Memory and amount of reward in the modulation of spider monkeys' foraging decisions[1,2]

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Abstract

Temporal Weighting Rule (TWR) is a mathematical model used to predict foraging decisions based firstly on recency and secondly on the quality of a patch (amount of food). The objective of this study was to investigate whether those variables modulate the decisions of spider monkeys (*Ateles geoffroyi*) using a foraging task. Sixteen adult individuals completed a series of three experiments where they had to recover a reward from one of three containers that simulated foraging patches. The first experiment showed that spider monkeys prefer higher quality patches over recently visited patches. The second experiment showed that spider monkeys take the total amount of reward into account, not the amount of reward per trial. Finally, in the third experiment, the data showed that spider monkeys do not choose patches based on effort, but on quality. We concluded that spider monkeys choose a patch based firstly on quality, and secondly on recency, contrary to what is proposed by the TWR. Additionally, the quality values of the patches are stored globally, and they remember the quality and location of patches for periods as long as 24 hrs, which implies the involvement of a long-term memory process.

Key words: *Memory, recency, foraging, quality, decision making*

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Resumen

La Regla de Peso Temporal (RPT) es un modelo matemático que predice las decisiones de forrajeo basado en la recencia con que se han visitado y la calidad de las parcelas de forrajeo (cantidad de alimento). El objetivo de este estudio fue investigar si estas variables modulan las decisiones de monos araña (*Ateles geoffroyi*) en una tarea de forrajeo. Dieciséis individuos adultos completaron una serie de tres experimentos donde debían recuperar alimento de uno de tres contenedores que simulaban parcelas de forrajeo. El primer experimento mostró que los monos araña prefieren las parcelas con mayor calidad sobre las parcelas visitadas recientemente. El Segundo experimento mostró que los monos araña toman en consideración la cantidad total de recompensa y no la cantidad de recompensa que reciben en cada ensayo. Finalmente, en el tercer experimento, los datos mostraron que los monos araña no eligen una parcela basándose en el esfuerzo que realizan para conseguir el alimento, sino en la cantidad de alimento que consiguen en cada parcela. Se concluye que los monos araña eligen parcelas de forrajeo basándose en la calidad de la parcela y posteriormente en la recencia de la visita, lo cual contrasta con lo propuesto por la RPT. Adicionalmente se puede concluir que los monos araña almacenan la información de la calidad de las parcelas de forma global y son capaces de recordar esta calidad y donde se localiza la parcela por periodos de 24 hrs, lo que implica un proceso de memoria a largo plazo.

Palabras clave: *Memoria, recencia, forrajeo, calidad, toma de decisiones*

Introduction

Research on foraging has emphasized the role of ecological and physiological variables on the selection of items that are part of the diet and the foraging patches of primates and other animal species (Chapman et al., 2012). Examples of these studies are those that involve food availability (Chaves & Bicca-Marques, 2016), the effect of secondary compounds of food items (Glander, 1982), and the chemical and mechanical properties of food items (Berthaume, 2016), among others.

A mathematical model called temporal weighting rule (TWR) has been proposed to explain choices based on the recent memory and the quality of the patch (Devenport & Devenport, 1993; Devenport & Devenport, 1994; Devenport, Patterson, & Devenport, 2005). Recency is an effect on memory related to the order in which information is presented and means that information at the end of a series or recently presented information is more easily recognized or recalled (Bolhuis & Van Kampen, 1988). The quality of a patch is estimated as the average value of the food ingested or the reward available in a patch, which decays over time and is calculated using the following formula (Devenport, Hil, Wilson, & Ogden, 1997; Devenport et al., 2005):

$$V_w = \{\Sigma\ [Qi(1/Ti)]\}/[\Sigma(1/Ti)]$$

V_w represents the value of the patch, Qi is the quality of the patch, and Ti is the time since the patch was visited. Imagine a hypothetical case of four trials in which an animal visits a patch every 30s, and after an interphase interval (IPI) of 30s, the animal visits another patch for the same amount of trials at the same rate. At the end of these visits, the animal has to wait 30s to decide in which patch to forage again. For this example, the animal eats a piece of food of the same quality in each patch in every visit.

In this situation we have to calculate the value of each patch, beginning with the effect of time (Ti) on the pieces of food that our hypothetical animal received in every visit. First, we have to consider that the first visit was a long time ago, so we have to take into account three ITIs from the first patch (90s), plus the IPI (30s), the three ITIs from the visits to the second patch (90s) and the time to decide (30s). This gives us a total amount of 240s. Each subsequent visit, the time is less since it is closer to the decision point, as Table 1 shows. Qi $(1/Ti)$ is calculated by dividing the quality of the patch in each visit by the amount of time since the food was consumed (1/240 = 0.0041), and adding the values together (Patch A= 0.0215, Patch B= 0.0694).

Table 1

Outcomes of the patches and TWR

Patch A

Trial	T1	T2	T3	T4	$\Sigma[Qi(1/Ti)]$
Qi	1	1	1	1	
Ti	240	210	180	150	
$Qi(1/Ti)$	0.00416667	0.0047619	0.00555556	0.00666667	0.0211508

Patch B

Trial	T5	T6	T7	T8	$\Sigma[Qi(1/Ti)]$
Qi	1	1	1	1	
Ti	120	90	60	30	
$Qi(1/Ti)$	0.00833333	0.01111111	0.01666667	0.03333333	0.06944444

Note: The Qi of every trial is 1, which means that the animal eats a piece of food with the same characteristics in every visit. Ti (in seconds) reduces in time as the time approaches the decision point. $\Sigma[Qi(1/Ti)]$ represents the sum of the values, which decays over time.

The second part of the equation $[\Sigma(1/Ti)]$ is calculated using the sum of the time since the beginning of the experience with each patch until the decision point. For Patch A, the sum is 240s, and for Patch B, 120s as Table 2 shows. We divide both parts of the equation to calculate the value of a patch (V_w).

Table 2.

