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"The effect of different food rewards on performance in a string-pulling task and subsequent theft avoidance in Japanese macaques (*Macaca fuscata*)"

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# Abstract

Getting food rewards is a common motivation for animals to participate in experimental studies. The type of food reward might further be of relevance for performance in a task. I confronted a group of ~150 semi-free living Japanese macaques (*Macaca fuscata*) with a string-pulling task for the first time. When a single string is pulled the bottom of the installed apparatus collapses and releases two rewards. Throughout the test sessions I used six distinct combinations of low-, medium- and high- valued food as rewards. I tested the monkeys within their social group and did not hinder their access to the apparatus at any time, thus creating a producer-scrounger situation. The monkeys‘ efficiency in solving the task improved with time. Additionally they developed strategies to increase their pay-off and prevent thievery. Successful individuals left significantly more pieces of low-valued food items than high-valued ones and stopped participating for a low-valued reward. Hence the findings of this study indicate that low-valued food rewards might prevent monopolization. Thus it allows inexperienced individuals access and the chance to participate, whereas subsequent motivation in experienced individuals only remains in response to high-valued rewards.

# Zusammenfassung

Tiere, die in kognitiven Experimenten Aufgaben lösen, werden meist mit Futter belohnt. Die Art des Futters könnte einen Einfluss auf die Motivation und die Performance der Tiere haben. In der vorliegenden Masterarbeit habe ich eine Gruppe semi-freilebender Japanmakaken (*Macaca fuscata*) mit einem “string-pulling” Problem konfrontiert. In einer Hütte mitten im Affengehege wurde eine Box installiert, deren Falltüren sich öffneten und zwei Futterstücke freigaben, wenn ein Affe an einem Seil zog. Die beiden Futterstücke waren zufällige Kombinationen aus sehr (Banane, Ananas, Orange), mittel (Apfel) und wenig (Karotte) beliebtem Futter. Die Tiere wurden nicht von ihrem sozio-ökologischen Umfeld getrennt und zu keiner Zeit daran gehindert die Hütte zu betreten. Dadurch entstand eine “producer-scrounger” Situation, in der erfolgreiche Individuen einen Teil oder sogar die ganze Belohnung an andere Affen verlieren konnten. Die Japanmakaken lösten die Aufgabe mit der Zeit immer effizienter, d.h. sie benötigten weniger Züge am Seil, um die Belohnung zu bekommen. Zusätzlich entwickelten sie Verhaltensstrategien, um Diebstahl der Belohnung zu vermeiden. Erfolgreiche Individuen ließen signifikant öfter wenig beliebtes Futter zurück und verweigerten schließlich die Teilnahme am Experiment, wenn kein hoch präferiertes Futter in der Box war. Dies lässt vermuten, dass die Verwendung von wenig präferiertem Futter eine Monopolisierung durch einzelne Individuen verhindert und dadurch unerfahrenen Affen die Möglichkeit gibt den Apparat zu erkunden und die Aufgabe zu lösen. Hoch präferiertes Futter bewahrt hingegen das Interesse von erfahrenen Individuen am Experiment.

# Introduction

Animal Cognition is a rapidly growing field, with more than 5800 papers (based on a Web of Science search) covering this topic in the last decade only. Cognitive abilities in animals are commonly tested by confronting the animals with tasks that require some sort of solution, in order to get a reward. Usually pieces of food are used as such rewards. Surprisingly it does not seem to be a major concern which food to use, since the choice is rarely discussed in the literature. If comments are given they mostly concern the animals‘ motivation. Hence highly preferred food is mainly used to capture the animals’ attention and get them to participate in the given task. A broad variation of food rewards can be found in the literature including different kinds of fruit (e.g. Albiach-Serrano, Bugnyar, & Call, 2012; Cronin, Kurian, & Snowdon, 2005), nuts (e.g. Visalberghi, Quarantotti, & Tranchida, 2000) and even sweets such as caramel or chocolate (e.g. Brosnan et al., 2009). However, apparently no study has investigated whether differently preferred food influences motivation and thus individual performance in a given task. This is surprising since research about inequity aversion shows that animals may react negatively after an unequal distribution of food rewards, when considering quantity but also quality of food. Negative reactions can be rejection of the reward and unwillingness to participate in further trials (Brosnan & de Waal, 2003). Furthermore, such reactions are more likely to occur after animals solved a task in comparison to receiving a food item without a task beforehand (reviewed in Brosnan & de Waal, 2014). Such inequity aversion considers a social comparison of one’s own reward with that of someone else and has received quite some attention lately. The influence of reward quality on the performance in a task of just a single individual, however, remains relatively understudied.

Furthermore, the majority of previous studies on reward-driven tasks were conducted under laboratory conditions. Here, motivation via certain highly preferred food might be less of an issue than it is when testing animals in their natural habitat. Even more so if they have not been confronted with an experimental task before, unlike regularly tested animals. Using only highly preferred food in field conditions, where animals are not separated during testing, may lead to monopolization of the task by single individuals.

Nevertheless, testing animals in their natural species-typical social group has several positive aspects. Keeping the environment as natural as possible during testing may be essential for learning and cognitive performance (Drea, 2006). Moreover, only such ecologically valid and psychologically informed experiments can truly shed light on the

proximate mechanisms and evolution of a certain behaviour (McAuliffe & Thornton, 2015). For example, isolating an individual from its group may increase (or decrease, see Stocker et al., 2016) its stress level and consequently not only influences the results, but also the animal's welfare (Olsson & Westlund, 2007). Despite their positive aspects, cognitive studies in a social setting are currently in the minority, but their number is steadily increasing (Cronin et al., 2017). There are of course difficulties that have to be faced when testing animals in field conditions. When participating in a task is optional, motivation is essential. Previous studies did not consider the influence of differently preferred food on motivation in a social setting. Yet, testing different kinds of food may be beneficial in such a situation as it could serve to minimize aggression and to motivate inexperienced individuals to participate in a task – especially in despotic groups, where the risk of monopolization by single (high ranking) individuals is high.

To investigate which food rewards can be used in a study in a social group setting, I tested a semi-free living group of ~150 Japanese macaques (*Macaca fuscata*), a highly despotic non-human primate species (Thierry, 2000) in a string-pulling task. String-pulling tasks have a very long history, with the first studies conducted over a century ago (Hobhouse, 1915; Kinnaman, 1902; Köhler, 1925; Shepherd, 1910, 1915). An object of desire (e.g. food) is placed out of reach, but a physical connection to reach it (e.g. an attached string) is offered. Variations of this task have since been used with different approaches in at least 163 mammal and bird species (reviewed in Jacobs & Osvath, 2015) and recently even in insects (Alem et al., 2016). Besides birds (e.g. Heinrich & Bugnyar, 2005; Hofmann, Cheke, & Clayton, 2016; Schuck-Paim, Borsari, & Ottoni, 2009; Seibt & Wickler, 2006; Taylor et al., 2010; Werdenich & Huber, 2006), primates are most commonly studied in such string-pulling tasks (e.g. (Anikaev, Chalyan, & Meishvili, 2015; Halsey, Bezerra, & Souto, 2006; Harlow & Settlage, 1934; Molina & Mimó, 2017). The majority of these studies used captive animals, and only a few were conducted in the field (e.g. Molesti & Majolo, 2016). The group of Japanese macaques tested in the present study were not confronted with any experimental task before and received food provision on a daily basis. Hence, capturing their interest on the task via highly preferred food rewards was essential. To test whether food quality has an effect on the motivation, less preferred food items entered the experiment as well. Less preferred food may get rejected by experienced individuals and consequently may prevent monopolization by these individuals. The food items (provided in different combinations and in a random order) were placed in a transparent box (c.f. Visalberghi et al., 2000) to enable visual inspection of the reward. A trapdoor in this box could be opened by pulling a string, making the reward accessible for the monkeys.

