Scrounging marmosets eat more when the finder's share is low without changing their searching effort

Thalita Siqueira Sacramento [1] , Júlio César Bicca-Marques [*]

Laboratório de Primatologia, Escola de Ciências da Saúde e da Vida, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil

Animals that forage in groups may either search actively for food sources (producers, P) or monitor other members of the group in an attempt to consume resources that producers have encountered (scroungers, S). One factor that may influence the choice of foraging strategy is the finder's share, defined as the proportion of the resource consumed by the producer before the arrival of scroungers. Several models predict that when the finder's share is relatively small, the frequency of scrounging will be high because producing gives only a small benefit compared to playing scrounger. A model based on a linear operator learning rule confirmed this prediction and further predicted that individuals would change their foraging strategy gradually in response to environmental changes. We tested these predictions in an experiment involving three groups ($N = 18$ individuals) of free-ranging black-tufted marmosets, *Callithrix penicillata*. We manipulated the finder's share at artificial feeding stations by controlling the distribution of food rewards (slices of banana) among baited platforms. We divided our field experiments into two conditions — low finder's share (few food-rich patches) and high finder's share (many food-poor patches). Most (15/18) marmosets consumed more banana slices as scroungers in the low finder's share condition than in the high finder's share condition, as expected by the theory. However, individuals did not modify their frequency of use of the strategies in both conditions and did not show gradual learning as expected by the linear operator learning rule. We suggest that in social groups with high levels of tolerance and cooperation, such as those of marmosets, scrounging individuals can have higher foraging success without increasing their searching effort by sharing productive food patches with producers and other scroungers.

© 2021 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Group living imposes potential costs and benefits. One of the benefits is an increase in the efficiency of foraging behaviour if group members can integrate both ecological information (e.g. the location or the relative productivity of feeding sites) and social cues (e.g. food calls and the sight of a group member feeding) in their search for resources (Bicca-Marques & Garber, 2005). In a social context, the discovery of food by some individuals may increase the feeding success of conspecifics (Vickery et al., 1991). When observing other members of the group, individuals may obtain information (e.g. if patches are depleted or not) that increases their ability to decide where to forage and when to scrounge patches encountered by others (Kok et al., 2017). Depending on the amount and distribution of food, scrounging generates costs, such as an increase in resource competition and social conflicts (Barnard & Sibly, 1981; Barta & Giraldeau, 1998; Liker & Barta, 2002; McCormack et al., 2007).

One valuable theoretical approach for the investigation of foraging decisions in social species is the producer–scrounger (P–S) game (Giraldeau & Caraco, 2000; Maynard-Smith, 1979). The P–S game predicts individual foraging decisions based on the optimal cost–benefit ratio in a social context (Barnard & Sibly, 1981). In this game, individuals choose between producer (P) and scrounger (S) strategies. While producers search actively for resources, scroungers monitor the behaviour of producers to share/ steal the food that producers encounter (Barnard & Sibly, 1981; Giraldeau & Beauchamp, 1999). These strategies are temporally exclusive, that is, an animal can only adopt one strategy at a time (Giraldeau & Caraco, 2000). However, an individual can act as a producer at one source of food and then immediately become a scrounger at the next resource, and so on (King et al., 2009).

The P–S model also predicts that individuals face a 'frequency-dependent' scenario, in which the amount of food ingested (hereafter, success) resulting from their choices depends on the

* Corresponding author.
  E-mail address: jcbicca@pucrs.br (J. C. Bicca-Marques).
[1] thalitasiqueira.bio@gmail.com.

ecological characteristics of the environment (e.g. the size, abundance and distribution of food sources) and the frequency with which each strategy is adopted by other members of the group (Barnard & Sibly, 1981; Giraldeau & Caraco, 2000). On one hand, when the frequency of the scrounger strategy increases in the group, fewer animals are searching for food, so scroungers need to compete among more scroungers for fewer scrounging opportunities. On the other hand, when the frequency of the producer strategy increases, so does the number of opportunities to scrounge and, therefore, the success of the scrounger strategy increases too (Giraldeau & Livoreil, 1998). Therefore, when food is not abundant and scroungers are rare, scroungers do better than producers if the food is not quickly depleted by the producers, such as solitary prey, but they do worse than producers when scroungers are common, creating a stable equilibrium frequency somewhere in between, where the two strategies have equal payoffs (Giraldeau & Caraco, 2000; Giraldeau & Livoreil, 1998).

Foraging models based on the theory of the evolutionarily stable strategy (ESS) predict how the P–S strategies can coexist over time in a population and reach an evolutionarily stable equilibrium in which both strategies are equally profitable (Giraldeau & Beauchamp, 1999). These simple models assume that an individual's behaviour is fixed genetically (that is, the use of each strategy is restricted by the individual's genotype) and will not adjust appropriately to changing conditions of the social and ecological environment. Therefore, the models simulate simplified, static conditions (Afshar & Giraldeau, 2014). While captive house sparrows, *Passer domesticus* (Barnard & Sibly, 1981), and great tits, *Parus major* (Aplin & Morand-Ferron, 2017), may in fact present a relatively fixed strategy use, individuals of other species alternate between the P–S strategies in response to environmental changes (e.g. chacma baboons, *Papio ursinus*: King et al., 2009; Lee & Cowlishaw, 2017; spice finches, *Lonchura punctulata*: Coolen, 2002; Morand-Ferron, Varennes et al., 2011; Morand-Ferron, Wu et al., 2011).

An alternative approach involves the development of learning models (Dubois, Morand-Ferron, & Giraldeau, 2010; Katsnelson et al., 2012; Morand-Ferron & Giraldeau, 2010), such as an agent-based model using a linear operator learning rule (Afshar & Giraldeau, 2014) that includes the effects of environmental complexity on social foraging. As in previous models, this agent-based model predicts that the proportion of scroungers will shift in response to the variation in ecological factors, including the finder's share (Giraldeau & Livoreil, 1998; Vickery et al., 1991). The finder's share is the proportion of the resource consumed by the producer before the arrival of scroungers (Vickery et al., 1991) and is inversely proportional to the amount of food available in the feeding patch (De la Fuente et al., 2019; Di Bitetti & Janson, 2001; Kok et al., 2017). On one hand, models predict that when the amount of food in the patch is small (and the finder's share is high), the producer will consume most or all of the food reward, and the producer strategy will have the best cost–benefit ratio in terms of the amount of food consumed per unit time. On the other hand, when the resource patch is large (and the finder's share is low), the producer will not exhaust the patch, which remains available to scroungers (Afshar & Giraldeau, 2014; Giraldeau & Livoreil, 1998). Additionally, this agent-based model predicts that the members of a social group will gradually adjust the frequency of their strategies over time, with the proportion of the most advantageous strategy increasing progressively when individuals gain experience about the environment, using a linear operator learning rule (Afshar & Giraldeau, 2014).