Subjective value at the time of decision

	Patch A	Patch B
$\Sigma\ [Qi(1/Ti)]$	0.0211508	0.06944444
$\Sigma(1/Ti)$	240	120
Vw	0.000081	0.000578

Finally, for the decision moment we compare the relative values of the patches using the following equation (Devenport et al., 2005):

$$V_{wB}= V_{wB}/\ (V_{wA} + V_{wB})$$

$$V_{wB} =0.000578\ /\ (0.000081+0.000578)$$

$$V_{wB} = 0.87$$

The result is V_{wB}= 0.87. Since the total value of the patches is equal to 1, we can calculate V_{wA} by subtracting V_{wB}. (V_{wA} = 1-V_{wB}). If the value falls outside of the indifference zone (greater than 0.40, but less than 0.60), the animal will choose the patch with the grater relative value (Devenport et al., 1997).

In the case that the decision has to be made after a longer period of time, like 24hrs later, we have to add that time to the *Ti,* So T1: $Ti = 210 + 86400$, T2: $Ti = 180+ 86400$, T3: $Ti = 150 + 86400$…T7: $Ti = 30+ 86400$, T8: $Ti= 86400$. Under these circumstances, the relative values at the decision moment $[V_{wB}= V_{wB}/ (V_{wA} +V_{wB})]$ will be $V_{wB}=0.5$ *and* $V_{wA}=0.5$, which means that both patches fall in the indifference zone following the rule of Devenport et al. (1997).

TWR does not explain how animals keep track of information about patches (outcomes, subjective values, and spatial position), but the evidence points to the use of a memory process. TWR assumes that the value of patches decays over time (Devenport & Devenport, 1993; Devenport & Devenport, 1994), similar to memory decay (Kraemer & Golding, 1997), and during experiences with patches, the organism has to remember how to get there, how much food they consumed there, and when to go there. Previous experiments have shown that TWR can predict the foraging decisions of carnivores (Devenport & Devenport, 1994), granivores (Devenport & Devenport, 1993), and grassland herbivores (Devenport et al., 2005), but this rule has not been tested on animals with frugivorous habits. Based on this, spider monkeys are ideal for testing TWR since fruits are the key component of their diet (Rimbach et al, 2014).

Spider monkeys (*Ateles geoffroyi*) are Neotropical primates that live in large groups and their foraging strategies include fission-fusion dynamics which increase the probability of finding fruits in heterogeneous environments (González-Zamora et al., 2009; Rimbach et al, 2014, Pinacho-Guendulain & Ramos-Fernandez, 2017). They feed mainly at the canopy, and fruits compose around 20 - 90% of their diet, which means that their feeding habits can be described as frugivorous (González-Zamora et al., 2009; Rimbach et al, 2014), and food items are chosen based on their nutritional content (Laska, Hernández-Salazar, & Rodriguez-Luna, 2000). However, research about how information is processed and stored for future foraging decisions is still scarce. The objective of this study was to test how well TWR can predict the foraging decisions of spider monkeys in a series of three experiments using a foraging task that varies the amount of reward and the delay to recover the reward.

Experiment 1

Since TWR was able to predict foraging decisions in animals with different feeding habits based on recency and quality, the objective of this experiment was to test whether TWR can predict the foraging decisions of a frugivorous species like the spider monkey using the design of a previous experiment with horses (Devenport et al., 2005).

Method

Individuals

We worked with 16 adult individuals (*Ateles geoffroyi*), eight females and eight males. The individuals were divided into four groups with two males and two females per group ($n = 4$). All of the individuals were living in captivity in a reserve managed by the Instituto de Neuroetología. The age range of the individuals at the moment of the experiment was from 6 to 20 years old ($\mu =11.43$, ± 3.63 years). The experiments followed the guide for the care and use of laboratory animals (National Institutes of Health Publication no. 86-23, revised, 1985), and we have a license from the Mexican government (SEMARNAT 09/GS-2132/05/10).

During the experiments, the monkeys were not deprived of food or water and their diet was based on fruits, vegetables, and leaves to satisfy their nutritional requirements. The monkeys were not physically restricted to do the task and could abandon the experiment at any moment.

The spider monkeys lived in pairs and interacted with other individuals that lived in adjacent enclosures. The size of each enclosure was 8 x 4 x 4 m (l, w, h). The walls of the enclosure were made of chain-link fencing that allowed the individuals to look outside and to move their arms, legs, and tail outside their enclosure. The individuals were previously trained to stay at the fence in front of the researcher and interact with different objects such as containers and absorbent papers (Laska, Hernández-Salazar, & Rodriguez-Luna, 2003), water bottles (Larsson, Maitz, Hernández-Salazar, & Laska, 2014), and plastic tubes (Motes Rodrigo, Ramirez-Torres, Hernández-Salazar, & Laska, 2018). During the experiments, the individuals were separated by a chain-link fencing barrier to work individually, and after the experiment ended, the individuals were reunited again. The pair of individuals was always the same and the individuals were not able to change partners.

Materials

We used a 50 cm apparatus with three plastic containers, each with a metal lid. The containers were held in a specific spatial position and had a specific color (white, gray, or black), as Figure 1 shows. The containers were distributed pseudo-randomly between the three spatial positions. This distribution of colors was presented to all the individuals and never changed during this experiment. We used cereal (Cheerios®) as a food reward.