The setup, installed in the middle of the monkeys‘ 40 000 m² enclosure, allowed free access to the bowl with the reward from all sides. Together with testing in the natural group setting this open setup may promote thievery, and therefore creates a producer-scrounger situation. The producer-scrounger paradigm describes two different strategies to obtain resources. Producers invest time and energy to search for resources themselves, whereas scroungers exploit the investments of aforementioned producers by watching them and using the same food source. In social animals scrounging food is widely spread and considered to be almost universal (Aplin & Morand-Ferron, 2017). If producing resources is accompanied with higher costs, more individuals adopt the scrounger strategy (Barrette & Giraldeau, 2006; Giraldeau, Soos, & Beauchamp, 1994; Morand-Ferron, Giraldeau, & Lefebvre, 2007). In larger groups a higher frequency of scrounging can be sustained (Coolen, 2002), although the effect of group size is weak (Afshar & Giraldeau, 2014). Since this study was conducted in a large group of individuals and obtaining the food reward is connected with some effort, I expected high levels of scrounging behaviour. However, this should not necessarily prevent social learning of producing (Aplin & Morand-Ferron, 2017).

Japanese macaques are known for their social learning and passing on (both vertically and horizontally) behaviors like washing sweet potatoes (Kawai, 1965), forming snowballs (Eaton, 1972) and stone handling (Huffman & Quiatt, 1986). These behaviours have been picked up and spread among a number of individuals in a troop and are considered as pre-cultural (Whiten & van Schaik, 2007). I therefore expected individuals in this study to learn by watching other individuals solve the task.

In conclusion, the present study investigates the willingness to participate in a string-pulling task of a group of semi-free ranging Japanese macaques (*Macaca fuscata*), who were never confronted with any comparable experiment before. I investigated their motivation and performances during the task in response to differently preferred food items used as a reward. Moreover, given the open character of the task, I also investigated the different strategies, be it producer or scrounger, used by different animals. Specifically, I focused on (i) which monkeys showed interest in the task, (ii) how their performance in the task developed over time and (iii) whether experienced animals developed certain behavioural strategies to cope with thievery.

I developed the following predictions:

- Female monkeys show more interest in the task than male ones, due to females tendency to concur for resources, rather than mates like males do, for successful reproduction (Fedigan, 1983).

- The monkeys' performance gets better with time, i.e. they
    - need fewer pulls to open the box
    - look into the box more often to evaluate the food reward
    - pull more often if the box is filled than when it is empty
    - wait before participating and consequently prevent thievery
- Experienced monkeys react to differently valued rewards, i.e. they
    - leave low-valued rewards more often than high-valued ones
    - stop participating for low-valued rewards
- Monkeys show more aggression when a high-valued reward is stolen than when it is a low-valued one.

# Material and Methods

## Study Site and Animals

The study was conducted at the Affenberg Landskron, Austria (GPS: 46.643°, 13.899°) - a park that houses ~150 semi-free living Japanese macaques (*Macaca fuscata*) in a 40 000 m² enclosure. The population originates from 39 monkeys, which were relocated from a wild troop in Osaka prefecture, Japan (GPS: 34.693°, 135.502°) in 1996. The Affenberg is open to visitors from the beginning of April until the end of October. During this time groups of visitors are guided through the park via defined pathways. Physical interactions, such as feeding or touching the animals, are prohibited. Two thirds of the enclosure remain inaccessible to visitors, giving the monkeys the chance to avoid humans. Food is provided twice a day by the animal care staff and consists of wheat, different kinds of vegetables and fruits. Additionally the vegetation of the park allows foraging for e.g. leaves, seeds and insects. During data collection the park housed 151 individuals living in one group. The group consisted of 64 adult females, 32 adult males, 19 sub-adult males, 26 juveniles and 10 infants. Following the classification of Takahata (1980) and Wolfe (1978) females were considered adult over the age of 3.5 years, and males over 8.5 years as soon as they reached socio-sexually maturity. The term „sub-adult males“ refers to physiologically matured individuals over the age of 4.5 years. Juveniles range from one to three years and infants include all individuals born in the year under investigation (< 1 year). All monkeys were individually identifiable on a visual basis. The monkeys had never before been confronted with a string-pulling task. The present study followed a voluntary approach (for more details see section “Experimental Setup”) and was therefore of non-invasive nature.

## Experimental Setup

For research purposes a wooden hut was built inside the enclosure. The hut’s four doorways on two opposite walls were always open, giving the animals free access and the possibility to leave at all times (Figure 1). During a four-month pilot study the monkeys were familiarized with the building and the setup (for details see section „Experimental Procedure“).


*Figure 1: The wooden hut inside the monkeys' enclosure housing the experimental apparatus has four doorways, which remained open at all times, giving the monkeys the possibility to enter and leave at all times.*

For the current study, an apparatus was installed inside the hut, that allowed the animals to perform a string-pulling task with food items as reward (c.f. Köhler, 1925). The top of the apparatus consisted of a transparent box with a lockable lid, through which the rewards were placed inside (Figure 2). A rope was fixed to two wire ropes leading through copper pipes to one metal latch on each side of the box (Figure 3). Pulling the rope strong enough would release the latches and subsequently led the wooden bottom of the transparent box to collapse. This bottom consisted of two trap doors, which dropped sideways against the wooden frame resulting in a specific noise (which could attract other individuals in the vicinity). The rewards inside the transparent box would then fall into a wooden bowl (Figure 2). The monkeys could approach the box and bowl from all four sides, making monopolization of the reward difficult, but not impossible.

*Figure 2: The apparatus consists of a transparent box at the top in which the food reward is filled and a bowl underneath into which the reward drops after the rope in front is pulled. The apparatus is accessible from all sides.*

*Figure 3: The opening mechanism consists of two metal latches on each side. Here the left one is in the "closed" position and the right one in the "open" position.*

Three cameras were installed inside the hut, two on opposite walls at each side of the box and one wide-angle camera beneath the bowl, which had a transparent bottom (Figure 4). Recordings were aligned and merged using Blender (www.blender.org; version 2.77) and avconv (www.libav.org; version 11.5), to allow watching all three views simultaneously.

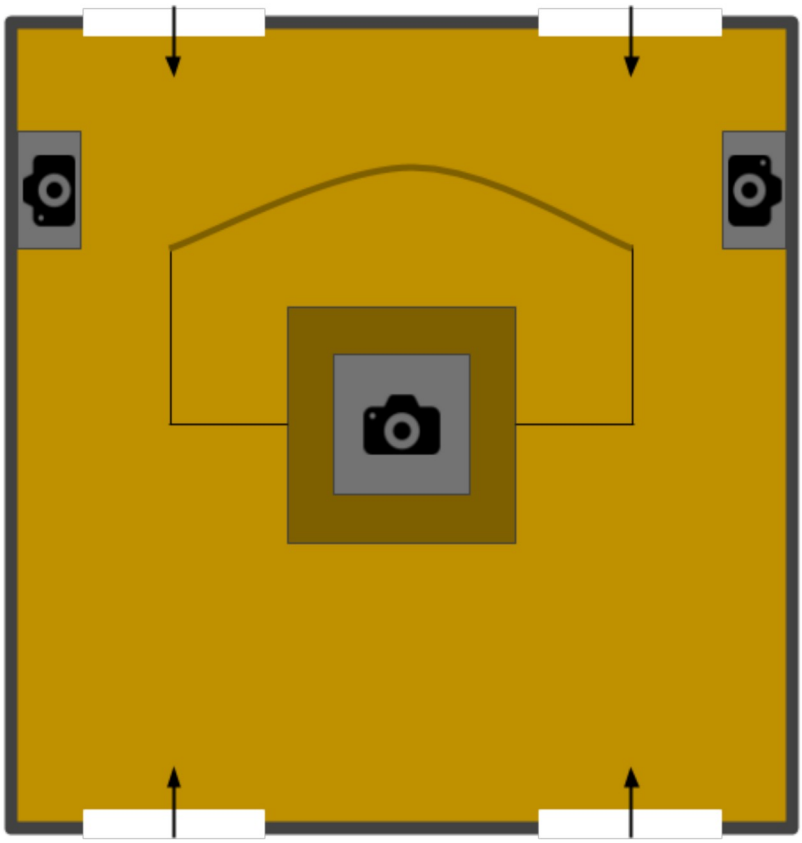

*Figure 4: A sketch of the hut and the apparatus inside. The camera symbols show the positions of the three used cameras. Arrows indicate the openings in the hut through which the monkeys could enter and exit at all times. The bent brown line indicates the rope.*

## Food Rewards

Three differently valued fruits and vegetables familiar to the animals were used as reward. Carrots entered the experiment as low-valued reward and bananas, pineapples and oranges as high-valued reward. The latter three were changed regularly to maintain their high status and prevent satiety. Green apples as medium-valued food represented an intermediate. Preferences were tested regularly by presenting various monkeys (especially those interested in the experiment) with two different pieces of food and noting which they took and ate first. All food pieces were cut to equal size to prevent preferences based on size of the reward. Furthermore, I ensured that the pieces were big enough to not fit into the monkeys'

pouches unchewed in order to avoid immediate storage of the food reward.