Empirical studies are essential to test the hypotheses and predictions of these theoretical models under a range of social foraging scenarios, which are more similar to the conditions in which the

behaviours are likely to have evolved (Afshar & Giraldeau, 2014; Di Bitetti & Janson, 2001; Giraldeau & Beauchamp, 1999). Most of these experiments have been conducted on captive birds (Afshar et al., 2015; Giraldeau & Livoreil, 1998; Morand-Ferron, Varennes et al., 2011). Research on wild animals, including primates (mammals with variable social systems), is still particularly scant (Di Bitetti & Janson, 2001; King et al., 2009; Lee & Cowlishaw, 2017). Moreover, few studies have analysed the adjustment process that occurs via learning in response to environmental conditions (Afshar et al., 2015; Belmaker et al., 2012; Morand-Ferron & Giraldeau, 2010).

Learning is the most likely mechanism to enable animals to optimize their behaviour to cope with changing local environmental conditions (Belmaker et al., 2012; Giraldeau & Dubois, 2008). Reinforcement learning is a possible mechanism for the choice of foraging strategy. In this type of learning, individuals try both P–S strategies and develop a preference for the most successful one (Beauchamp, 2000; Belmaker et al., 2012). House sparrows (Belmaker et al., 2012), nutmeg mannikins, *L. punctulata* (Morand-Ferron & Giraldeau, 2010), and zebra finches, *Taeniopygia guttata* (Afshar et al., 2015), show reinforcement learning. Zebra finches appear to use a linear operator learning rule by gradually changing the proportion of scrounging in response to changes in patch quality (Afshar et al., 2015).

In addition to these avian studies, wild tamarins (*Saguinus imperator* and *Leontocebus weddelli*, formerly *Saguinus fuscicollis weddelli*) were reported to combine social (e.g. the identity of groupmates that tolerate co-feeding), temporal (e.g. recent feeding success and failure) and ecological (e.g. expectations on the amount and distribution of food rewards) information in choosing a social foraging strategy (Bicca-Marques, 2003; Bicca-Marques & Garber, 2005; Garber et al., 2009). This decision-making process likely involves learning (Garber et al., 2009).

In the present study, we explore the application of P–S models to the social foraging of free-ranging black-tufted marmosets, *Callithrix penicillata*, and test whether these Neotropical primates adjust their group level proportion of use of the scrounger strategy under different environmental conditions (variation in the finder's share) by learning the payoffs associated with each strategy. Callitrichines are a good model to test the use of P–S strategies. They form small cohesive multimale-multifemale groups that forage together and access patches that are usually divisible, like fruit trees (Faria, 1986; Fonseca & Lacher, 1984; Miranda & Faria, 2001; Vilela & Faria, 2004). We begin by describing baseline patterns of producer and scrounger behaviour. Then, we test the following hypotheses: (1) the finder's share influences the choice of P–S strategies based on the assumption that individual marmosets increase their proportion of use of the scrounger strategy when the finder's share is low, and (2) that this adjustment occurs gradually over time if individuals follow a linear operator learning rule (Afshar & Giraldeau, 2014).

METHODS

Study Area and Subjects

We studied three multimale-multifemale groups of *C. penicillata* (with 6, 6 and 9 individuals; total of 19 adult and 2 juvenile individuals). Marmosets are characterized by low levels of aggression (Bicca-Marques & Garber, 2005; De la Fuente et al., 2019; Digby, 1995). Their social groups feed on a varied diet of fruits, flowers, exudates, invertebrates and small vertebrates (Faria, 1986; Fonseca & Lacher, 1984; Miranda & Faria, 2001; Vilela & Faria, 2004), resources whose availability varies seasonally. Groups typically include a single breeding female (but see Garber et al., 2016), who is

behaviourally dominant to all other group members (De la Fuente et al., 2019; Decanini & Macedo, 2008; Garber, 1997).

We captured all members of the study groups (except the six dependent infants, $N = 21$) using the Peruvian method (Encarnación et al., 1990), and anaesthetized them by the inhalation of 2% isoflurane in a universal open-flow vaporizer with oxygen flow fixed at 1 litre/min. We marked the marmosets with colour-coded beaded collars and tail trichotomy (shaving rings of hair in different portions of the tail; Honess & Macdonald, 2011) for individual identification. We waited a minimum of 20 days after capture to begin behavioural observations. Three individuals left Group 3 and did not participate in any experimental session.

The three study groups inhabited a gallery forest in the Brasília National Park (15°38′28″S, 48°01′15″W; 42 355 ha, approximately 1000 m above sea level) in Brasília, Federal District, Brazil. The local climate is tropical and seasonal, with a rainy season from October to March, and a dry season from April to September (Ferreira, 2003). The vegetation is typical of the cerrado savannah biome of central Brazil and its various phytophysiognomies.

Ethical Note

The Ethics Committee for the Use of Animals in Research (CEUA) of the Pontifical Catholic University of Rio Grande do Sul (project number 7838) approved the study and the federal Chico Mendes Institute for Biodiversity Conservation (ICMBio) authorized the capture of marmosets through the Biodiversity Authorization and Information System (SISBio, licence number 56960).

Experimental Design

We exposed each study group to the same experimental procedure in loco in its home range. Within each area, we built a feeding station composed of a grid of 12 or 18 wooden platforms (30×45 cm) that were 1.3 m high and spaced approximately 1.5 m from the nearest adjacent platforms (Fig. 1a). The total area occupied by each feeding station was ca. 24.5 m^2. We arranged the platforms so that the marmosets could view all the other platforms from any position within the feeding station. We installed the platforms near trees and shrubs to facilitate access. The number of platforms in each feeding station was equal to twice the number of members in each respective study group (except for dependent infants). We baited the platforms with slices of banana divided in the middle, which weighed approximately 3 g each. We placed these pieces of banana in round, opaque white plastic boxes, each having six holes. We covered each hole with brown cloth so that the marmosets could not determine visually whether the box contained food or not. We used two types of boxes. One type had six large square holes (3×3 cm) through which the marmosets could reach the banana slices (Fig. 1b). The other type had small circular holes (ca. 0.5 cm in diameter), which did not allow the marmosets to reach inside but allowed the release of banana scent (Fig. 1c). This design controlled the ability of the marmosets to use olfactory cues alone in selecting which platform(s) contained a food reward.

