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SOCIAL FORAGING AND TIME OF ACCESS TO PATCH ZONES IN RATS

FORRAJEO SOCIAL Y TIEMPO DE ACCESO A LAS ZONAS DE PARCHE EN RATAS

Laurent Ávila-Chauvet[1], Yancarlo Lizandro Ojeda Aguilar[2], Óscar García-Leal[3], Diana Mejía Cruz[1] y Carlos Esparza[4]

[1]*Instituto Tecnológico de Sonora, Laboratorio de Comportamiento Adictivo y Antisocial*

[2]*Universidad Autónoma de Aguascalientes, Departamento de Psicología*

[3]*Universidad de Guadalajara, Centro de Estudios e Investigaciones en Comportamiento*

[4]*Universidad Marista de Guadalajara*

Abstract

In social foraging situations, some group members tend to search their food sources (producers), while others tend to join a previously discovered food source (scroungers). Rate maximization model and agent-based models predict that the proportion of scroungers within the group should increase as the finder share decreases. We propose a novel experimental preparation to study the effects of the finder share on the proportion of scroungers in a social foraging situation by controlling the access time to the patch zones. As the access time to discovered patch zones decreased, the opportunity to join patch zones decreased too, and the finder share increased. Our results matched the models' prediction in the sense that the proportion of producer responses decreased, and the number of scroungers increased as the access time to the patch zones increased.

Keywords: social foraging, producer, scrounger, mathematical modeling, agent-based models, access time

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Resumen

En las situaciones de forrajeo social, algunos miembros del grupo tienden a buscar sus fuentes de alimento (productores), mientras que otros tienden a unirse a las fuentes previamente descubiertas (parásitos). El Modelo de maximización de la tasa y los modelos basados en agentes predicen que en la medida que disminuye la ventaja de descubrimiento, la proporción de parásitos incrementa dentro del grupo. Proponemos una preparación experimental novedosa para estudiar el efecto de la ventaja de descubrimiento sobre la proporción de parásitos en el forrajeo social a través del control del tiempo de acceso a las zonas de parche. Al disminuir el tiempo de acceso a las zonas de parche descubiertas, la oportunidad de unirse a las zonas de parche disminuye también y la ventaja de descubrimiento aumenta. Como predicen los modelos, nuestros resultados muestran que en la medida en que aumenta el tiempo de acceso a las zonas de parche, la proporción de respuestas de productoras disminuye y el número de parásitos aumenta.

Palabras clave: forrajeo social, productores, parásitos, modelación matemática, modelos basados en agentes, tiempo de acceso

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In social foraging situations, some group members tend to search for their food sources (Producers), while others tend to join a previously discovered food source (Scroungers). The relationship between these strategies has been referred as Producer-Scrounger Game (Barnard & Sibly, 1981). It assumes that 1) the organism can choose between two mutually exclusive strategies (i.e., producing or scrounging), 2) the proportion of producers and scroungers within a group tends to reach a balance in which all members maximize the amount of resources, and 3) The amount of energy resources obtained through a particular strategy maintains an inverse relationship with the number of subjects that choose the same strategy. So, when there are more producers, scroungers get more resources, and vice versa (Beauchamp & Giraldeau, 1996).

Mathematical models and Agent-Based Models (ABM) have been developed to predict the optimal proportion of producers and scroungers that should exist within a group in order to reach an Evolutionarily Stable Strategy or to maximize the amount of resources with both strategies (Afshar & Giraldeau, 2014; Beauchamp, 2000; Dubois & Richard-Dionne, 2020; Vickery et al., 1991). One of the most common mathematical models used to make predictions about the producer-scrounger game is the Rate Maximization Model (Alfaro & Cabrera, 2021; Vickery et al., 1991). This model assumes that producers partially consume some food units in a patch zone before scroungers join the patch zone (finder’s share), and the remaining food units in the patch zone will be equally distributed among the members of the group (G). The model predicts the proportion of producers (p^) based on the group size (G), food units in the patch zones (F), and the finder's share (a) (Giraldeau & Livoreil, 1998; see Equation 1). If the finder's share (a) remains constant and the number of food units (F) in a patch zone increases, the number of food units that the scroungers (G^s) will take also increases ($[F$-a$]/G^s$).