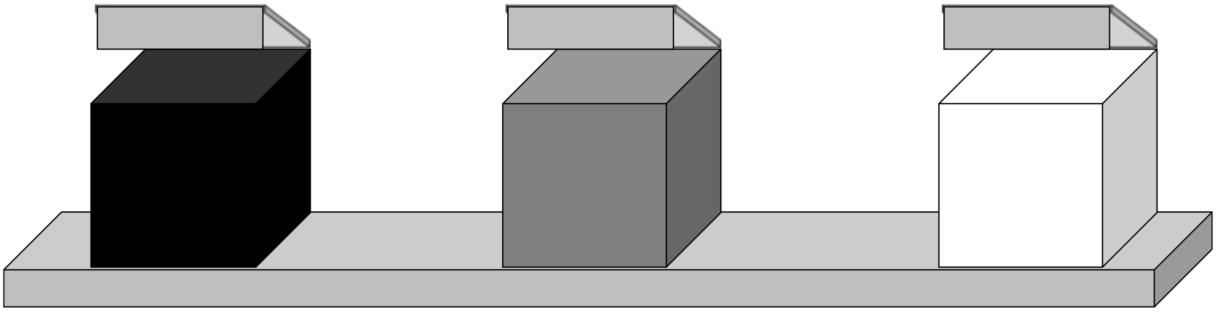

Figure 1. Design of the apparatus employed with the monkeys during Experiment 1. Each container had a distinct color and the order of the containers stayed constant during Experiment1. The plastic containers were 6 x 6 x 6 cm (l, w, h) and had an inner space of 5.5 x 5.5 x 1 cm (l, w, d). The distance between the central container and the lateral containers was 10 cm. A similar apparatus with two containers was used previously in olfactory experiments with our spider monkeys (Laska, et al., 2003).

Procedure

We used a 2 x 2 factorial design with the variables a) amount of reward (1 piece of cereal vs 4 pieces of cereal), and b) delay of the single-trial test (0-hr and 24-hr). The groups were named G1, G2, G3, and G4; and four monkeys (two males/two females) were pseudo-randomly assigned to each group. Table 3 shows the groups and the conditions of the task.

Table 3

Experiment 1 design

Group	**Condition**	P1	P2	**Delay**
G1	A = B	A+ B- C-	A- B+ C-	0-h
G2	A = B	A+ B- C-	A- B+ C-	24-h
G3	A > B	A++++ B- C-	A- B+ C-	0-h
G4	A > B	A++++ B- C-	A- B+ C-	24-h

Note. The signs (+/-) represent the presence or absence of reward and the number of signs represents the number of cereal pieces per trial.

The experiment was divided into two phases of eight trials each (P1 and P2) and a single-trial test at the end of the second phase (Devenport et al., 2005). The monkeys' task was to retrieve a reward from a container on the apparatus by opening the containers and looking inside. In both phases, the ITI was 30s, the interval between phases was 60s and the interval between subjects was 3 min. In each phase, one container was selected pseudo-randomly and called A or B respectively, and the food reward was placed in those containers during each phase: in A during P1 and in B during P2. Groups G1 and G2 received the same amount of reward in both phases (one piece of cereal per trial), while groups G3 and G4 received four pieces of cereal per trial during P1 and one piece of cereal during P2. Half of the monkeys did the single-trial test 30s after the end of the experimental phases (0-hr delay [G1 and G3]) and the other half did the test 24 hrs after (G2 and G4).

We followed several control procedures during the experiment. 1) The containers were baited outside of the monkeys' views using the back of the researcher to block the baiting process. After that, the researcher turned and showed the apparatus to the individuals. 2) To avoid the spider monkeys using odor cues to solve the task, the apparatus was presented approximately 20 cm outside of the monkeys' enclosures, held by the researchers. This prevented the monkeys from sniffing the apparatus and forced them to use their hands to open the containers and solve the task. 3) The sound of the baiting process was not a cue since the spider monkeys did not have the information necessary to match a specific sound with a specific container.

We recorded latencies to retrieve the reward and which container was opened first during the trials in each phase. The trial ended when the monkey opened all of the containers. We repeated this procedure until we completed all the trials in both phases. During the single-trial-test we followed the baiting process outside of the monkeys' views, doing the movement as if we had been baiting a container, but no reward was hidden in the containers. We recorded which container was opened first during the single-trial-test, following the procedure used in previous experiments (Devenport & Devenport, 1993; Devenport & Devenport, 1994; Devenport et al., 200).

During the experiment, one container was never baited (container C) and worked as a control in the experiment. If an individual opened container C during the single-trial-test, this showed that the individual solved the task with strategies not related with recency or quality of the patch, such as random selection of a patch.

TWR predicts this distribution of selections during the single-trial-test: a higher percentage of the monkeys in G1 and G3 should choose container B (recency), the individuals in G2 should choose indifferently between containers A and B (same quality), and a higher percentage of G4 individuals should choose container A (higher quality). TWR also predicts that none of the individuals should choose container C since this container was never baited (Table 4).

Results and discussion

We calculated the mean of the latencies of the trials for each of the four groups and the SEM. Figure 2 shows that the latencies were shorter as trials progressed and there was an increase when the phase changed because some individuals looked in container A first. The reduction in latency has been taken as an index of learning since the monkeys opened the container with the reward faster (Devenport & Devenport, 1993; Devenport & Devenport, 1994; Devenport et al., 2005).

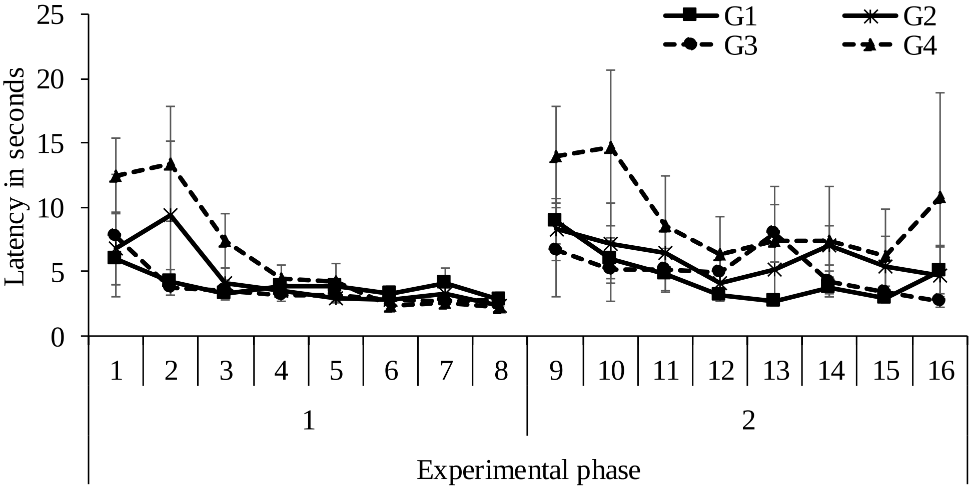

Figure 2. Mean latencies and the SEM of the groups to find the hidden reward in relation to the trials. The spider monkeys took more time to find the reward during P2 since at the beginning of P2 the individuals opened container A first, but after 4 to 6 trials the individuals opened the new container first.