We designed the experiment assuming that a visiting marmoset could not adopt the producer and scrounger foraging strategies simultaneously, and could not identify, from a distance, which platforms contained accessible food. In other words, the marmoset had to either play producer and visit an unoccupied platform to determine whether it contained accessible food or play scrounger and monitor the behaviour of producers to decide which conspecific to join. The first author monitored the visits of each group to the feeding stations from a cloth-covered hide at a distance of approximately 3 m from the nearest platforms (see Fig. 1a) with the help of field assistants. A single observer was present during each experimental session. We filmed the platforms with a closed-circuit television (CCTV) system, which used professional security cameras (Sony 312 and Bullet AHD 20MT 1MP 1/4 BR 5280B Luxvision) with 2.8, 6 and 60 mm lenses. We protected the cameras inside aluminium boxes fixed to wooden stakes at a height of approximately 1.5 m. We positioned each camera to film two or three platforms simultaneously at a distance of 1 m.

Procedures

We habituated each group to its feeding station and to feed on the platforms over a period of 15–20 days prior to beginning the experiment. During this habituation period, we baited the boxes on all platforms with four banana slices (ca. total of 144–216 g depending on the number of platforms) and monitored the feeding stations. All study subjects visited the feeding stations and fed at all platforms. They inspected all platforms in 90% of the visits to the stations. We trained the marmosets to access the food rewards placed inside the boxes in four steps during the habituation. First, we placed the banana slices on the platforms. Second,
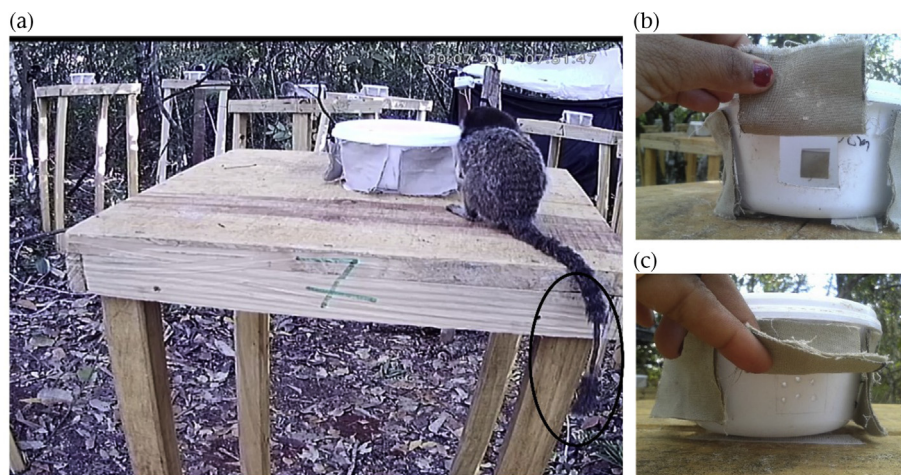

Figure 1. (a) View of a feeding station, showing a marmoset on a platform in the foreground (see tail trichotomy, circled). The white tent in the right background is the observer's hide, where equipment was stored. The plastic boxes were either (b) accessible, with holes large enough to allow the marmosets to insert a hand and reach the bait or (c) inaccessible, with small holes that allowed the release of banana scent but did not allow the marmosets to access the food. In both cases, the holes were covered with opaque brown cloth.

we placed them inside open boxes. Third, we closed the lids of the boxes so the marmosets had to insert their hands inside the box holes to access the rewards. And, finally, the marmosets had to lift the cloth to insert their hand in the hole and take a banana slice from inside. We finished each step when all study subjects had fulfilled the task.

After the habituation period, we ran two experimental sessions (when rewards were placed inside the boxes) per day on each group, one at 0600 hours and the other at 1300 hours. We considered a session as any group visit to the feeding station. A session began when the first marmoset arrived at a feeding platform and it ended when the last individual had left and no group member returned to the station within 10 min. We analysed the sessions in which at least two group members visited platforms and at least one fed at a reward platform.

We tested two conditions in each group: (1) high finder's share (HFS) and (2) low finder's share (LFS). We manipulated the finder's share in the two conditions by altering the distribution of a constant amount of food (Table 1) among the feeding platforms. In the case of the HFS (dispersed) condition, we distributed the rewards on 10 platforms (Groups 1 and 2) or 15 platforms (Group 3). During the LFS (concentrated) condition, we distributed the rewards on four platforms (Groups 1 and 2) or six platforms (Group 3; Table 1). We used Excel functions to randomize across sessions which platforms contained accessible food. We set the constraint that the location, but not the number, of nonrewarding platforms should differ from the previous session in the HFS, when we baited most platforms. In contrast, the location of rewarding platforms differed randomly between sessions during the LFS condition, when we baited 1/3 of the platforms. We offered 20 g of food per individual for each group, based on the mean consumption of food recorded during the habituation period.

We ran the study during the dry seasons (April–September) of 2017 and 2018 to minimize the possible influence of seasonal variation in the availability of natural food sources within the home range of each group on the foraging behaviour of the study subjects. We chose the dry season as the study period because food availability is lower during this time (Oliveira & Paula, 2001). This decision limited the study to a single switch from HFS to LFS, as the switch in the opposite direction (LFS back to HFS) to confirm the marmosets' responses to our experimental design, would have taken place, at least partially, during the wet season, when food availability in the group's home range would have been higher, and represent a confounding factor in their foraging behaviour, as could also be the case of seasonal changes in behavioural state. However, we believe that our results are reliable because all three study groups responded similarly to the change in finder's share despite the fact that they inhabited distinct home ranges. We ran the experiment simultaneously on Groups 1 and 2 on 54 consecutive days in July and August, 2017, and on Group 3 on 49 consecutive days in July and August, 2018. The groups did not visit the feeding stations on 14–19 days during

the experiments, although there were never more than two consecutive days in which the marmosets failed to visit the feeding station.