$$p\hat{}= a/F+1/G \tag{1}$$

Agent-Based Models, on the other hand, simulate virtual habitats that include patch zones and transition zones. In these simulated environments, agents move through the habitat represented by a matrix in search of resources. These agents have decision rules (i.e., maximization or matching) and learning rules (i.e., linear operator or perfect memory) that determine their behaviors (Beauchamp, 2000). Decision rules guide agents' strategies, encompassing actions like movement, search, consumption, and more. Meanwhile, learning mechanisms assign weights to the values of each strategy. When a producer discovers a patch zone, the finder's share will depend on the time-steps required by scroungers to join the discovered patch zone (Afshar & Giraldeau, 2014; Beauchamp, 2000). If food units within the patch zone remain available for long, scrounging opportunities increase and the producers' finder's share decreases. In this sense, it is possible to hypothesize that as the access time to the patch zone increases, the proportion of producers in the group will tend to decrease.

While no studies have not directly manipulated the access time to patches, some have manipulated the finder's share by altering the distribution of patch zones or the amount of resources. Alfaro et al. (2010) observed that when patch zones with food are scattered throughout the habitat, the opportunities to find the patch zones and the proportion of scroungers increase, in contrast to the conditions in which patch zones with food were clustered. This reduces the distance subjects must travel to scrounge a patch zone and increases the finder's share. On the other hand, Sacramento & Bicca-Marques (2022) observed that when the amount of food units in patch zones is decreased, the number of food units consumed as scroungers tends to decrease. As the number of food units in a patch zone increases, the scrounging opportunities also increase.

Typically, experimental preparations to assess social foraging strategies consist of platforms with holes arranged matrically where food is deposited, and experimental sessions end when available food in foraging platforms is depleted (Alfaro & Cabrera, 2021; Giraldeau et al., 1994). These preparations are limited by the size of the foraging platform and the number of non-refillable patches. Once a producer discovers a patch zone, it remains accessible to the group the whole time, increasing the opportunity of the subjects to scrounge and limiting the number of opportunities to produce (Alfaro & Cabrera, 2021; Dubois & Richard-Dionne, 2020).

In this experiment, we devised a new preparation that limits the access to discovered patch zones to evaluate the effect of access time to the patch zone over the proportion of producer responses. As the access time to patch zones increases, it is expected that subjects will have more opportunities to scrounge, and the finder's share of producers will tend to decrease. Therefore, the number of scroungers should increase as the finder's share decreases.

Method

Subjects

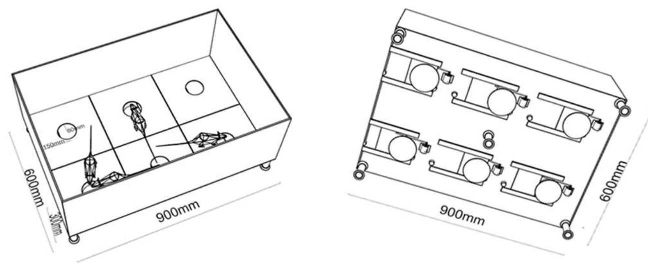
Eight male Wistar rats (*Rattus norvegicus*) with previous experience in social foraging situations, approximately three months old at the beginning of the experiment. They were housed in two groups of four subjects each, with *ad libitum* access to water, under conditions of 11 hours of light and 13 hours of darkness at room temperature (21°±4). Over two weeks, the subjects were gradually limited in their daily food intake until they reached 80% of their *ad libitum* weight. The subjects were marked with a vegetable paint color spot on their back. We followed the recommendations for the acquisition of laboratory animals, technical staff and animal health of the official Mexican norm NOM-062-ZOO-1999 "Technical specifications for production, care and use of laboratory animals".

Devices and materials

We designed a 90 cm x 60 cm wood foraging platform, surrounded by four 30cm high polycarbonate walls. The platform featured six holes, each with an 8 cm diameter, arranged in a 2 x 6 matrix configuration with a center-to-center distance of 15 cm. Within each hole, a feeder constructed from PVC pipe was installed to a depth of 3 cm, and it was equipped with a sliding door gate for cover (see Figure 1). Each door was connected to a 12-volt DC motor through a belt and a pulley wheel. The doors could be easily opened by the subjects pulling them with their paws, and they were closed based on instructions from a program developed in "LabVIEW 2012". The doors were controlled by a low-cost interface assembled by the authors, utilizing the parallel port of a computer (Escobar et al., 2012). However, it is important to note that this technology has become outdated. To replicate the experiment, it is recommended to use more up-to-date technology (see Gurley, 2019; Pérez-Herrera, et al., 2018). The source code and the files for laser cutting and 3D printing of an upgraded equipment version can be requested from the first author. Sessions were recorded with a video camera mounted on an aerial harness on top of the instrument.