We compared the latencies of the phases with a paired-samples Wilcoxon test for each group in the statistical software R (V. 3.6.1). The results did not show significant differences in the distribution of latencies between P1 and P2 for G1 ($Z = 9$, $p = 0.25$, $r= 0.40$), G2 ($Z = 4$, $p = 0.058$, $r = 0.66$), or G3 ($Z = 4$, $p = 0.05,4$ $r = 0.67$), only for G4 ($Z = 0$, $p = 0.007$, $r = 0.94$).

The spider monkeys made mistakes opening other containers without the reward first. Table 4 shows, in E_{P1} and E_{P2}, in how many trials the spider monkeys opened other containers without the reward first. The number of mistakes was smaller during P1(E_{P1}) than during P2(E_{P2}). Even if the spider monkeys did not open the correct container on the first attempt, they were allowed to open the other containers until they found the reward. In this sense, the experience with the reward was similar in both phases since they could always open all of the containers and retrieve the reward, acquiring the information about the quality of the containers during each phase of the process.

Table 4.
Predictions of TWR and decisions of the spider monkeys during Experiment 1

Group	*Monkey*	*Sex*	E_{P1}	E_{P2}	V_{wA}	V_{wB}	*Prediction*	*Decision*
G1	PAULINA	F	2	6	0.0956	0.9044	B	B
	MAG	F	3	5	0.0956	0.9044	B	B
	NETO	M	4	4	0.0956	0.9044	B	A
	NERY	M	3	5	0.0956	0.9044	B	B
G2	CAMILA	F	3	6	0.4985	0.5015	I	B
	GRUÑON	M	5	6	0.4985	0.5015	I	A
	LLUVIA	F	3	5	0.4985	0.5015	I	B
	BRUTUS	M	3	4	0.4985	0.5015	I	A
G3	PATAS	M	2	4	0.2972	0.7028	B	A
	KIKA	F	4	5	0.2972	0.7028	B	B
	FRIDA	F	4	5	0.2972	0.7028	B	A
	CEJITAS	M	3	6	0.2972	0.7028	B	A
G4	MARY	F	4	5	0.799	0.201	A	A
	SORUYO	M	4	6	0.799	0.201	A	B
	YAYO	M	2	4	0.799	0.201	A	A
	CHABELA	F	4	4	0.799	0.201	A	A

Note. In the column *Sex*, "F" indicates the females and "M" the males. E_{P1} and E_{P2} show in how many trials the monkeys opened containers other than the one with the reward first. V_{wA} and V_{wB} represent the subjective values of the patches at the moment of selection. The "I" in the prediction column indicates indifference between patches since they have a similar value and means that the individual could choose any container since both have the same value.

Concerning the single-trial test, we can see in Table 4 that TWR was able to predict the choices for 3 out of 4 groups. In the case of G3, TWR predicted that the individuals should choose container B (recency), but 75% of the individuals chose container A, the one with higher quality. None of the individuals chose container C during the test, which indicates that the individuals remembered the containers and their qualities, and the spider monkeys chose only the containers where the reward had previously been hidden, avoiding container C. Since none of the spider monkeys chose container C, the data indicates that they do not choose by chance. The data from Table 4 indicate that the spider monkeys preferred higher quality patches over those recently visited. The spider monkeys differed significantly from TWR since the model assumes that recency is more important than quality (Devenport & Devenport, 1993; Devenport & Devenport, 1994; Devenport et al., 1997; Devenport et al., 2005).

Experiment 2

The data from Experiment 1 showed that spider monkeys prefer containers with higher quality over recently visited ones, and do not choose containers by chance. However, during Experiment 1, two groups received a total amount of reward and a reward per trial four times higher during P1 than in P2. In the literature, the total amount of reward (Williams & Royalty, 1989) and the structure of trials play a key role in decision-making (Alvarado, Jara, Vila, & Rosas, 2006). Therefore, it is important to test whether spider monkeys choose a patch based on the total amount of reward or the amount of reward per trial.

Method

Individuals

Sixteen adult spider monkeys (Ateles geoffroyi), the same as in Experiment 1, participated in this new experiment. The individuals were pseudo-randomly distributed into four groups (G1, G2, G3, and G4) with two males and two females per group, establishing groups with different individuals from the ones in Experiment 1.

Materials

We used a 50 cm apparatus with three containers that were oriented vertically to make this apparatus different from the one used in Experiment 1 and to prevent the individuals using the previous configuration to solve the task. The containers and their colors were the same as in Experiment 1, and as in the previous experiment, the configuration of the apparatus was the same for all of the individuals and the position of the colors never changed during the experiment (Figure 3). As in the previous experiment we used cereal (Cheerios®) as a reward.

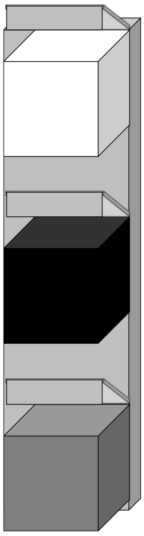

Figure 3. Apparatus design used in Experiment 2. Every container had a color and the order stayed constant during the experiment, as in Experiment 1.

Procedure

The procedure had two phases and a single-trial test, as in Experiment 1. A 2 x 2 factorial design was used with the variables: a) amount of trials during P1 (16 and 32 trials), and b) delay of the single-trial test (0-hrs and 24-hrs), as Table 5 shows. All of the individuals received one piece of cereal per trial and the total amount of reward depended on the number of trials per phase. In this experiment, half of the individuals completed 16 trials and the other half completed 32 trials during P1. All the individuals completed 8 trials during P2, and at the end of this phase they completed the single-trial-test, half of the individuals 0-hrs and half 24-hrs after the last trial. As in Experiment 1, we recorded the latencies to find the reward during each trial and which container was opened first. The procedures and experimental controls were the same as in Experiment 1. This experiment started 60 days after Experiment 1.