## Experimental Procedure

Since the monkeys were never confronted with a string-pulling task and not used to a hut, which they could access freely at all times, a habituation phase was necessary. To accustom the monkeys to the wooden hut a part of their food was placed inside and around it during feeding turns every day. To gain their interest for the apparatus the transparent box was filled with high-valued cereal pellets. After a one-month habituation phase, data collection commenced for 28 days in October and November 2016. Apart from a 14-day long break in the middle of October the maximum time gap between testing was three days. Testing started one hour after the morning feeding turn following an auditory signal, i.e. the noise the trap doors of the bottom made when the box was opened. A typical testing day started between 10:00 and 11:00 AM and lasted until 30 trials were completed. Because of the voluntary approach the duration of testing varied between 1 hour to 6.5 hours a day with on average 2.7 hours until 30 trials were completed.

I filled the box with two pieces of food using the six distinct combinations of high-, medium- and low-valued food in a random order. To achieve the same number of tests for all six combinations I balanced them over 90 trials (three days). The animals were not influenced or hindered in their interaction with each other and the box by me at any time. I refilled the box after both reward pieces had been taken out of the bowl by a monkey. I canceled a trial after 15 minutes if no monkey had been successful and none were participating at the time.

## Behavioural Variables

During each trial I recorded the behaviour of all present monkeys (Table 1). This involved those monkeys who were present inside the hut as well as those sitting in front of the four doorways within one meter distance. Behavioural data was collected with continuous focal sampling (c.f. Martin & Bateson, 1993) using a digital voice recorder and video records of the three cameras (see section “Experimental Setup”).

*Table 1: Ethogram of the recorded behaviour variables.*

| ***Variable*** | ***Definition*** |
|---|---|
| *Waiting* | *Monkey approached the apparatus, but stopped by sitting or standing in front of it or the hut for at least ten seconds before participating* |
| *Participating* | *Monkey holds the rope with one or more extremities (i.e. hand or foot) while moving it toward the body resulting in putting the rope under tension* |
| *Pulling toward the box* | *Monkey has its back to the box containing the reward while manipulating the apparatus, i.e. pulling the rope* |
| *Pulling away from the box* | *Monkey faces the box containing the reward while manipulating the apparatus, i.e. pulling the rope* |
| *Looking into the box* | *Monkey brings its eye level to the height of the transparent parts of the box either by straightening up in front of the box or lowering the head when it sits or walks on one of the joists on either side of the transparent box* |
| *Stealing the reward* | *A monkey arrives before or at the same time with the pulling individual at the bowl and takes at least one part of the reward* |
| *Leaving the reward* | *The successful monkey is the first at the bowl, but does not take both pieces of the reward (or none at all) before moving away from the bowl* |
| *Refusing to participate* | *A monkey already successful in the past leaves the hut after looking into the box without participating and without being forced to leave by another monkey* |

I recorded each pull from the moment of the first filling of the box in a session until the box was opened for the last time in the same session. This also includes the pulls happening before the box was filled again, i.e. when the box was empty in between trials. All pulls during a trial, i.e. when the box was filled with a reward, were recorded for each participating individual, i.e. each monkey that pulled the string. This resulted in a “number of pulls” for each trial for the successful individual, i.e. the monkey whose pull opened the box and released the rewards. By dividing the number of trials by the number of pulls for each day and each individual I calculated a rate of efficiency (c.f. Cronin et al., 2005). The maximum rate of efficiency was 1, meaning the number of trials equaled the number of pulls (i.e. the

monkey needed only one pull to open the box in each trial that day).

For the three variables “Looking into the box”, “Pulling toward the box” and “Waiting” I calculated a ratio for each day and each individual by dividing the number of occurrences per day through the number of trials per day. Therefore the ratios range between 0 (participating monkey didn’t show the behaviour in any trial on this day) and 1 (participating monkey showed the behaviour in each trial on that day).

For reliability analysis a subset of 15 % of the successful trials (N = 128) were analysed by a second observer familiar with the animals. All variables (Table 2) show a Cohen’s κ of more than 0.81 and are therefore categorised as (almost) perfect agreement (Landis & Koch, 1977).

*Table 2: Agreement of the behaviour variables between two observers in percent and Cohen’s κ.*

| ***Variable*** | ***Agreement in %*** | ***Cohen’s κ*** |
|---|---|---|
| *Pulling individual* | *100.0* | *1.00* |
| *Direction of the pull* | *100.0* | *1.00* |
| *Number of pulls of successful individual until opening of the box* | *90.6* | *0.81** |
| *Looking into the box before pulling* | *99.2* | *0.98* |
| *Individual who took the reward* | *98.1* | *0.96* |
| *Reward was stolen or left* | *99.2* | *0.99* |

*difference max. one pull

## Statistical Analysis

All statistical analyses were performed using IBM SPSS Statistics 24 with α set at 0.05.

To detect any relationship between age and interest for the experiment, the age of all individuals and their presence in the hut were correlated using Spearman’s Rho.

Linear Mixed Models (LMM) were used to investigate whether the rate of efficiency, “Looking into the box”, “Pulling toward the box” and “Waiting” increased or decreased over time. The rates (per day) of these behaviours were used as response variables. The number of the

testing day (1 to 28) entered the model as fixed covariate and the pulling individual as random factor.

For each sort of food reward, the number of all items left by the successful individual (see definition for leaving reward behind in “Behavioural Variables”) were divided by the total number of items of the same sort the individual was confronted with during all successful participated trials. The resulting rates for each sort of food per individual were compared pairwise with Friedman’s two factorial Anova.

To test if male and female thieves steal to different degrees a Mann Whitney U-Test with sex as the group variable was computed. A Chi-Square Test was used to determine whether thieves stole the higher valued reward more often than the lower valued reward when the box was filled with two pieces of different value.

Finally, a Generalized Linear Mixed Model (GLMM) investigated the influence of „Waiting“ on thievery. Thievery was coded binary and set as the response variable. The pulling individual entered the model as random factor.

# Results

## Descriptive overview

I found a significant negative relationship between age and presence in the experimental hut ($r_s = -0.656$, $N = 141$, $p < 0.001$; Figure 5), with younger monkeys present more frequently than older ones. Of all 141 individuals, 26 (11 males between 1 and 4 years old, 15 females between 1 and 9 years old) participated at least once, i.e. pulled the rope (not necessarily successfully though). Of these participants, ten (4 males between 1 and 4 years old, 6 females between 1 and 9 years old) succeeded at least once, i.e. opened the box. However, four of these succeeded only once, leaving six regular participants (4 females between 4 and 9 years old, and 2 males, 3 and 4 years old), whose altogether 823 trials were used for the main statistical analyses. The four adult females all succeeded for the first time already during the habituation phase, whereas the two subadult males only started to participate during the testing period (for more information see Table 3).