We ran 30 consecutive sessions using the HFS condition followed by an interval of 5 days, during which we continued to provision the feeding stations. We offered the same total amount of food (120 g for Groups 1 and 2 and 180 g for Group 3) during this interval. We baited the boxes on all platforms with 10 g of bananas to ensure that the groups continued to visit the stations. Following the interval, we ran 30 consecutive sessions of the LFS condition.

We analysed one individual per experimental session to ensure the independence of the samples (Afshar et al., 2015; Coolen, 2002). We randomly selected this focal individual a posteriori using Excel formulas. We recorded the number of times (frequency) that the focal individual played producer (i.e. arrived at an unoccupied platform) and the number of times that it played scrounger (i.e. arrived at a platform occupied by another marmoset). Given that the marmosets visiting a station often arrived together, the focal individual could play either producer or scrounger at the beginning of most sessions. We recorded a new event when a marmoset 're-encountered' an unoccupied platform or 're-scrounged' an occupied one. We also recorded the number of visits in which a marmoset fed using each foraging strategy. In addition, we counted the number of banana slices that the focal individual consumed when it played producer and scrounger. We calculated foraging success separately for each strategy as the number of food items obtained by the focal forager through the use of one strategy divided by the cumulative frequency of use of that strategy at the end of a session. We calculated the mean value and the standard deviation of the foraging success of all focals over the set of all sessions per condition. We also calculated the proportion of feeding by the focal individual when playing scrounger in each session by summing all the banana slices that it scrounged and dividing this number by the total number of slices it consumed (scrounged +produced). (The data on social behaviour on the platforms remain to be analysed to assess whether individuals' social rank influenced P–S strategies.).

Sample size

We omitted six HFS sessions and eight LFS sessions because of lack of visibility of some platforms due to mist or the displacement or malfunction of at least one camera. These exclusions resulted in a sample of 164 sessions (82 in each condition) and 18 focal individuals. Therefore, we obtained 49 valid observation sessions for Group 1, 55 for Group 2 and 60 for Group 3. Males were focal subjects in 104 sessions and females in 60. Over half of the members of each study group participated in 87% of the sessions (Appendix, Table A1). Two adult females in Group 3 disappeared and never visited the feeding station during the experiment. Excluding this membership change, the composition of the three groups remained the same throughout the study and 17 marmosets participated in most sessions (Table 2). However, one adult female

Table 1
Experimental conditions used to test the influence of the finder's share on the frequency of scrounging in three groups of marmosets (*C. penicillata*)

Group	Group size	Number of platforms	Total amount of food	Finder's share			
				High		Low	
				Number (proportion) of platforms with food	Number of banana slices (biomass) per platform	Number (proportion) of platforms with food	Number of banana slices (biomass) per platform
1	6	12	120 g	10 (0.83)	4 (12 g)	4 (0.33)	10 (30 g)
2	6	12	120 g	10 (0.83)	4 (12 g)	4 (0.33)	10 (30 g)
3	9	18	180 g	15 (0.83)	4 (12 g)	6 (0.33)	10 (30 g)

Table 2
Composition of study groups and number of sessions each individual participated in as focal

Group	Individual	Age	Sex	Total sessions participated	Number of sessions as focal		
					HFS condition	LFS condition	Total
1 ADM	MR1	A	M	46	5	5	10
	PV	A	M	39	5	5	10
	VR	A	BF	38	5	5	10
	AB	A	M	32	5	5	10
	AV	A	M	44	4	5	9
	VA1[a]	A	F	3	0	0	0
2 CASA	RR	A	M	53	5	6	11
	MV	A	BF	51	5	5	10
	LA	A	M	51	5	5	10
	PB	A	M	42	5	5	10
	VA2	J	F	52	5	4	9
	RL	A	F	15	3	2	5
3 MATA	AA	A	M	59	5	4	9
	AR	A	M	57	5	4	9
	MR3	A	M	59	4	5	9
	RA	A	M	59	4	5	9
	ML	A	BF	59	4	4	8
	LV	J	F	58	4	4	8
	CI	A	M	53	4	4	8
				Total	82	82	164

A = adult; J = juvenile; M = male; F = female; BF = breeding female.
[a] Individual not included in the analyses.

in Group 1 only participated in three HFS sessions, and, therefore, we did not include her as a focal individual.

Statistical Analyses

We used two approaches in our analyses. First, we described the foraging behaviour of marmosets. We compared the mean frequency of use of each strategy, their food consumption and their success between experimental conditions using Mann−Whitney *U* tests. Second, we tested the hypothesis that the finder's share and the session (experience) influence the proportion of playing scrounger by running generalized linear mixed models (GLMMs) with binomial distribution and logit link (Bolker et al., 2009; Zuur et al., 2009). We considered the proportion of feeding as scrounger by each focal individual as an index of the use of the scrounger strategy as reported elsewhere (Afshar et al., 2015; Coolen, 2002; Morand-Ferron, Varennes et al., 2011; Morand-Ferron, Wu et al., 2011). We began with the complete model with three explanatory variables (condition, session, group), the interaction between session (experience) and condition, and focal individual as random factor. We then kept the random factor and conducted model comparisons via sequential ANOVA using the 'anova' function of the 'stats' package (R Core Team, 2020). In addition, we compared subsets of best models based on the estimate of maximum likelihood using the Akaike's information criterion corrected for small samples, AICc (Burnham & Anderson, 2002; Zuur et al., 2009). We used the 'AICctab' function of the 'bbmle' package in the R platform to run this analysis (R Core Team, 2020). We selected the model with the lowest AICc and ΔAICc values (delta = the difference between the observed model and the most parsimonious model) that did not lose explanatory power (*P* < 0.05; Zuur et al., 2009). We also used the full-model averaging analysis because we had more than one model with ΔAICc < 2, all of which are equally parsimonious (Grueber et al., 2011).

We used the 'dredge' function in the 'MuMIn' package to create a set of models based on the complete model, and the 'model.avg' function (also in MuMIn) to identify the averaged-model and the relative importance of each variable (Σwi). The GLMM analysis allowed us to control for the temporal autocorrelation generated by the sampling of the same individuals repeatedly over time.