Figure 1

Scheme of Foraging Platform



Note. The left panel shows a top view of the platform. The right panel shows a view of the bottom of the platform. Under each feeder, there were aluminum door guides, the pulleys, and the DC motors that closed the sliding doors.

Procedure

Each experimental session started with the sliding doors closed. To ensure an adequate food supply throughout the session, 240 g of food was evenly distributed across the experimental platform, with 40 g placed in each feeder. The available food amount was computed based on previous pilot studies. Subjects were simultaneously placed in the middle of the experimental platform with the aid of two assistants. The experiment consisted of two conditions (5min and 1min) of five sessions each.

Each session lasted for 30 minutes. In Condition 5min, the doors were automatically closed every five minutes and the maximum number of times the doors could be opened was 30 if the six doors had been opened at every five available opportunities. In Condition 1min, the doors were automatically closed every minute, thus providing a maximum of 174 opportunities to open the doors if the six doors had been opened at every 29 available opportunities. Group 1 was first exposed to Condition 5min and then to Condition 1min , while Group 2 was first exposed to Condition 1min and then to Condition 5min. The doors were not equipped with a switch to indicate their closure; therefore, all the doors closed simultaneously, regardless of when the subjects opened them.

Data collection and analysis

The sessions were analyzed using an observational approach. Each session was recorded using the observational recording software "Lince 1.2.1" (Gabín et al., 2012). To ensure the reliability of the observations, two separate observers individually coded the sessions. Cohen's kappa reliability index among observers was greater than 0.90.

Two behavioral categories were established: 1) *Opening*, defined as displacing the door using the front paws; and 2) *Arrival to the feeder*, defined as introducing the snout in a currently opened feeder. The *opening* behavior was considered the producer response (R^p), while the arrival to a previously opened patch zone by other subjects was considered a scrounger response (R^s). We computed a producer index (Pi), where we considered the frequency of producer and scrounger responses for each subject ($Pi = [(R^p-R^s)/(R^p+R^s)]$). A Pi value close to 1 suggests that the subject tended to produce, while a Pi value close to -1 suggests that the subject tended to scrounge (Harten et al., 2018). Subjects with a Pi greater than or equal to 0.33 were classified as producers, while subjects with a Pi less than or equal to -0.33 were classified as scroungers. Subjects with a Pi between -0.33 and 0.33 were classified as mixed-strategy subjects.

Equation 2 was used to calculate the predictions for producer index based on the Rate Maximization Model. Since the subjects could not deplete the patch zones during the session, the food units (*F*) were replaced by 1 (total of the food units that could be consumed by the group) and the finder's share (a) was replaced by a proportion of the food units that producers consumed before scroungers joined the patch zone ($0 < a < 1$). Finally, the result was scaled to match the producer index ([p^-.5]*2).

$$p\hat{}=[(a/1+1/G)-.5]*2 \qquad (2)$$

In order to test whether the number of scroungers increases as the availability of patch zones increases, we calculated the time that patch zones remained opened when one, two and three scroungers joined the patch zones. Furthermore, we calculated the average number of scroungers per open patch zone and the latency between the opening of the patch zone and the arrival of the first scrounger.

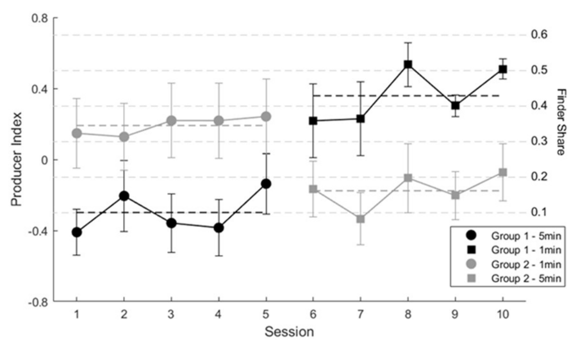
Statistical analysis was conducted using the JASP software package. A thorough normality assessment was performed to determine the appropriate statistical tests, including the Shapiro-Wilk test. Additionally, the homogeneity of variances was evaluated using Levene's test. The mean producer index, the average number of scroungers, and the arrival of the first scrounger were analyzed using the Mann-Whitney U test. Furthermore, an ANOVA was conducted to investigate the impact of scroungers joining the patch zones.