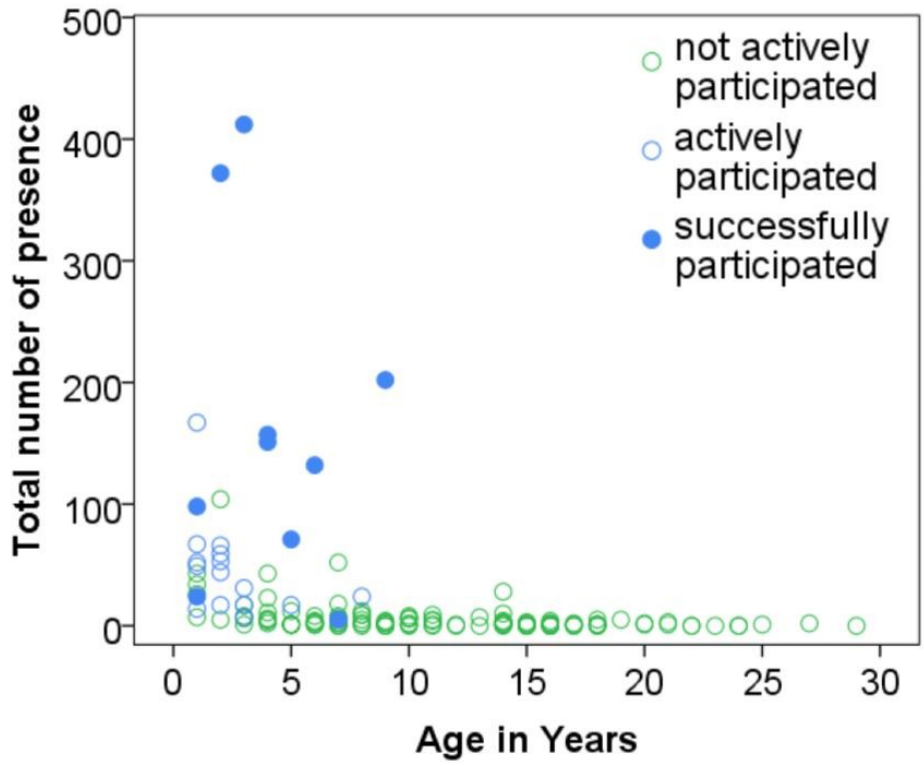


*Figure 5: Overall presence ordered by the monkeys' age. Each dot represents a single individual. Monkeys who never participated in the experiment are represented by a green circle, those who pulled the rope at least once by a blue one and those who opened the box at least once by a filled blue circle.*

*Table 3: List of regularly participating monkeys. Given are their names, sex, year of birth, day they participated for the first time and day of their first success.*

| ***Name*** | ***Sex*** | ***Year of Birth*** | ***First participation*** | ***First success*** |
|---|---|---|---|---|
| *Aladdin* | *male* | *2012* | *Day 9* | *Day 11** |
| *Alina* | *female* | *2007* | *Habituation* | *same day* |
| *Finn* | *male* | *2013* | *Day 1* | *Day 5** |
| *Jessy* | *female* | *2010* | *Habituation* | *same day* |
| *Julia* | *female* | *2012* | *Habituation* | *next day* |
| *Kate* | *female* | *2011* | *Habituation* | *same day* |

*equals his second participation day

These six individuals opened the box in nearly every trial they participated in (89.9 % - 100 %; see Table 4). On average they needed 1.8 pulls per trial (range 1 - 24). An LMM showed that the rate of efficiency increases over time (Num. Df = 1; Denom. Df = 120.5, $\beta$ = 0.0131 ± 0.003, p = 0.001, Figure 6); i.e. the number of pulls they needed to open the box decreased over time. All four female monkeys pulled more often when the box was filled than when it was empty. Both males on the other hand pulled more often when the box was empty than when it was filled (Table 4).

*Table 4: List of regularly participating monkeys. Given are their names, sex, number of successful trials and rate of success, as well as the number of pulls when the box was filled with a reward and when the box was empty.*

| ***Name (sex)*** | ***Successful trials*** | ***Successful/ Participated trials*** | ***Pulls (filled box)*** | ***Pulls (empty box)*** |
|---|---|---|---|---|
| *Aladdin (m)* | *62* | *89.9 %* | *170* | *369* |
| *Alina (f)* | *170* | *98.8 %* | *269* | *28* |
| *Finn (m)* | *302* | *98.1 %* | *518* | *943* |
| *Jessy (f)* | *111* | *100.0 %* | *130* | *22* |
| *Julia (f)* | *120* | *97.6 %* | *221* | *74* |
| *Kate (f)* | *58* | *95.1 %* | *171* | *68* |

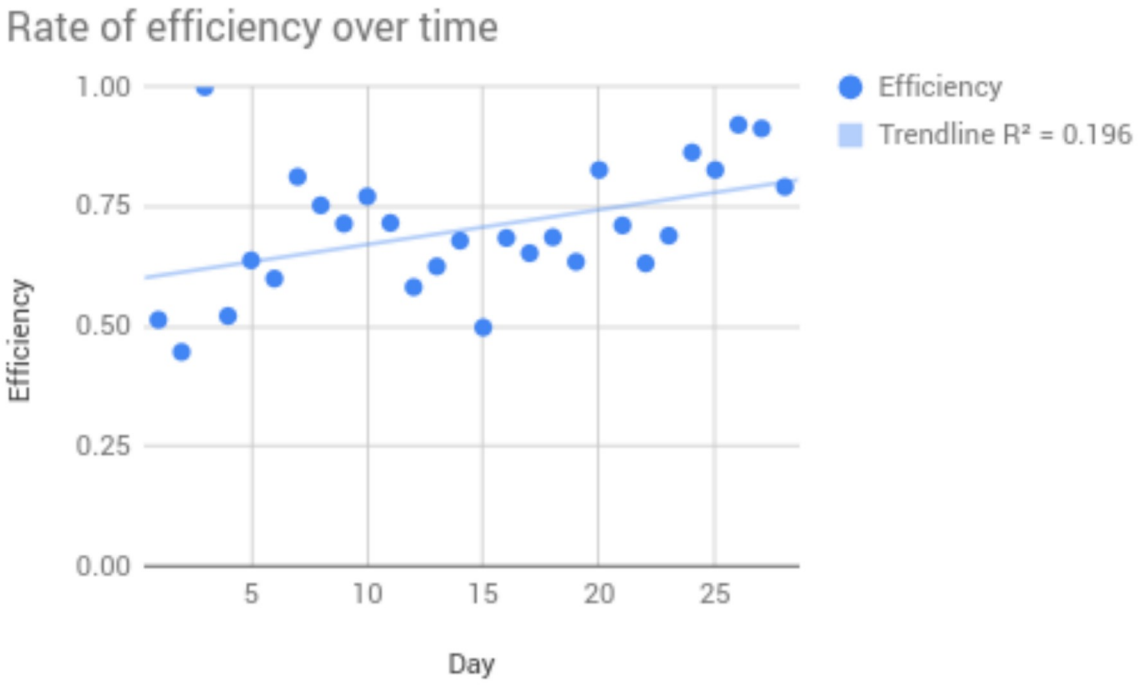


*Figure 6: The rate of efficiency averaged over all six regularly participating monkeys over the period of testing.*

Successful individuals were able to monopolize the reward in 38.8 % of all 823 cases. In 49.0 % of the cases the successful monkey got half the reward and in 12.2 % no reward at all (Figure 7). Stealing occurred in 60.5 % of the 502 cases, in which the successful individual was not able to monopolize the reward. In the remaining cases the successful monkey left part of, or even the whole reward in the bowl (Figure 8).