Finder's success

We calculated the finder's success, that is, the proportion of food obtained by the producer, including what it ate after scroungers arrived, in each session relative to the total amount of food available in the platforms that it produced, using the formula: total number of banana slices consumed by the producer/number of sources produced × *x*, where *x* is the total number of banana slices available per platform in each condition (that is, *x* = 4 in the HFS condition and *x* = 10 in the LFS). We also used a GLMM with binomial distribution and logit link (Bolker et al., 2009; Zuur et al., 2009) to compare the finder's success between the HFS and LFS conditions, including the identity of the focal individual as a random factor.

RESULTS

Patterns of Producing and Scrounging

The marmosets used both P−S strategies, and they played producer more frequently than scrounger in both conditions (Table 3). Producers ate a mean ± SD of 5.1 ± 2.6 banana slices (ca. 15 g) during the HFS condition (*N* = 82) and 3.0 ± 2.9 slices (ca. 9 g) during the LFS condition (*N* = 82). Scroungers ate a mean ± SD of 1.1 ± 1.5 slices (ca. 3 g) during the HFS condition and 3.1 ± 3.2 slices (ca. 9 g) during the LFS. Scroungers showed high variation in food consumption between sessions (Fig. 2). The mean individual food consumption per session, irrespective of foraging strategy, was similar in both conditions (HFS = 6.3 ± 2.4, LFS = 6.1 ± 2.4, ca. 18 g; Mann−Whitney *U* test: *U* = 3361.5, $N_1 = N_2 = 82$, *P* = 1). The success of scroungers was higher during the LFS condition than during the HFS condition (Table 3).

Finder's success

The finder's success was, on average, 50% greater in the HFS condition (mean ± SD = 0.52 ± 0.23) than in the LFS condition (0.22 ± 0.23; β = −1.37, *z* score = −3.49, *P* = 0.0004). The model differed from the null model (likelihood ratio test: AIC = 182.29, $\chi^2_3 = 13.63$, *P* = 0.0002).

The marmosets quickly dispersed among the platforms playing mostly producer and rarely scrounging during the HFS sessions. The first three marmosets visiting the feeding station in the LFS

Table 3
Mean ± SD of the variables in each experimental condition

Variables	Condition		Mann—Whitney U
	HFS	LFS	
Frequency of scrounging	1.7 ± 2.1	2.0 ± 2.3	2986, $P=0.20$
Frequency of producing	6.2 ± 3.7	6.2 ± 4.0	3412 $P=0.87$
Scrounging success	0.5 ± 0.6	1.3 ± 1.4	2351.5, ***$P<0.001$***
Producing success	1.0 ± 0.7	0.8 ± 1.2	4581.5, ***$P<0.001$***
Proportion of feeding by scrounging	0.18 ± 0.25	0.50 ± 0.43	2105.5, ***$P<0.001$***

HFS = high finder's share; LFS = low finder's share. Significant P values are shown in bold.
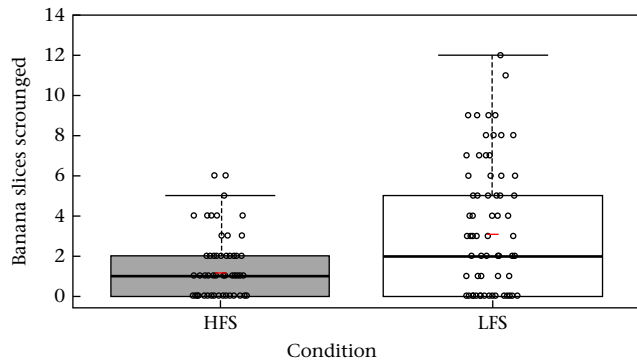
Figure 2. Number of banana slices scrounged by marmosets (*C. penicillata*) in two experimental conditions: high finder's share (HFS) and low finder's share (LFS) ($N = 18$ focal individuals). The box represents the first and third interquartiles (IQR), the whiskers represent the maximum values excluding outliers, the red line within each box represents the mean and the black line represents the median. The dots represent the actual number of banana slices scrounged in each session by the focal individual.
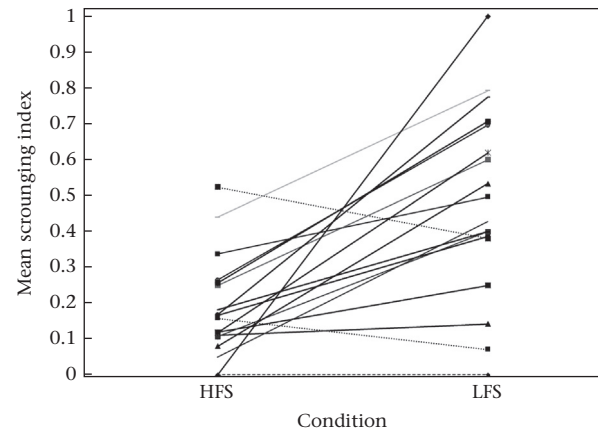

Figure 3. Mean individual scrounging index (mean proportion of food eaten when playing scrounger) by the study marmosets ($N = 18$) under experimental conditions of high finder's share (HFS) and low finder's share (LFS). Trends HFS → LFS: increase (continuous lines), decrease (dotted lines) and scrounging index equal zero (dashed line).

sessions also often played producer, while the remaining group members moved directly to the platforms where producers were eating, playing scrounger. On average, only two of the six adult females scrounged less in LFS than in HFS sessions (Fig. 3). Almost all individuals (15 of 18) fed more as scroungers in the LFS condition compared with the HFS condition, while a single adult male never fed when playing scrounger.

Scrounging index

We found two equally parsimonious models (Table 4). The probability of selecting the best model ($w_i = 0.35$), which included experimental condition only, was similar to the second-best model ($w_i = 0.30$), which included both experimental condition and group. The averaged-model included all potentially explanatory variables. However, it differed from the null model (maximum likelihood ratio: AIC = 178.36, $\chi^2{}_3 = 31.65$, $P < 0.0001$) due exclusively to the experimental condition (Table 5). Therefore, we found support for the first hypothesis but not for the second one. The marmosets changed their scrounging index between conditions, but this change did not fit a linear response. The study subjects maintained a high level of producing throughout the HFS condition. They also began the LFS condition playing mostly producer. However, the success of scrounging exceeded the success of producing during many sessions, beginning in the sixth session, and they tended to maintain higher levels of scrounging than in the HFS until the end of the experiment (Fig. 4).