TWR predicts the following choice distribution during the single-trial-test: a higher percentage of the individuals in G1 & G3 should choose container B, and a high percentage of individuals in G2 & G4 should choose container A (Table 6). If the individuals choose a patch based on the total amount of reward, all monkeys should choose container A, but if the individuals choose a patch based on the local rates of reward, all of the groups should be indifferent to containers A and B. All three predictions propose that none of the individuals should open container C.

Table 5
Experiment 2 design

Group	Trials P1	Trials P2	Delay
G1	32	8	0-h
G2	32	8	24-h
G3	16	8	0-h
G4	16	8	24-h

Note. The individuals received one piece of cereal in each trial and the total amount of reward depended on the number of trials per phase.

Results and discussion

The mean latencies decreased as the trials progressed, but increased during the change of phases (Figure 4). We ran a paired Wilcoxon test in R (V. 3.6.1) comparing the latencies from P1 and P2. This analysis showed statistically significant differences only for G1 ($Z = 0$, $p = 0.007$, r = 0.94) and G4 ($Z = 0$, $p = 0.007$ $r = 0.94$), but not in the other groups (G2 [$Z = 5$, $p = 0.078$, $r = 0.62$]; G3 [$Z = 7$, $p = 0.148$, $r = 0.51$]).

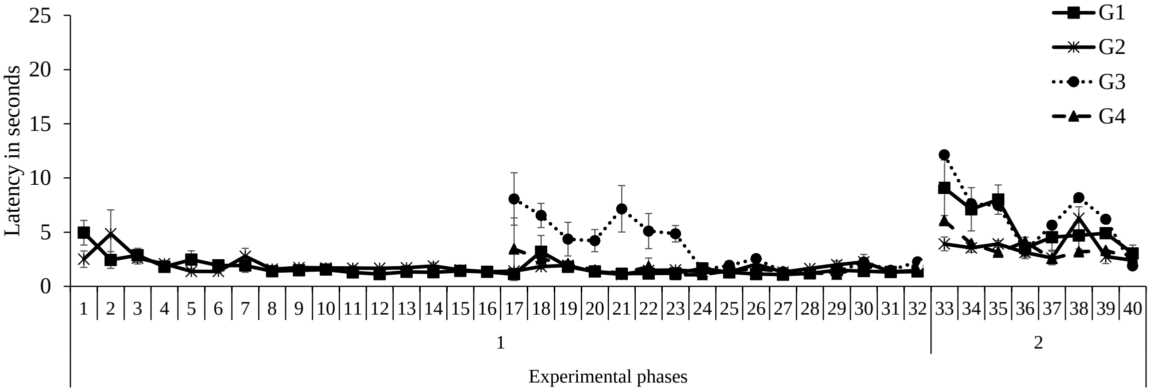

Figure 4. Mean latencies and the SEM of the groups to find the hidden reward in relation to the trials. The spider monkeys took more time to find the reward during P2, since at the beginning of P2 the individuals opened container A first, but after 2 to 5 trials the individuals opened the new container first. Since G3 & G4 did only 16 trials during P1, these are shown starting with trial 17.

As in Experiment 1, the individuals made some mistakes during P1 and P2, opening containers without the reward before the one with the reward, as Table 6 shows (E_{P1} and E_{P2}), but after a few trials, all of the individuals opened the container with the reward first. During P1 and P2, the monkeys opened all of the containers during each trial, which gave them the information about the outcome of each container.

Table 6

Predictions of TWR and decisions of the spider monkeys during Experiment 2

Group	*Monkey*	*Sex*	E_{P1}	E_{P2}	V_{wA}	V_{wB}	*Prediction*	*Decision*
G1	MARY	F	3	5	0.0956	0.9044	B	A
	MAG	F	3	4	0.0956	0.9044	B	A
	PATAS	M	2	3	0.0956	0.9044	B	A
	CEJITAS	M	2	3	0.0956	0.9044	B	A
G2	YAYO	M	2	4	0.7971	0.2029	A	A
	NERY	M	1	4	0.7971	0.2029	A	B
	KIKA	F	3	2	0.7971	0.2029	A	A
	PAULINA	F	4	4	0.7971	0.2029	A	A
G3	GRUÑON	M	4	3	0.1041	0.8959	B	A
	SORUYO	M	3	5	0.1041	0.8959	B	A
	CHABELA	F	3	5	0.1041	0.8959	B	A
	CAMILA	F	2	2	0.1041	0.8959	B	B
G4	NETO	M	3	3	0.6643	0.3357	A	A
	FRIDA	F	3	4	0.6643	0.3357	A	A
	BRUTUS	M	4	3	0.6643	0.3357	A	A
	LLUVIA	F	3	3	0.6643	0.3357	A	A

Note. In the column *Sex*, "F" indicates the females and "M" the males. V_{wA} and V_{wB} represent the subjective values of the patches at the moment of selection. E_{P1} and E_{P2} show in how many trials the monkeys opened containers other than the one with the reward first.

Concerning the single-trial test, the data from Table 6 show a preference in all groups (14 of 16 monkeys) for the higher quality container (A). In the case of G1 and G3, TWR predicts a preference for the recently visited container (B), but almost all of the individuals chose the higher quality one. As in Experiment 1, none of the individuals chose container C, which implies that spider monkeys used the qualities of the containers to choose between them. The data suggest that spider monkeys take the total amount of reward into account, not the amount of reward per trial, and remember this information for at least 24 hrs. The preference for the higher reward option has been reported previously in other primates like chimpanzees, capuchin monkeys, and humans (Proctor et al., 2014) which could imply a general preference across primates.