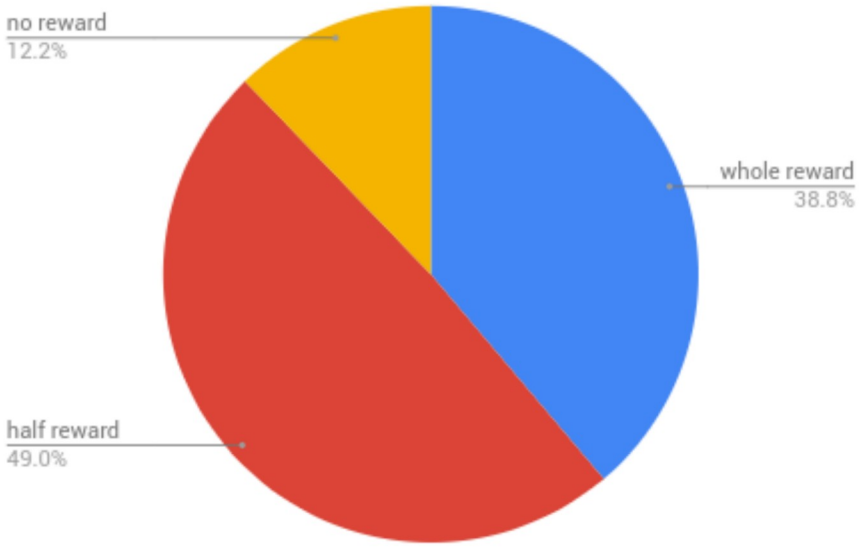


*Figure 7: Percentage of how often the successful individuals acquired the whole reward (blue), half of the reward (red) and no reward at all (orange).*

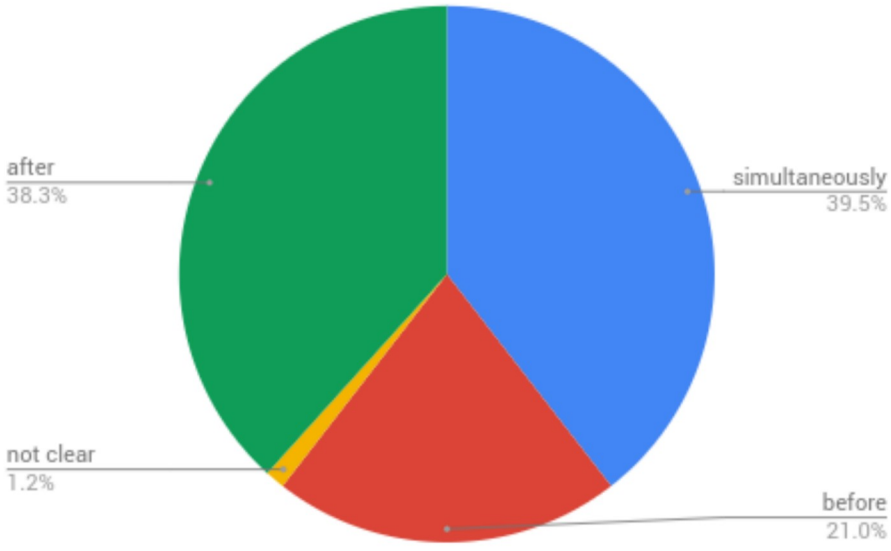


*Figure 8: Percentage of all cases in which the successful individual did not monopolize the reward. Given are how often the reward was taken by other monkeys before (red), simulatenously (blue) and after (green) the successful individual arrived at the box and when the situation was not clear (orange).*

## Behavioural Strategies

Pulling the rope toward the box rather than away from it was originally not intended. Doing so allows the successful individual to be closer to the bowl, and consequently, to the reward. The monkeys did so in 48 cases of 823. An LMM showed a trend toward an increase of using this technique over time (Num. df = 1; Denom. df = 121.7, $\beta$ = 0.0043 ± 0.002, p = 0.069, Figure 9). However, a more detailed analysis showed that half the trials with a successful pull toward the box were performed by a single individual (Figure 9). One regular participant never pulled toward the box and another only once. Therefore this seems to be a strategy mainly performed by one specific individual (Julia).

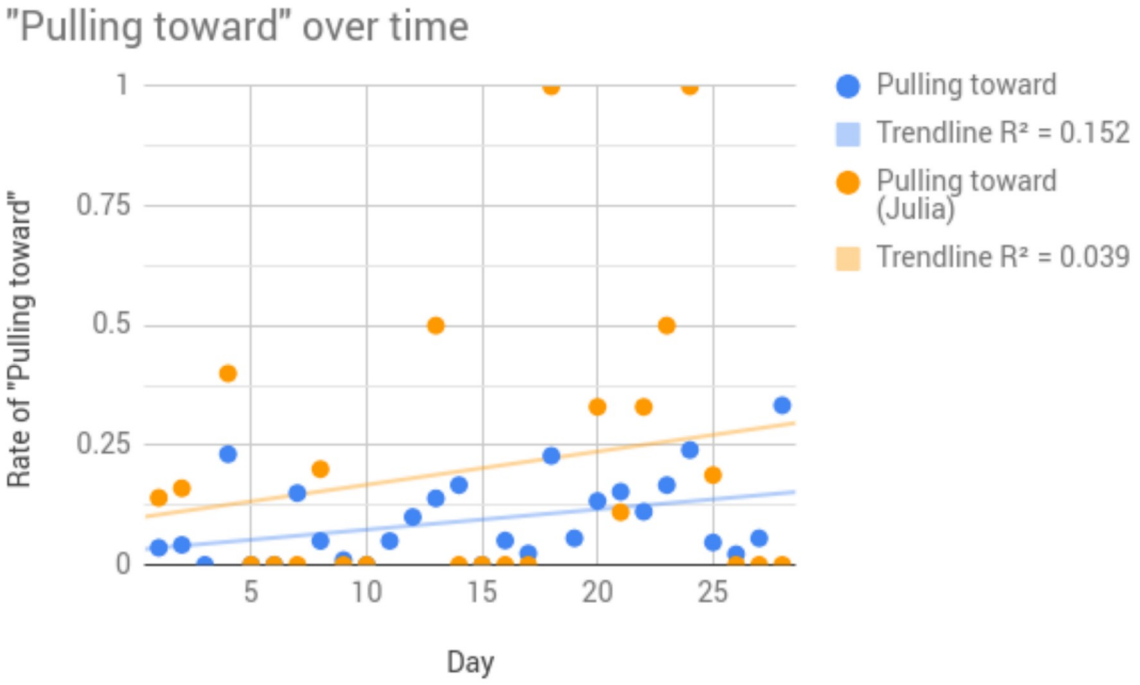


*Figure 9: The rate of pulling toward the box averaged over all six regularly participating monkeys (blue) and for a single individual (Julia, orange) over the period of testing.*

Looking into the transparent box before participating allowed the monkeys to check whether the box was filled and if so, with what kind of food rewards. Monkeys looked into the box in 34.4 % of all cases (283 of 823). An LMM showed that this behaviour increased over time (Num. df = 1; Denom. df = 119.2, $\beta$ = 0.0216 ± 0.003, p < 0.001, Figure 10). The behaviour „Waiting“ before participating occurred in 26.6 % of all cases (219 of 823) and fluctuated over time (Num. df = 1; Denom. df = 123.0, $\beta$ = 0.0018 ± 0.003, p = 0.512, Figure 11). Furthermore, a GLMM did not show an effect of this behaviour on preventing thievery ($F_{1,821}$ = 0.009, $\beta$ = 0.017, p > 0.1, Figure 12).