DISCUSSION

Producer and scrounger strategies were 'available' to all study subjects and almost all marmosets (17) adopted both. As expected,

most marmosets (15) were more successful as scroungers when the food was more concentrated and the finder's share proportionally smaller (LFS condition). Therefore, the finder's share influenced marmosets' success as scroungers. However, this influence occurred without a change in their frequency of use of the P—S strategies, failing to support the linear operator learning rule of the agent-based model predicted by mathematical simulations (Afshar & Giraldeau, 2014) and observed in captive zebra finches (Afshar et al., 2015).

The marmosets tended to play producer more often than scrounger throughout the study. On average, for each platform visited as scroungers under both experimental conditions, individuals inspected three platforms as producers. Their exploitation of easily depletable food sources (e.g. exudates and nonsocial prey; Miranda & Faria, 2001; Vilela & Faria, 2004) may play a strong selective force that favours this tendency to producing. Additionally, the close proximity between all platforms in our experimental design did not impose distinct energy costs between producing and scrounging (indeed, energy costs of locomotion are reported to be negligible; Steudel, 2000).

The success of playing producer was 100% higher than that of playing scrounger when the finder's share was high, whereas the success of playing scrounger was 62% higher than that of playing producer when the finder's share was low. However, given differences in the investment of producing and scrounging under both experimental conditions, marmosets ate only 18% of the food by playing scroungers in HFS compared to 50% in LFS. That is, producing and scrounging were equally profitable at rich food patches. This pattern is possible because marmosets show high levels of within-group tolerance at feeding sites (De la Fuente et al., 2019), a

Table 4
Best generalised linear mixed models (GLMM) for explaining the proportion of feeding as scrounger in three groups of black-tufted marmosets, including the comparison with the null model

Rank	Model	df	logLik	AICc	ΔAICc	w_i
1	Condition	3	85.1	176.4	0.0	0.35
2	Condition + group	4	−84.2	176.6	0.3	0.30
3	Condition + session	4	−85.1	178.4	2.1	0.12
4	**Condition + session + group**	**5**	**−84.2**	**178.7**	**2.4**	**0.10**
5	Condition + session + condition*session	5	−85.1	180.6	4.2	0.04
6	Condition + session + group + condition*session	6	−84.1	180.8	4.5	0.03
7	Session	3	−88.7	183.6	7.2	0.009
8	Session + group	4	−87.7	183.7	7.3	0.009
	Null GLMM	2	−100.0	204.1	27.7	<0.001

The random effect was individual identity. An asterisk (*) represents an interaction between variables. The averaged-model is shown in bold. AICc = Akaike's information criterion corrected for small samples; ΔAICc = the difference between the observed model and the most parsimonious model; w_i = probability of model selection.

Table 5
Estimates and significance of the explanatory variables of the averaged-model that included the proportion of feeding as scrounger as response variable and the focal individual as random variable

	β	SE	Z	P	$\sum w_i$
Intercept	−1.09	0.22	4.78	**<0.001**	
Condition	2.06	0.50	4.09	**<0.001**	1.00
Group	−0.21	0.35	0.59	0.55	0.40
Session	0.01	0.30	0.04	0.96	0.16

β = coefficient of partial regression of the mean model; SE = standard error; $\sum w_i$ = relative importance of each predictor variable; P = probability. Significant P values are shown in bold.
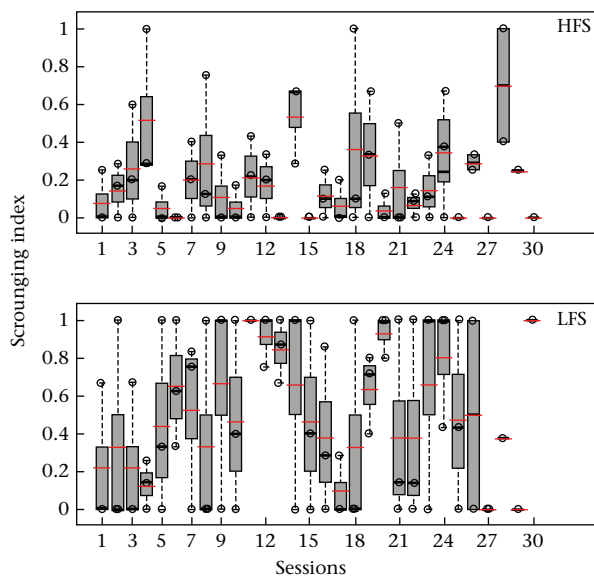

Figure 4. Scrounging index (the proportion of food eaten when playing scrounger) of focal individuals of three marmoset (*C. penicillata*) groups per session in two experimental conditions: high finder's share (HFS) and low finder's share (LFS). The box represents the first and third interquartiles (IQR), the whiskers represent the minimum and maximum values, the red line within each box represents the mean and the black line represents the median. The dots represent the proportion of banana slices eaten by the focal individual in each session that were scrounged.

social trait whose evolution may be linked to the dependence on nonbreeding individuals for the success of raising the twin offspring in the cooperative-breeding callitrichines (Garber, 1997). The high risk of predation faced by marmosets (Duarte & Young, 2011) may also play a role in their foraging behaviour (Bicca-Marques, 2003). Co-sharing a feeding site may reduce the perceived predation risk via improved vigilance, leading both producers and scroungers to stay longer and obtain more food rewards when visiting a platform together, similar to what was reported for northwestern crow, *Corvus caurinus*, scroungers (Robinette & Ha, 2001).

Overall, we found that the social foraging behaviour of free-ranging black-tufted marmosets is consistent with the P–S model, and that variation in the finder's share played an important role in the success of producer and scrounger strategies. On one hand, the prediction on the success of scrounging was supported by the foraging behaviour of the study marmosets. On the other hand, the prediction on the frequency of use of the P–S strategies was not. Future analyses of the role of social rank and interaction networks on individual foraging decisions may improve our understanding on how marmosets decide whom to avoid and whom to scrounge from at feeding sites. In summary, we provide new insights into how social and ecological information affect the dynamics of social foraging in free-ranging highly cooperative animals.

Author Contributions

Thalita Siqueira Sacramento: designed the study; collected, curated and analysed the data; wrote and revised the manuscript. **Júlio César Bicca-Marques**: designed the study; provided equipment and financial support; wrote and revised the manuscript.

Declarations of Interest

None.