Experiment 3

Optimal Foraging Theory (OFT) proposes that animals optimize their foraging efforts to maximize the number of resources acquired with a low investment of energy (Reynolds, 2012; Blanchard & Hayden, 2015). Experiments 1 and 2 showed that spider monkeys prefer higher quality patches over recently visited ones. Based on this, it is important to assess what happens when both patches have the same overall quality, but in one of the patches, they need to do more trials to obtain the same total amount of reward. The objective was to investigate whether spider monkeys are sensitive to the effort they expend for each reward.

Method

Individuals

We worked with 16 adult spider monkeys (*Ateles geoffroyi*). The individuals were the same as in Experiments 1 and 2 and were pseudo-randomly assigned to four groups (G1, G2, G3, and G4) with two males and two females, establishing groups with different individuals from the ones in Experiment 1 and 2.

Material

We used a three-container apparatus with a triangle shape. We changed the array of containers, as in Experiment 2, to make it different from the apparatus used in previous experiments and to prevent the individuals from using the previous configurations to solve the task. As in the two previous experiments, the containers were distributed pseudo-randomly to the different spatial positions and the configuration of colors was the same for all the individuals through the entire experiment (Figure 5). The containers had the same measurements as in previous experiments, but the distance between containers was 15 cm. We used Cheerios® as a reward.

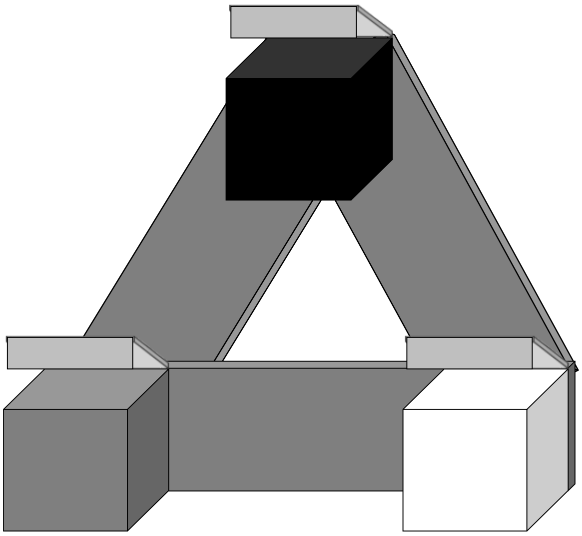

Figure 5. Apparatus design for Experiment 3.

Procedure

We used a 2 x 2 factorial design (Table 7). The variables were: a) amount of reward per trial (one or two pieces) and b) delay of the test (0-hr and 24-hr). G1 and G2 received one piece of cereal per trial during P1 and two pieces during P2. G3 and G4 received two pieces of cereal per trial during P1 and one piece during P2. G1 and G3 did the test with a 0-hr delay, and G2 and G4 did the test with a 24-hr delay. For all groups, the total amount of reward per phase was 16 pieces of cereal. We followed the same procedures and controls during the trials and the single-trial-test that were used previously in Experiments 1 and 2. This experiment began 45 days after Experiment 2.

TWR predicts this distribution of selections during the single-trial-test: a higher percentage of the individuals in G1 and G3 should choose container B (Recency), while the individuals in G2 and G4 should choose indifferently between containers (Table 8). If the spider monkeys choose patches based on the quality, the prediction indicates that the individuals of all groups should be indifferent between patches since both patches have the same value. If the individuals choose a patch based on optimization, the individuals in G1 and G2 should chose container B (greater reward per trial), while the individuals in G3 and G4 should choose container A (greater reward per trial). As in previous experiments, the predictions propose that none of the individuals should open container C.

Table 7
Experiment 3 design

Group	Trails P1	Trials P2	Delay
G1	16 $_{(1)}$	8 $_{(2)}$	0-h
G2	16 $_{(1)}$	8 $_{(2)}$	24-h
G3	8 $_{(2)}$	16 $_{(1)}$	0-h
G4	8 $_{(2)}$	16 $_{(1)}$	24-h

Note. The number in brackets represents the pieces of cereal per trial. All of the groups received the same number of cereal pieces in both experimental phases.

Results and discussion

The mean of the latencies showed the reduction tendency of the previous experiments (Figure 6). We ran a paired-samples Wilcoxon test in R (V. 3.6.1) and this test showed statistically significant differences in the latencies for G2 ($Z = 36$, $p = 0.007$, $r = 0.94$), but not for the other groups (G1 [$Z = 4$, $p = 0.05469$, $r = 0.67$]; G3 [$Z = 26$, $p = 0.3125$, $r = 0.35$] and G4 [$Z = 8$, $p = 0.195$, $r = 0.45$]).

In relation to the mistakes opening the containers without the reward first, the individuals made fewer mistakes (E_{P1} and E_{P2}) compared with the previous experiments. The mistakes increased during P2 compared with P1, but after 2 to 4 trials, they started to open container B first (Table 8).

In Table 8, the data show that during the single-trial test, half of the individuals in three groups (G1, G3 & G4) chose container A and half chose container B. In G2, a higher percentage of the individuals chose container B (recency). The data show again that spider monkeys take the total amount of reward into account when they have to choose between patches since a higher percentage of the monkeys did not systematically choose the container that gave two rewards per trial. Spider monkeys can remember the quality of a patch even if this quality is determined in only eight trials.