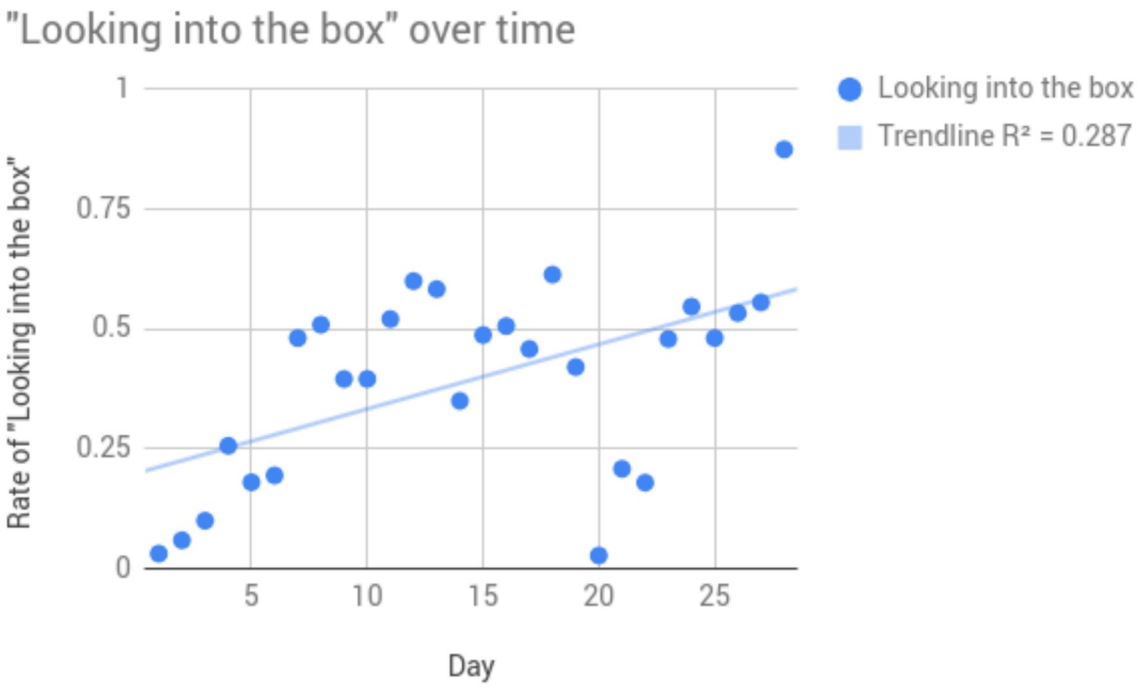


*Figure 10: The rate of „Looking into the box“ averaged over all six regularly participating individuals over the period of testing.*

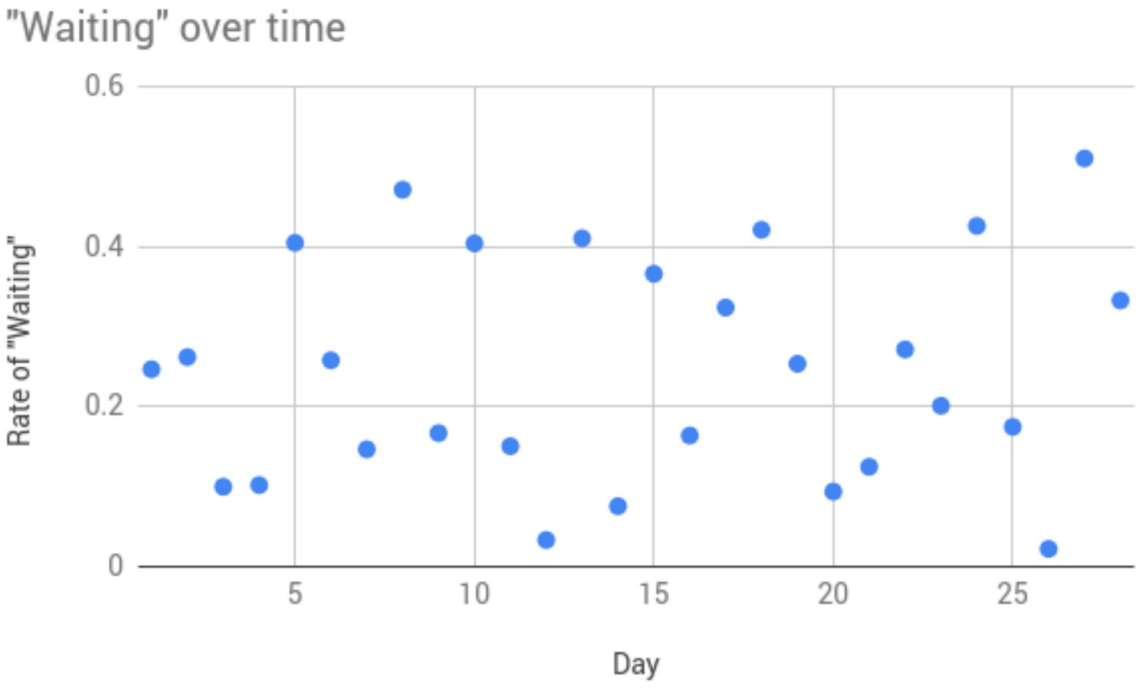


*Figure 11: The rate of „Waiting“ averaged over all six regularly participating individuals over the period of testing.*


*Figure 12: Amount of Thievery (in percent) when the participating individual waited or did not wait before participating.*

## Thievery

In total 302 cases of stealing were recorded from 42 different monkeys (21 male and 21 female, between 1 and 14 years old). Every one of the six main participants were also thieves themselves. Twenty-one of the thieves never actively participated at all, whereas 15 did so, with three of them (besides the main participants) once successfully opening the box. This results in 50 % of the thieves following solely the scrounging strategy. The other half of the thieves followed both strategies, i.e. producing and scorunging, if participating in the experiment is considered as producing irrespective of whether the monkey succeded in the trial or not. Only four monkeys solely followed the producing strategy with only one succeeding once. (Figure 13)

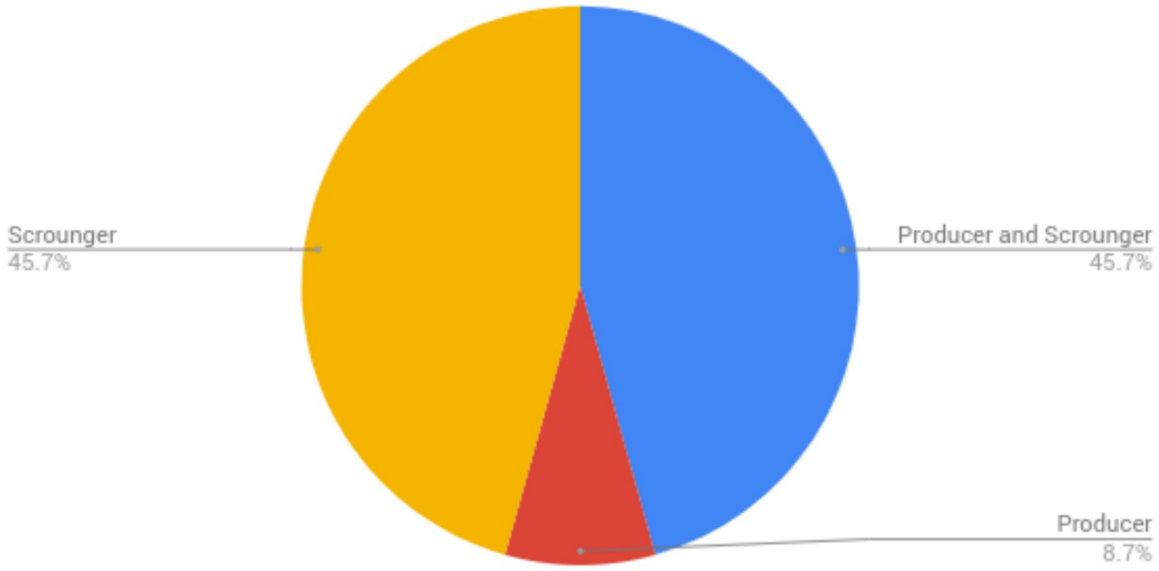


*Figure 13: Percentage of monkeys that solely followed the producing strategy (i.e. pulling the string whether successful or not and never stole a reward, red), that solely followed the scrounging strategy (i.e. never pulled the string, but stole at least one reward, orange) and that followed both strategies (i.e. pulling the string whether successful or not and stealing a reward, blue).*

Each thief stole on average in 8.1 cases (with a minimum of 1 and a maximum of 153 times). Male thieves stole with an average of 13.6 cases significantly more often than females with an average of 2.6 cases (Mann-Whitney's U = 131.0, N = 42, p = 0.021).