Acknowledgments

References

Afshar, M., & Giraldeau, L.-A. (2014). A unified modelling approach for producer–scrounger games in complex ecological conditions. *Animal Behaviour, 96*, 167–176. https://doi.org/10.1016/j.anbehav.2014.07.022

Afshar, M., Hall, C. L., & Giraldeau, L.-A. (2015). Zebra finches scrounge more when patches vary in quality: Experimental support of the linear operator-learning rule. *Animal Behaviour, 105*, 181–186. https://doi.org/10.1016/j.anbehav.2015.04.016

Aplin, L. M., & Morand-Ferron, J. (2017). Stable producer–scrounger dynamics in wild birds: Sociability and learning speed covary with scrounging behaviour. *Proceedings of the Royal Society B: Biological Sciences, 284*, 20162872. https://doi.org/10.1098/rspb.2016.2872

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour, 29*, 543–550. https://doi.org/10.1016/S0003-3472(81)80117-0

Barta, Z., & Giraldeau, L.-A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: A phenotype-limited producing-scrounging game. *Behavioral Ecology and Sociobiology, 42*, 217–223. https://doi.org/10.1007/s002650050433

Beauchamp, G. (2000). Learning rules for social foragers: Implications for the producer–scrounger game and ideal free distribution theory. *Journal of Theoretical Biology, 207*, 21–35.

Belmaker, A., Motro, U., Feldman, M. W., & Lotem, A. (2012). Learning to choose among social foraging strategies in adult house sparrows (*Passer domesticus*). *Ethology, 118*(11), 1111–1121. https://doi.org/10.1111/eth.12013

Bicca-Marques, J. C. (2003). Sexual selection and the evolution of foraging behavior in male and female tamarins and marmosets. In C. B. Jones (Ed.), *Sexual selection and reproductive competition in primates: New perspectives and directions* (pp. 455–475). Norman, OK: American Society of Primatologists.

Bicca-Marques, J. C., & Garber, P. A. (2005). Use of social and ecological information in tamarin foraging decisions. *International Journal of Primatology, 26*, 1321–1344. https://doi.org/10.1007/s10764-005-8855-9

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution, 24*, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Burnham, P. K., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York: Springer-Verlag.

Coolen, I. (2002). Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Lonchura punctulata*). *Behavioral Ecology and Sociobiology, 52*, 232–238. https://doi.org/10.1007/s00265-002-0500-4

Decanini, D. P., & Macedo, R. H. (2008). Sociality in *Callithrix penicillata*: I. Intragroup male profile. *International Journal of Primatology, 29*, 433–447. https://doi.org/10.1007/s10764-007-9173-1

De la Fuente, M. F., Schiel, N., Bicca-Marques, J. C., Caselli, C. B., Souto, A., & Garber, P. A. (2019). Balancing contest competition, scramble competition, and social tolerance at feeding sites in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology, 81*, Article e22964. https://doi.org/10.1002/ajp.22964

Di Bitetti, M. S., & Janson, C. H. (2001). Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Animal Behaviour, 62*, 47–56. https://doi.org/10.1006/anbe.2000.1730

Digby, L. J. (1995). Social organization in a wild population of *Callithrix jacchus*: Intragroup social behaviour. *Primates, 36*, 361–375. https://doi.org/10.1007/BF02382859

Duarte, M. H. L., & Young, R. J. (2011). Sleeping site selection by urban marmosets (*Callithrix penicillata*) under conditions of exceptionally high predator density. *International Journal of Primatology, 32*, 329–334. https://doi.org/10.1007/s10764-010-9468-5

Dubois, F., Morand-Ferron, J., & Giraldeau, L.-A. (2010). Learning in a game context: Strategy choice by some keeps learning from evolving in others. *Proceedings of the Royal Society B: Biological Sciences, 277*, 3609–3616. https://doi.org/10.1098/rspb.2010.0857

Encarnación, F., Moya, L., Soini, P., Tapia, J., & Aquino, R. (1990). La captura de Callithrichidae (*Saguinus* y *Cebuella*) en la Amazonia Peruana. In N. E. Castro-Rodrigues (Ed.), *La primatologia en el Peru* (pp. 45–56). Iquitos: Proyecto Peruano de Primatología.

Faria, D. S. (1986). Tamanho, composição de um grupo social e área de vivência (home-range) do sagui *Callithrix jacchus penicillata* na mata ciliar do córrego Capetinga, Brasília-DF. In M. T. Melo (Ed.), *A primatologia no Brasil (2)* (pp. 87–105). Brasília: Sociedade Brasileira de Primatologia.

Ferreira, M. E. (2003). *Análise do modelo linear de mistura espectral na discriminação de fitofisionomias do Parque Nacional de Brasília (bioma cerrado)* (M.S. dissertation). Brasília: Universidade de Brasília.

Fonseca, G. A. B., & Lacher, T. E. L. (1984). Exudate-feeding by *Callithrix jacchus penicillata* in semideciduous woodland (Cerradão) in Central Brazil. *Primates, 25*, 441–450. https://doi.org/10.1007/BF02381667

Garber, P. A. (1997). One for all and breeding for one: Cooperation and competition as a tamarin reproductive strategy. *Evolutionary Anthropology, 5*, 187–199. https://doi.org/10.1002/(SICI)1520-6505(1997)5:6<187::AID-EVAN1>3.0.CO;2-A

Garber, P. A., Bicca-Marques, J. C., & Azevedo-Lopes, M. A. O. (2009). Primate cognition: Integrating social and ecological information in decision-making. In P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. W. Heymann, & K. B. Strier (Eds.), *South American primates* (pp. 365–385). New York: Springer.

Garber, P. A., Porter, L. M., Spross, J., & Di Fiore, A. (2016). Tamarins: Insights into monogamous and non-monogamous single female social and breeding systems. *American Journal of Primatology, 78*, 298–314. https://doi.org/10.1002/ajp.22370

Giraldeau, L.-A., & Beauchamp, G. (1999). Food exploitation: Searching for the optimal joining policy. *Trends in Ecology & Evolution, 14*, 102–106. https://doi.org/10.1016/S0169-5347(98)01542-0

Giraldeau, L.-A., & Caraco, T. (2000). *Social foraging theory*. Princeton University Press.

Giraldeau, L.-A., & Dubois, F. (2008). Social foraging and the study of exploitative behavior. *Advances in the Study of Behavior, 38*, 59–104.