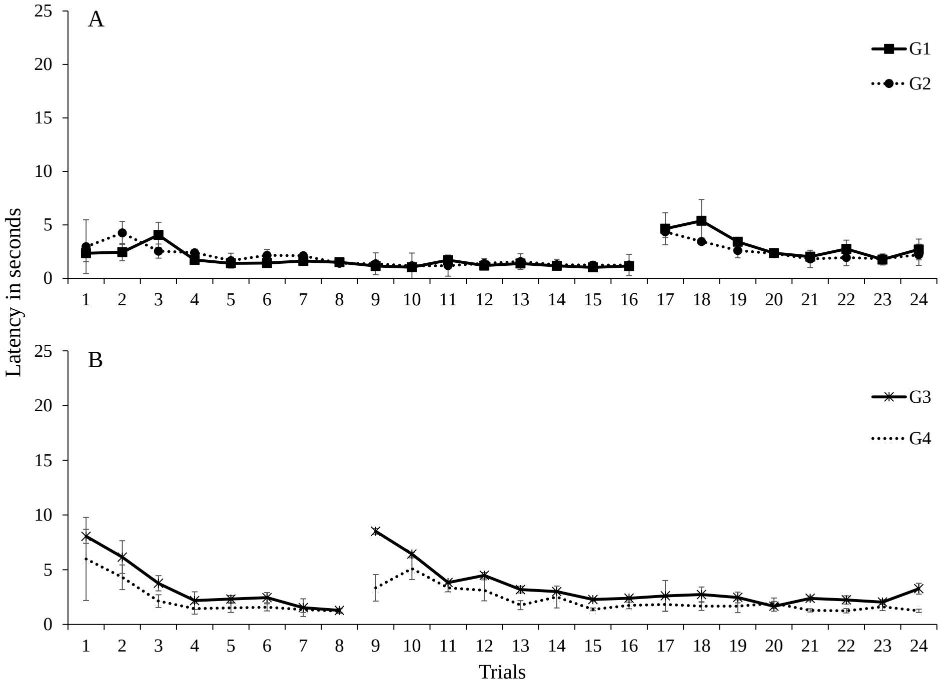

Figure 6. Mean latencies and the SEM of the groups to find the hidden reward in relation to the trials. The spider monkeys took more time to find the reward during P2 since at the beginning of P2 the individuals opened container A first, but after 2 to 4 trials the individuals opened the new container first. A) For G1 and G2 P2 started at Trial 17; B) for G3 and G4 P2 started at Trial 9.

Table 8

Predictions of TWR and decisions of the spider monkeys during Experiment 3

Group	*Monkey*	*Sex*	*EP1*	E_{P2}	V_{wA}	V_{wB}	*Prediction*	*Decision*
G1	CHABELA	F	3	3	0.0549	0.9451	B	B
	LLUVIA	F	1	4	0.0549	0.9451	B	A
	GRUÑON	M	2	2	0.0549	0.9451	B	A
	SORUYO	M	2	3	0.0549	0.9451	B	B
G2	NETO	M	3	4	0.4974	0.5026	I	A
	MARY	F	2	2	0.4974	0.5026	I	A
	YAYO	M	2	3	0.4974	0.5026	I	A
	FRIDA	F	2	2	0.4974	0.5026	I	B
G3	PAULINA	F	4	4	0.2696	0.7304	B	B
	CAMILA	F	3	5	0.2696	0.7304	B	B
	NERY	M	3	3	0.2696	0.7304	B	A
	BRUTUS	M	1	3	0.2696	0.7304	B	A
G4	PATAS	M	2	2	0.4984	0.5016	I	B
	MAG	F	3	3	0.4984	0.5016	I	A
	KIKA	F	2	3	0.4984	0.5016	I	B
	CEJITAS	M	3	3	0.4984	0.5016	I	A

Note. In the column *Sex*, “F” indicates the females and “M” the males. V_{wA} and V_{wB} represent the subjective values of the patches at the moment of selection. The “I” in the prediction column indicates indifference between patches since they have a similar value. E_{P1} and E_{P2} show in how many trials the monkeys opened containers other than the one with the reward first.

The results of this experiment and Experiment 2 indicate that spider monkeys are not sensitive to the amount of effort and choose between patches based on the total amount of reward. None of the spider monkeys chose container C during the single-trial-test. TWR was able to predict the choices of only two groups; in this sense, the model is not a good predictor of the foraging decisions of spider monkeys.

Since in the first two experiments the data show the spider monkeys' preference for the patches with higher quality, we performed a generalized linear mixed model analysis (GLMM) to analyze the relationship between recency and quality in the three experiments using the statistical software R (V. 3.6.1). To fit the model, we used the library *lme4* and the function *glmer,* and we calculated the r^2 values using the library *r2glmm*. The fixed effects were recency and quality, and the random effect was the monkeys in the experiment. P-values were obtained by the maximum likelihood approach, and the test was run under a binomial distribution. The results of this analysis show a significant but small effect of the quality (Z = -1.895, p = .058, r^2 = .102), but not the delay (Z =.441, p = .659, r^2 = .015). The random effects results show that fixed effects were modulated by the monkeys *(SD* = 1.63), which means that some monkeys preferred patches visited recently.

General discussion

Our data from the three experiments suggest that spider monkeys choose patches based on their quality and the recency of information, but the quality is more important than recency, which contrasts with TWR (Devenport & Devenport, 1993; Devenport et al., 1997; Devenport et al., 2005). The data from the GLMM also show this preference for quality, but also indicate that some monkeys will choose a patch based on recent information. For example, one of our individuals (Camila) systematically chose the more recent container during all three experiments, and four other monkeys (Nery, Paulina, Kika, and Soruyo), chose the more recent container in two out of three experiments as the TWR model predicts.

Under natural conditions (Felton et al., 2009) and in experimental settings (Laska et al., 2000), spider monkeys have shown a preference for items with high nutritional content (like sugar, protein or fat). The preference for high-quality options based on the results of Experiments 2 and 3 showed that most of the spider monkeys maximize the outcomes but do not take into account the rate of rewards earned in each trial, which implies that the individuals do not optimize their choices as the OFT proposes (Reynolds, 2012; Blanchard & Hayden, 2015), suggesting that other variables play a role during decision making.