The six regularly participating monkeys differ greatly in how often they were subjects to thievery (Minimum of 7.2 % to a maximum of 69.4 % of their successful cases). In most cases (61.7 %) the thief was 1-2 years younger than the successful individual and they were not related (65.5 %). If the successful monkey and thief were related, they were rather siblings (20.3 %) than parent or offspring (13.6 %).

If the box was filled with two pieces of reward of different value the thieves did not steal the higher-valued more often than the lower-valued one ($\chi^2$ = 0.231, N = 156, p > 0.1). Due to very few occasions of aggression, it was not possible to address whether successful individuals showed more aggression if a high- compared to a low-valued reward was stolen.

## Influence of reward value

In 171 cases the successful monkey left a piece of reward in the bowl, in twenty cases even both pieces of reward. The rates of left food items of each sort for each main participant were compared and showed a significant difference (Friedman's $\chi^2$ = 10.17, N = 6, p = 0.006, Figure 14). Post hoc analysis showed that successful individuals left more pieces of low-

valued food than high-valued food (Friedman's $\chi^2$ = 1.750, N = 6, $p_{Bonferroni}$ = 0.007). There was no significant difference between low-valued and medium-valued food (Friedman's $\chi^2$ = 1.250, N = 6, $p_{Bonferroni}$ = 0.91) nor between medium- and high-valued food (Friedman's $\chi^2$ = 0.500, N = 6, $p_{Bonferroni}$ = 1.00).

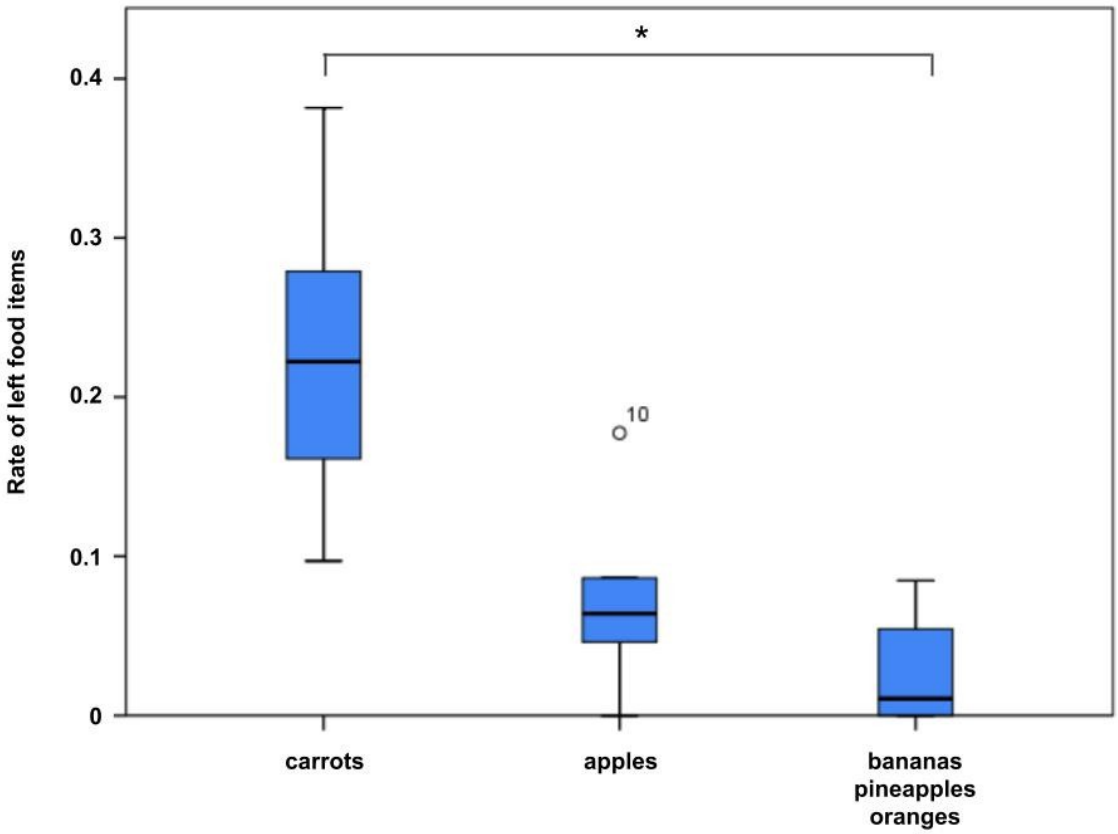


*Figure 14: Difference between the three differently valued food rewards regarding how often they were left by a successful individual.*

Five of the six experienced monkeys refused to participate after looking into the filled box in altogether 30 trials (between 3 and 9 cases per individual). This was more likely when the box did not contain a piece of high-valued food than when it did ($\chi^2$ = 4.800, N = 30, p = 0.028; Figure 15).

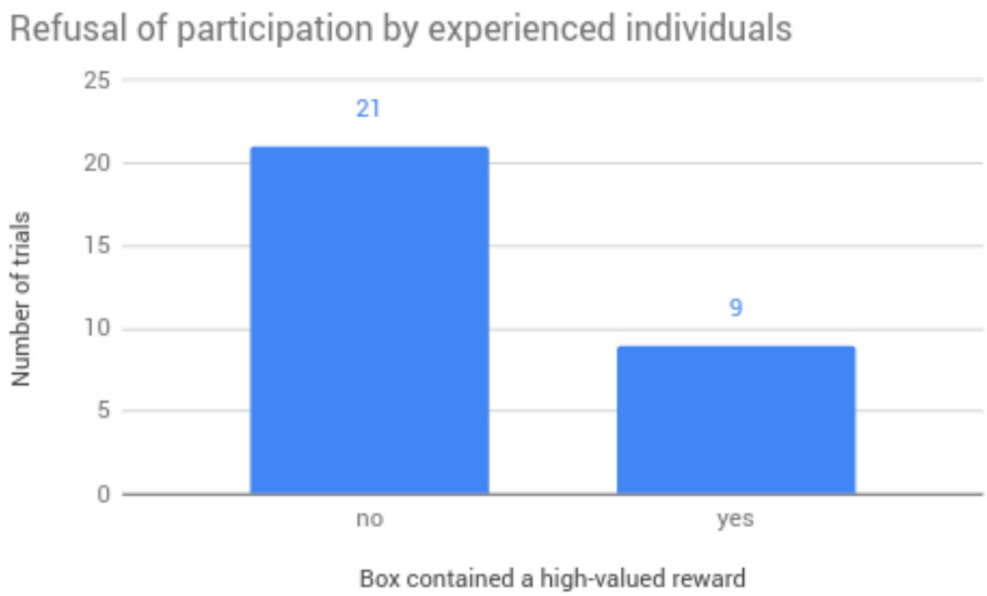


*Figure 15: Experienced monkeys refused significantly more often to participate in the task when the box contained no reward of high value (N=30).*

To see whether inexperienced monkeys also show a reaction to differently valued rewards I looked at their first trial. Of the 26 individuals that participated at least once, two pulled solely when the box was not filled. After excluding the individuals already successful in the habituation phase (4 of the 6 main participants) the first trial of the remaining 20 monkeys was investigated in a subsequent analysis. Of those, only six had been confronted with a piece of high-valued food in their first trial. In the remaining 14 cases the box had been filled with pieces of low- and/or medium-valued food. However, this difference did not reach significance ($\chi^2 = 3.200$, N = 20, p = 0.074).