Results

Figure 2 shows the mean producer index per group across sessions and the Rate Maximization Model predictions for each producer index. The mean producer index for Group 1 (M = -0.29, SD = 0.12) was lower than for Group 2 (M = 0.19, SD = 0.05) in the first five sessions, while the mean producer index was greater for Group 1 (M = 0.35, SD = 0.15) than for Group 2 (M = -0.17, SD = 0.10) in the last five sessions. Mann-Whitney tests showed significant differences between Group 1 and Group 2 in the first five sessions (U = 0, p = 0.008) and in the last five sessions (U = 25, p = 0.008). Regarding Rate Maximization predictions, the predicted proportion of food units consumed only by producers was 0.10 for Group 1 and 0.34 for Group 2 in the first five sessions and 0.42 for Group 1 and 0.16 for Group 2 in the last five sessions. The predicted finder's share was less than half in Condition 5 min, compared to Condition 1min.

Figure 2

Mean producer index per group and Rate Maximization Model predictions

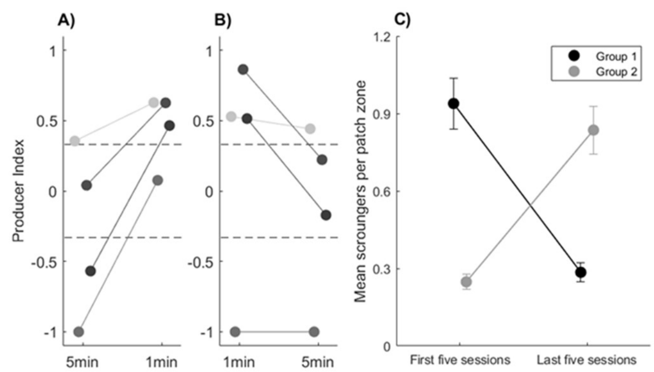


Note. Solid lines represent the mean producer index for each group in each session and condition. Dotted lines show the finder's share predicted by the model for the mean producer index in each condition and group.

Figures 3A and 3B show the mean producer index considering the last three sessions for each condition and each subject in groups 1 and 2 respectively. The sessions from 3 to 5 and 8 to 10 were analyzed, assuming stability in the subject's response. In 1min conditions, the number of producers (Pi >= 0.33) was three, while in 5min conditions, the number of producers was one. Figure 3C shows the average number of scroungers per produced patch zone per group and condition, including the patch zones that a scrounger did not visit. The average number of scroungers was greater for Group 1 ($N = 98$, $M = 0.93$, $SD = 0.98$) than for Group 2 ($N = 278$, $M = 0.24$, $SD = 0.50$) in the first five sessions, while in the last five sessions, the average number of scroungers was lower for Group 1 ($N = 214$, $M = 0.28$, $SD = 0.55$) than for Group 2 ($N = 128$, $M = .83$, $SD = 1.04$). Mann-Whitney tests showed significant differences between Group 1 and Group 2 in the first five sessions ($U = 7997$, $p < 0.001$) and in the last five sessions ($U = 9804$, $p < 0.001$).

Figure 3

Individual Producer Index and Average Number of Scroungers per Produced Patch Zone

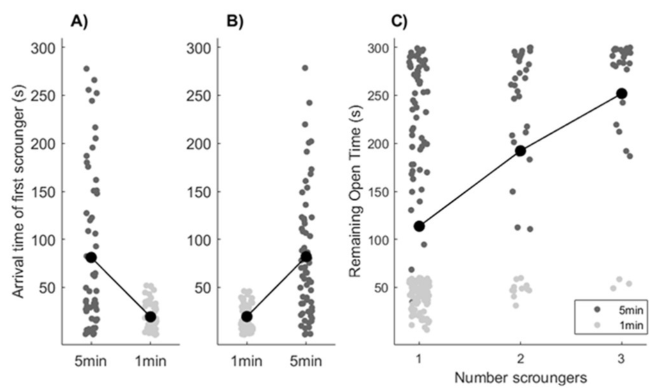


Note. Subjects with a producer index greater or equal to 0.33 were considered as producers, while subjects with a producer index less or equal to -0.33 were considered as scroungers. A) Individual producer index for Group 1 in both conditions. B) Individual producer index for Group 2 in both conditions. C) average number of scroungers per produced patch zone between groups for all sessions in both conditions.