The preference for higher quality options is a characteristic reported previously in other species like rodents, pigeons, and humans using time discounting tasks (Vandervel et al., 2006). In these three species, high-reward options are preferred over low-reward since the subjective value of the higher reward options can be maintained over longer periods (Green et al., 1997; Mazur, 2000). Experiments on decision-making have shown that capuchin monkeys (*Cebus apella*) display the endowment effect (Lakshminaryanan et al., 2008), or estimate quantities based on past experiences (Beran et al., 2012), in a similar way to humans. These studies indicate that the characteristics of decision-making are shared by primates, even in those less related to humans, like New World monkeys, and the processes and mechanisms are likely shared among primates. This opens the possibility of studying the evolutionary roots of decision-making in species like spider monkeys

Besides TWR and the OFT, one alternative to explain how spider monkeys choose between foraging patches is the Marginal Value Theorem (MVT) which assumes that as an organism forages in a patch, its value decreases over time since resources are limited. Once the value is marginal, the organism leaves the patch and begins to forage in another place (Charnov, 1976; Zimmerman, 1981; Wajnberg et al., 2000). The problem with this theorem is that it assumes that the organisms should optimize their decisions to maximize the outcomes decreasing the cost, but the data from our experiments show that the spider monkeys chose patches to maximize their outcome but not to reduce the cost.

Another alternative to explain the foraging decisions of spider monkeys could be the Ideal Free Distribution Theory (IFD) which explains foraging decisions for resources dispersed across different patches, and the goal of the organisms is to maximize the energy income and reduce the competition (Tyler & Hargrove, 1997; Matsumura, Arlinghaus, & Dieckmann, 2010). Based on our data, the foraging choices of spider monkeys could be explained by the IFD theory since 1) our data suggest that spider monkeys choose a patch to maximize the outcome; 2) spider monkeys use strategies of fission-fusion to increase the probability of finding food items (Pinacho-Guendulain & Ramos-Fernandez, 2017), and 3) the fission-fusion dynamics reduce the competition between spider monkey individuals (Asensio, Korstjens, Schaffner, & Aureli, 2008). Future experiments will clarify how well IFD theory predicts foraging decisions since our experiments were not designed to test the predictions of IFD.

Concerning memory, previous research on free ranging animals has shown that spider monkeys can remember and use foraging routes for periods longer than 6 years (Di Fiore & Suarez, 2007; Valero & Byrne, 2007). The long-term memory capacity of spider monkeys is not limited to foraging. Other studies show that spider monkeys use sleeping trees to rest during the night; the sleeping trees are visited every day at dusk, and the spider monkeys have to travel from where they are to the sleeping trees, which implies that the spider monkeys remember the location of the trees (Gonzalez-Zamora et al., 2012). With reference to our data, the three experiments indicate that spider monkeys have a long-term memory capable of keeping track of the location and the quality of the patches in the apparatus for periods as long as 24 hrs.

In our study, the total number of spider monkeys that participated is large (*N = 16*) compared to many other primate studies (Schwartz, Hoffman, & Evans, 2005; Basile, Hampton, Suomi, & Murray, 2009; Heyselaar, Johnston, & Pare, 2011), but the number of individuals per group was small (*n = 4*). This increases the effect of each individual on the group, where each monkey represents 25% of the data in a group. Even with this limitation, our data show a clear tendency towards higher quality patches.

One major concern in our experiments was the carryover effect in the individuals since we worked with the same monkeys during all three experiments. To decrease this effect, we conducted the experiments with a long pause between each one, with 60 days between Experiment 1 and Experiment 2, and 45 days between Experiment 2 and Experiment 3. Another control was the shape of the apparatus in each experiment. The different shapes made it impossible for the individuals to use the spatial location of the reward in previous experiments to find the reward in the new one. Finally, the combination of colors for Phases 1 and 2 was selected to avoid the individuals using color as a cue. For example, if the individuals had to find the reward in white and gray containers during Experiment 1, they had to find the reward in black and white containers during Experiment 2, and gray and white containers during

Experiment 3. The combination of these three controls decreases the probability of carryover effects and increases confidence in our data.

Based on the behavior of the spider monkeys and the conditions of the task, we believe that the individuals did not use olfactory cues to solve the task since they were not allowed to sniff the containers to identify the contents. The apparatus was presented outside of the monkeys' enclosure at a distance far from their noses, which made it difficult for the monkeys to use the odor of the reward as a cue. Sniffing behavior has been tested before with this species (Laska et al., 2003; Nevo et al., 2015), and the behaviors associated with sniffing (movements of the nose muscles and air inhalation) were not expressed by the monkeys during the task. Other cues like the sound of the containers could be associated with the reward, but since the individuals were not allowed to see the baiting process, they were not able to recognize what the precise sound of each container was in order to use that as a cue for which container to open.

Another concern was that the spider monkeys did not have enough trials in the phases to remember the outcomes of the patches, but previous work with other animals like squirrels (Devenport & Devenport, 1994), dogs (Devenport & Devenport, 1993), rats (Devenport et al., 1997), horses (Devenport et al., 2005), and human children (Alvarado, Juarez, Cabrera, Strempler, & Vila, 2012) has used a similar number of trials per phase. This suggests that eight trials were enough to acquire information about the patches' outcomes. During all three experiments, the spider monkeys opened all of the containers during each trial of the experiment, which allowed the individuals to learn the outcomes of the containers in each phase. Another point that confirms that there were enough trials is that the individuals never opened container C during the single-trial test. This shows that they remembered the containers and their outcomes, which was very clear during Experiments 1 and 3. In Experiment 1, the individuals that received a higher amount of reward in container A for eight trials opened that container during the single-trial-test even when they had to wait for 24 hrs. In the case of Experiment 3, most of the groups divided their choices between containers even with only eight trials of experience, since both containers gave the same total amount of reward.

Our data also show that the individuals learned where to find the reward since their latencies were smaller as the trials progressed. This trend occurred in both phases of the experiments. During Phase 2, some individuals opened Container A first (which held the reward in Phase 1), but also container C which indicates that the spider monkeys were not only looking for where the reward was hidden based on previous information but also, they were upgrading their information about the new location in this phase. After a few trials, the monkeys acquired information about the new location of the reward and began to open container B first. These data also show that eight trials were enough for the monkeys to learn the outcomes of the containers.

In conclusion, TWR is not capable of precisely predicting the different choices of spider monkeys when there are different qualities since it is the quality of a patch, not the recency, that is the most important variable for choosing between patches. Spider monkeys' memories store the quality of the patches based on the total amount of food consumed and the location of the patches, storing the information in the long-term memory.

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