# Discussion

I tested a troop of semi-free living Japanese macaques (*Macaca fuscata*) in a string-pulling task. The monkeys were tested within their social group (~150 Individuals) and had free access to the apparatus at all times. I used high-, medium- and low-valued food items as reward. Ten monkeys solved this task at least once and six individuals regularly. These monkeys' efficiency (i.e. the number of pulls they needed to solve the task) improved with time. Similarly, over time they increased behavioural strategies to improve their pay-off i.e. both behaviours "Looking into the box" (knowing if and what reward was filled into the box) and "Pulling toward the box" (being nearer to the reward when it was released) increased over time. By looking into the box before participating, the monkeys could avoid putting effort in the task for an unwanted reward. Pulling toward the box allowed the participating monkey to be closer to the bowl, in which the reward landed. Consequently the successful monkey could obtain the reward before anyone else could take it. A lot of thievery occurred during the sessions, yet the monkeys reacted with low rates of aggression, resulting in too few data points for sufficient analyses on aggression in response to different reward qualities. Experienced monkeys, however, did stop to participate for a low-valued reward, but did not stop participating altogether. Moreover, successful individuals left significantly more low-valued food items behind than high-valued ones. The setup with different valued rewards thus allowed access to the apparatus and to the rewards for less-experienced individuals.

The monkeys' age correlated negatively with their presence inside the hut housing the experimental apparatus. Not all of the young monkeys participated in the experiment, but played inside the hut or watched what was going on. Consequently, the monkeys who pulled the rope also were young, with the oldest participating monkey being a nine year old female. These findings are in line with findings on cultural behaviours in Japanese macaques, such as potato washing and stone handling, which are passed from younger to older individuals and often initiated by play (Huffman, 1984; Kawai, 1965). Similarly, young Japanese macaques display more stone handling than adults, which possibly helps to develop motoric and perceptual skills (Nahallage & Huffman, 2007). It must be noted that in the present study, the one- and two-year old monkeys did not solve the task, most probably because they were not yet strong and coordinated enough to succeed in this setup rather than due to a lack of interest. Moreover, like in a similar study conducted in Barbary macaques (*Macaca sylvanus*) (Molesti & Majolo, 2016), high ranked males showed no interest in the experiment. Due to the strict hierarchy in Japanese macaques, high ranked individuals have better

access to food (Takahata et al., 1999) and are therefore less dependent on additional food sources. Competition over food has more impact on females (Koenig, 2002), since in general females compete over food and males over mates for reproductive success (Fedigan, 1983). The participation of subadult males was therefore surprising, but since they were not yet socio-sexually matured, their reproductive effort was probably not yet relevant. Moreover, all adult participants (whether successful or not) were indeed females.

A previous study on Capuchin monkeys showed that they pulled a tray more often when it was loaded with a reward than when it was empty (Visalberghi et al., 2000). Accordingly, a transparent box was installed in the present study to allow the monkeys to check for a reward before participating. Despite the use of a transparent box, the two male participants pulled more often when the box was empty than when it was filled with a reward. The four females, however, did pull more often when the box was filled with a reward, than when it was empty. In some species pulling a string without the presence of a reward might be caused by their playful behaviour, resulting in pulling a string being self-rewarding (e.g. parrots Schuck-Paim et al., 2009 and cats Whitt et al., 2009). However, since only the males pulled more often in absence of a reward an explanation could be the tendency of the two males to pull in rapid succession instead of checking the box after one pull. Another plausible explanation for this sex difference could be the earlier first success and therefore longer experience of the females. In general, and irrespective of sex, the behaviour “Looking into the box” before participating increased over time, which can be considered as a learning effect in experienced individuals.

In general, the number of trials per individual were highly variable, with a single individual being accountable for over one third of all trials. This individual never displaced another one from the apparatus, but it is possible that it prevented especially the younger and lower ranking ones from participating. Such imbalance cannot be prevented when the animals are being tested in their social environment resulting in a reduced sample size - a common challenge of studies within more valid socio-ecological settings (Cronin et al., 2017). The small sample size of six regularly participating individuals in this study is probably due to the possibility of scrounging without the need to participate. Half of the scrounging monkeys never tried to participate (and therefore produce), but solely followed the scrounging strategy. Successful participants (i.e. “true” producer) were in the vast minority, however they also showed scrounging behaviour and can therefore be considered as “opportunists”. This opportunist strategy is expected to either occur alongside the scrounging strategy or the producing strategy (Vickery et al., 1991). This is in line with the present study as there were hardly any individuals following solely the producing strategy (and none of them were

successful), whereas scrounging and opportunistic individuals were equally widespread. Previous studies showed positive relationships between frequencies of scrounging and the cost accompanied to producing (e.g. Barrette & Giraldeau, 2006; Giraldeau et al., 1994; Morand-Ferron et al., 2007). The high frequencies of scrounging in the present study might therefore be a result of the need to invest time and effort to solve the task instead of waiting until the feeding turn to get food. Furthermore, larger groups allow higher frequencies of scrounging (Coolen, 2002). Compared to the average group size in the wild of about 40 individuals (Fooden & Aimi, 2006), the tested group of ~150 individuals is quite large. However, due to missing comparable studies with Japanese macaques, it can not be addressed whether the group size has an effect on frequencies of scrounging in a string-pulling task.

Some successful individuals figured out that the box could be opened by pulling the rope toward the box instead of away from it. By doing so the successful individual was closer to the reward when it was released. Especially one female applied this strategy, which might have helped prevent thievery. I suspected that the behaviour „Waiting“ before participating served the same purpose, but the data showed no influence on thievery. Although stealing occurred very often, none of the successful individuals stopped participating. Surprisingly, they also showed very little aggression towards thieves, although the despotic society of Japanese macaques with their strict hierarchy has a high potential for aggression in terms of food competition (Majolo et al., 2009), especially with densely clumped food sources (Rebout, Desportes, & Thierry, 2017). Low aggression rates in the present study might be explained by the fact that the group was provisioned on a regular basis twice a day. The experimental setup therefore provided only an additional but not essential food source. Furthermore, the setup installed in the 40 000 m² enclosure offered thieves the chance to leave the hut with the stolen reward and vanish into the forest. It would have been much more exhausting for the successful monkey to chase the thief than to simply turn around and participate in the next trial.

Thievery did not occur more often when the box was filled with high- compared to low-valued rewards (most probably because the thieves were unaware of what the box was containing). When the box was filled with two food items of different value, the thieves did not steal the high-valued reward more often than the low-valued one. They probably did not discriminate between the food items but rather ran away in order to avoid any encounters with group members.

It was unexpected that successful monkeys would leave part of the reward (or in some cases even the whole reward). Since they are provisioned and not free-ranging, they were

not dependent on the food rewards, which may have allowed them to be picky. It is important not to confuse this behaviour with sharing the reward. All food items were taken eventually by another monkey, which might have helped to attract other individuals to participate. A previous string-pulling study reported goldfinches not always eating the reward after a successful trial (Seibt & Wickler, 2006). In the present study, however, the monkeys left significantly more low-valued food items than high-valued ones. Consequently, I conclude that they simply were not keen on low-valued rewards. This notion is driven by the observation of successful individuals, who did not participate in a trial after looking into the box. They did so significantly more often when the box contained no piece of high-valued reward. Rejection of a reward and unwillingness to participate are typical reactions of inequity aversion (Brosnan & de Waal, 2014). There is, however, a trend for the box containing no piece of high-valued reward in the first trial of inexperienced individuals.

In summary, the present study showed that experienced monkeys eventually stop participating for low-valued rewards, but do not stop participating entirely. In such cases, inexperienced monkeys get a chance to participate and learn to solve the task. Allowing the monkeys access to the task at all times leads to high frequencies of scrounging from both participating and non-participating individuals.

Testing animals in their social group and not limiting their access to an experiment holds difficulties such as limited participation due to the ability to scrounge without participating and unequal numbers of trials per individual due to competition or interference (Cronin et al., 2017). Gaining interest from the animals for a task and maintaining their motivation can be achieved by using differently valued food items as reward. This appears to be particularly useful in despotic societies, such as found in Japanese macaques, where rank determines access to food. While high-valued rewards drive motivation for frequently participating monkeys, low-valued rewards reduce the risk of monopolization, giving inexperienced individuals a chance to participate in a task.

Despite many difficulties, keeping the animals' environment as natural as possible ensures ecological validity, which is crucial for shedding light on the proximate mechanisms and evolution of a certain behaviour (McAuliffe & Thornton, 2015).

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