Giraldeau, L.-A., & Livoreil, B. (1998). Game theory and social foraging. In L. A. Dugatkin, & H. K. Reeve (Eds.), *Game theory and animal behaviour* (pp. 16–37). Oxford University Press.

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology, 24*, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Honess, P. E., & Macdonald, D. W. (2011). Marking and radio-tracking primates. In J. M. Setchell & D. J. Curtis (Eds.), *Field and laboratory methods in primatology: A practical guide* (pp. 189–205). Cambridge University Press.

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. (2012). Evolution of learned strategy choice in a frequency-dependent game. *Proceedings of the Royal Society B: Biological Sciences, 279*, 1176–1184. https://doi.org/10.1098/rspb.2011.1734

King, A. J., Isaac, N. J. B., & Cowlishaw, G. (2009). Ecological, social and reproductive factors shape producer–scrounger dynamics in baboons. *Behavioral Ecology, 20*, 1039–1049. https://doi.org/10.1093/beheco/arp095

Kok, R. B., Stears, K., & Shrader, A. M. (2017). Does the removal of finder's share influence the scrounging decisions of herbivores? *Animal Behaviour, 133*, 229–235. https://doi.org/10.1016/j.anbehav.2017.09.023

Lee, A. E. G., & Cowlishaw, G. (2017). Switching spatial scale reveals dominance-dependent social foraging tactics in a wild primate. *Peer J, 5*, Article e3462. https://doi.org/10.7717/peerj.3462

Liker, A., & Barta, Z. (2002). The effects of dominance on social foraging tactic use in house sparrows. *Behaviour, 139*, 1061–1076. https://doi.org/10.1163/15685390260337903

Maynard-Smith, J. (1979). Game theory and the evolution of behaviour. *Proceedings of the Royal Society B: Biological Sciences, 205*, 475–488. https://doi.org/10.1098/rspb.1979.0080

McCormack, J. E., Jablonski, P. G., & Brown, J. L. (2007). Producer–scrounger roles and joining based on dominance in a free-living group of Mexican jays (*Aphelocoma ultramarina*). *Behaviour, 144*, 967–982. http://www.jstor.org/stable/4536491.

Miranda, G. H. B., & Faria, D. S. (2001). Ecological aspects of black-pincelled marmoset (*Callithrix penicillata*) in the cerradão and dense cerrado of Brazilian Central Plateau. *Brazilian Journal of Biology, 61*, 397–404. https://doi.org/10.1590/S1519-69842001000300008

Morand-Ferron, J., & Giraldeau, L.-A. (2010). Learning behaviorally stable solutions to producer–scrounger games. *Behavioral Ecology, 21*, 343–348. https://doi.org/10.1093/beheco/arp195

Morand-Ferron, J., Varennes, E., & Giraldeau, L.-A. (2011). Individual differences in plasticity and sampling when playing behavioural games. *Proceedings of the Royal Society B: Biological Sciences, 278*, 1223–1230. https://doi.org/10.1098/rspb.2010.1769

Morand-Ferron, J., Wu, G.-M., & Giraldeau, L.-A. (2011). Persistent individual differences in tactic use in a producer–scrounger game are group dependent. *Animal Behaviour, 82*, 811–816. https://doi.org/10.1016/j.anbehav.2011.07.014

Oliveira, P. E. A. M., & Paula, F. R. (2001). Fenologia e biologia reprodutiva de plantas de matas de galeria. In J. F. Ribeiro, C. E. L. Fonseca, & J. C. Sousa-Silva (Eds.), *Cerrado: Caracterização e recuperação de matas de galeria* (pp. 303–332). Brasília: Embrapa, CPAC.

R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org.

Robinette, R. L., & Ha, J. C. (2001). Social and ecological factors influencing vigilance by northwestern crows, *Corvus caurinus*. *Animal Behaviour, 62*, 447–452.

Steudel, K. (2000). The physiology and energetics of movement: Effects on individuals and groups. In P. A. Garber, & S. Boinski (Eds.), *On the move: How and why animals travel in groups* (pp. 9–23). University of Chicago Press.

Vickery, W., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., & Chapman, C. A. (1991). Producers, scroungers and group foraging. *American Naturalist, 137*, 847–863. https://www.jstor.org/stable/2462404.

Vilela, S. L., & Faria, D. S. (2004). Seasonality of the activity pattern of *Callithrix penicillata* (Primates, Callithichidae) in the cerrado (scrub savanna vegetation). *Brazilian Journal of Biology, 64*, 363–370. https://doi.org/10.1590/S1519-69842004000200023

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

Appendix

Table A1
Number of individuals of each study group participating in each experimental session

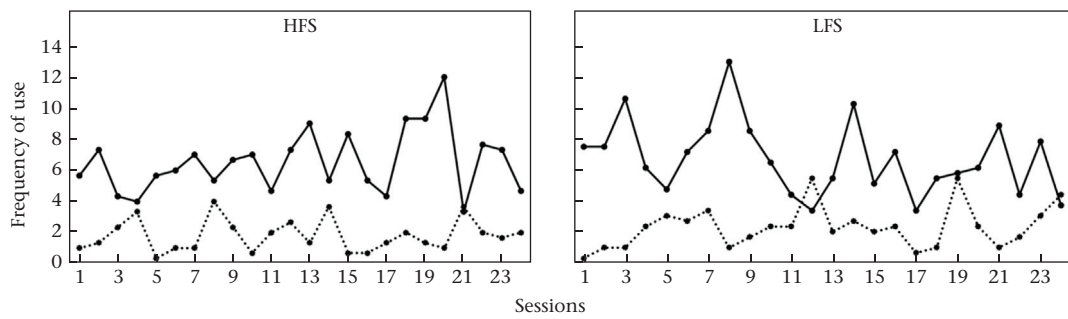| Number of individuals	Number of sessions			Total number of sessions	% Sample
	Group 1	Group 2	Group 3		
7	0	0	50	50	30
6	3	14	7	24	15
5	21	25	1	47	29
4	12	10	1	23	14
3	10	4	1	15	9
2	3	2	0	5	3
Total number of sessions	49	55	60	164	100

Figure A1. Mean frequency of use of the producer (continuous lines) and scrounger (dotted lines) strategies by three focal individuals, one of each group, of the high finder's share (HFS) and low finder's share (LFS) experimental conditions. This figure was based on 24 sessions per condition to allow calculating the mean frequency of all study groups for each session.