Figures 4A and 4B show the latency between the opening of the patch zone and the arrival of the first scrounger for all sessions in each condition for groups 1 and 2 respectively. The mean arrival time for the first scrounger was lower in the 1min conditions than in the 5min conditions for Group 1 (1min: $M = 19.34$, $SD = 15.50$; 5min: $M = 81.18$, $SD = 83.02$) and Group 2 1 (1min: $M = 19.62$, $SD = 13.07$; 5min: $M = 81.96$, $SD = 65.42$;). Mann-Whitney tests showed significant differences between conditions for Group 1 ($U = 87.58$, $p < 0.001$) and Group 2 1 ($U = 61.48$, $p < 0.001$). Figure 4C shows the average time that the gates remained open when one ($N = 165$, $M = 113.72$ s, $SD = 100.62$), two ($N = 40$, $M = 192.28$ s, $SD = 101.44$) or three ($N = 28$, $M = 251.83$ s, $SD = 77.30$) scroungers joined the patch zones. An ANOVA test showed statistically significant differences in remaining open time given the number of scroungers ($F(2) = 29.48$, $p < 0.001$, $\eta 2 = 0.20$). A Bonferroni post hoc analysis showed statistically significant differences between one and two, and one and three scroungers ($p < 0.001$). Similarly, significant differences were observed between two and three scroungers ($p = 0.04$).

Figure 4

Arrival Time of the First Scrounger and Remaining Open Door Time as a Function of the Number of Scroungers



Note. Latency between the opening of the patch zone and the arrival of the first scrounger for all sessions for each condition. A) Arrival time of the first scrounger for Group 1. B) Arrival time of the first scrounger for Group 2. C) Remaining open door time as a function of the number of scroungers. The continuous line represents the mean remaining open door time.

Discussion

In this experiment, we developed a social foraging procedure that allows restricting the access time to patch zones. This is a critical difference with other experiments in which sessions end once subjects deplete patch zones (Alfaro & Cabrera, 2021; Giraldeau et al., 1994). We were able to manipulate the opportunities to scrounge a patch zone by controlling the moment when a door was closed. As the access time to a discovered patch decreased, the producer's finder's share estimated by the rate-maximization model increased. Although the arrival times of the first scrounger were shorter in the Condition 1min, the average number of scroungers arriving at the patch zone was lower compared to the Condition 5min. The increase in the number of scroungers in a patch zone could have affected the resources the producers consume.

Results suggest that as the time available to access patch zones increased (because they remained open for a longer timespan), the proportion of producer responses decreased, consequently increasing the number of scroungers. When access time to the patch zone was longer, the number of scroungers tended to increase, decreasing the finder's share. The Rate Maximization Model (Vickery et al., 1991) predicts a higher proportion of consumed food units by the producers when the access time to patch zones is reduced. Conversely, in Beauchamp's (2000) Agent-Based Model, the finder's share depends on the time-steps that scroungers take to join the patch zone. If agents are far from the patch zone, it will take them a longer time to join the patch and consume the food units. In this sense, our preparation could be considered analogous to the habitat's richness or the distance to reach a patch zone. If patch zones remain open longer, the time required to find a patch zone is shorter.

An important aspect is the variation in individual producer indexes. In the group that shifted from Condition 5min to Condition 1min, a more marked change in the producer index was observed compared to the group that shifted from Condition 1min to Condition 5 min. This difference could be attributed to the behavioral flexibility of the subjects (Barou-Dagues, et al., 2020) or a possible effect of the value associated with each of the alternatives in the previous condition. Regarding this issue, the rate maximization model only predicts the group proportion of producer strategies during stable states, thus limiting its ability to confirm these claims. In the future, agent-based models that integrate the linear operator as a learning rule could be employed to explore behavioral flexibility or the impact of previous exposure. The linear operator includes a parameter that allows manipulation of the learning factor, determining how much agents prioritize current outcomes over the value of past strategies. In upcoming simulations, agents could experience a prior condition with a lower or higher finder's share and then be examined in the contrasting scenario.

In sum, as the access time to the patch zones increased, the proportion of scroungers within the group also increased. The experimental setup allowed for control over resource access. However, it still has some limitations, such as the absence of an input mechanism that enables independent door control. In this experiment, door opening times depended on the speed at which the producers opened the doors. In the future, an input mechanism should be implemented to control the opening of the doors independently, providing greater control over the finder share.

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