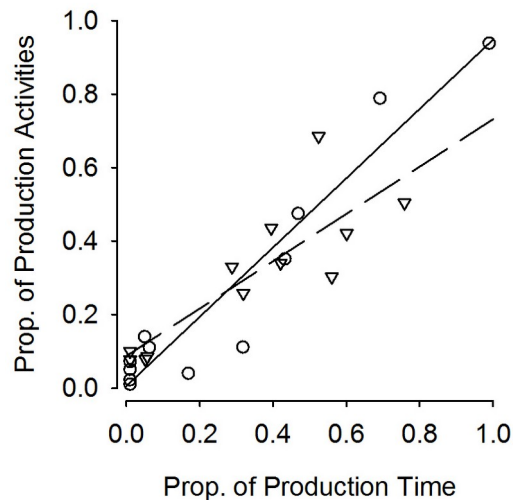


Figure 4. **Proportion of production activities plotted against proportion of production time for each individual rat in each of two food conditions (Seeds in circles, Pellets in triangles).** Lines are linear regressions within each food condition (Seeds is continuous, Pellets is dashed).

## Discussion

Results from the present experiment are consistent with the three hypotheses that motivated this study. First, larger food units (pellets) supported a higher proportion of production responses than smaller food units (seeds; Figure 2). Pellets were likely to yield a higher finder's advantage than seeds: Whereas the producer of pellets obtained a third of the food discovered, the producer of seeds obtained a negligible advantage (Caraco & Giraldeau, 1991; Vickery et al., 1991). For each rat, larger food units may thus reduce the payoff of scrounging relative to producing. As the frequency of the better-paying strategy increases, its marginal payoff declines until equilibrium in the distribution of strategies is attained (Giraldeau & Dubois, 2008). With larger food units, such equilibrium would favor more production (Vickery et al., 1991).

The effect of the finder's advantage on the proportion of production activities replicates one of the most reported effects in social foraging (Caraco & Giraldeau, 1991; Giraldeau, Hogan, & Clinchy, 1990; Giraldeau, Soos, & Beauchamp, 1994; Vickery et al., 1991). It is likely that, similar to other species such as three-spined sticklebacks (Hansen et al., 2016), baboons (King, Isaac, & Cowlshaw, 2009), spice finches (Wu & Giraldeau, 2005), house sparrows (Katsnelson et al., 2008, 2010), and pigeons (Giraldeau & Lefebvre, 1986), the social foraging strategy of rats is attuned by their outcomes. This replication advances the experimental paradigm implemented in the present study as an alternative tactic to study social foraging. Previous research has already suggested the utility of the laboratory rat in social foraging experiments (Tan & Hackenberg, 2012; Tan et al., 2014).

Second, the distribution of responses across strategies was correlated with distinct preceding responses: Regardless of the food pursued, rats that produced more food also made more unproductive contacts with potential food locations, whereas rats that scrounged more also followed other rats more often (Figure 3). This correlation suggests that foraging strategies are expressed as adaptive behavioral chains (Afshar et al., 2015; Coolen et al., 2001). Producing food is likely preceded by a host of activities that maximizes the likelihood of finding food, including contacting empty gates; scrounging for food is likely preceded by activities that maximize the detection of opportunities to join in the consumption of produced food. As with ground-feeding birds (Coolen et al., 2001), producing and scrounging in rats appear to be mutually exclusive activities; that is, rats do not seem capable of alternating between activities without first finishing the behavioral chain that defines that activity (Afshar et al., 2015; Giraldeau & Dubois, 2008). More concretely, rats contacting empty gates are unlikely to switch to following conspecifics before food is found in a gate; rats following conspecifics are unlikely to switch to contacting gates before scrounging from a gate found by a conspecific. Further examination of this hypothesis will require a more detailed analysis of the sequential organization of foraging strategies.

Finally, rats that engaged in more productive activities (productive responses and unproductive contacts) produced most of their food; rats that engaged in more scrounging activities (scrounging responses and following other rats) scrounged most of their food (Figure 4). This correlation suggests a simple regulatory feedback relation between social foraging strategies and their outcomes: Strategies that result in better outcomes are chosen more often (Belmaker et al., 2012). In a social foraging context, however, the average payoff of a strategy diminishes as the number of animals that choose that strategy increases (Giraldeau & Caraco, 2000; Hamblin & Giraldeau, 2009). The choice between foraging strategies, each yielding marginally decreasing payoffs, results in a stable distribution of strategies within groups of animals, in which choice of strategy and payoffs are closely correlated. Because in seminaturalistic foraging situations payoffs are only partially under experimental control, it is not yet possible to establish a clear direction for the causation arrow linking strategies to payoffs. It is possible that factors unrelated to strategy outcomes, such as dominance hierarchy within the group, influence each rat's choice of strategy (e.g., submissive rats may be more prone to scrounging, which leads to obtaining most food from this strategy). However, the alternation between production and scrounging in some rats (Figure 4) suggests that the choice of foraging strategy after each feeding is flexible and is unlikely to be solely determined by fixed social factors. Moreover, the proposed feedback mechanism is readily visible in experimental preparations in which strategies and payoffs are modeled as simple responses and experimentally-controlled reinforcers (Herrnstein, 1970; Kagel, Battalio, & Green, 1995).

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