

## UNIVERSITY OF PADUA

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## Spontaneous quantity discrimination in Capuchin, Spider and Howler monkeys: a preliminary investigation

Supervisor<br>Prof. Christian Agrillo<br>Submitted by<br>Alice Zini<br>n. 2002418

Abstract ..... 2

1. Introduction ..... 3-11
1.1. The importance of discrimination quantities in nature ..... 4-5
1.2.A review of the discrimination quantity abilities in animals ..... 5-8
1.3. The species under investigation ..... 8-11
2. Materials and methods ..... 11-15
2.1. Subjects ..... 11-13
2.2. Stimuli \& Apparatus ..... 13-14
2.3. Procedure ..... 14-15
2.4. Ethical note ..... 15
3. Results ..... 15-24
3.1. Analysis of the lateralization bias ..... 21-24
4. Discussion and Conclusion ..... 24-28
4.1 Limitation to the study ..... 25-28
5. Bibliography ..... 29-31


#### Abstract

In recent decades, a multitude of cognitive ethologists have engaged in extensive research testing the quantitative abilities exhibited by various animal species. The primary subjects under investigation are primates and birds; however, there remains a noticeable scarcity in the literature about New World monkeys, which constitutes the focal point of my research. This preliminary study investigates the cognitive abilities and quantitative skills of Capuchin (Cebus imitator), Spider (Ateles geoffroyi), and Howler (Alouatta palliata) monkeys through a series of tests using the free-choice method. The monkeys were presented with an inclined wooden plate on which two relevant stimuli, such as banana and beetroot sticks of different sizes were placed. The ratio between these sticks changed according to a pseudo-random sequence. In agreement with previous literature on several vertebrates, they were sensitive to the difference in quantities, they were expected to select the larger one. Data suggest that spider and howler monkeys can grasp this difference while for the capuchins the result is unclear. This study is a starting point for future investigation that can be useful to understand the similarity between human and non-human primates in quantitative skills.


## 1. Introduction

Numerous studies have investigated the ability of several animal species to discern differences in quantity. (Beran et al., 2015, 2008, Agrillo et al., 2007) The broad category of quantity discrimination refers to the ability of an individual to perceive and respond to quantitative differences between stimuli. In other words, it deals with an animal's ability to distinguish a magnitude of difference (continuous quantities, e.g., larger versus smaller area, longer vs. shorter) or discrete numerical information between two or more quantities of objects (e.g., 2 items vs. 3 items). This concept has been extensively studied by cognitive ethologists through test paradigms conducted on various animal species, including primates, birds, fish, insects and reptiles that examine when and how animals respond to differences in stimuli.

There are different methodologies for assessing quantities but most of them can be included in two broad categories, the observation of spontaneous behaviour in front of biologically relevant stimuli differing in quantities and the use of training procedures. Spontaneous assessments of quantities offer an advantage as they directly pertain to ecological functionality, encompassing aspects like discerning food quantities or availability and evaluating the composition of social groups. As a negative point, we have to underline that inter-specific comparison is quite limited because the relative salience of biologically relevant stimuli changes across the species. Nowadays we know that quantity judgments together with representation of numerosity, and perhaps even counting-like abilities (in different and limited degrees) are evident in nonhuman animals. (Beran, Parrish, \& Evans, 2015).

There are traditional ways of thinking about how animals can discriminate quantities, it is thought that they rely principally on two different mechanisms: the AMS, the Analogue Magnitude System, and the OFS, the Object-File System. The AMS is supposed to operate with both continuous and discrete quantities and follows Weber's law; this law states that the perception of variations in a stimulus is proportional to the baseline size of the stimulus itself; so what is perceived changes proportionally to the relative change compared to the initial stimulus rather than an absolute change. Using the AMS, the animal can do a rough estimation and compare quantities without actually counting them. So, sets with a lower ratio are easier to discriminate than sets with a higher ratio. In the meanwhile, when the absolute value of the magnitudes increases, sets become more difficult to discriminate (Cordes et al., 2001; Barth et al., 2003; Cantlon, 2012). In the AMS the quantities are only approximately represented, while in the OFS are individually represented as distinct entities. This latter system is thought to be available for higher-level cognitive processes and mainly related to discrete numerical abilities. In contrast to the AMS, the OFS would be a precise mechanism based
on a $1: 1$ correspondence between the object and the mental representation of numbers and would not follow Weber's law, so in very small sets (as smaller than four) accuracy would not vary depending on the ratio of the food quantities (Cantlon and Brannon, 2006). These two different prospective have been questioned a lot during the last years. However, it has been suggested that most animal species rely on the AMS and very few species use the OFS. (Caicova et al., 2021) Quantity discrimination in animals can vary significantly among species and even among individuals within the same species. Studies on this topic contribute to our understanding of the cognitive abilities of animals and the neural bases underlying these skills. This ability is, of course, present in humans, and the fact that some animals possess it may suggest a similarity in certain cognitive mechanisms. Cognitive research with infant monkeys is important for understanding human development because it can help to discover the evolutionary basis of human reasoning and the role of genetic and maturational factors in cognitive development (Bjorklund \& Pellegrini, 2002; Diamond, 1990, 1991; Gómez, 2005; Rosati, Wobber, Hughes, \& Santos, 2014).

### 1.1. The importance of discrimination quantities in nature

This skill plays a key role in various situations, such as decision-making while foraging, assessing the quantity of available resources, mating (mate preference), or responding to predator or competitor signals. Quantity discrimination contributes to increase the fitness of animals by increasing their foraging efficiency, breeding success, or survival. For instance, it has been demonstrated that there is a link between the ability to discern differences in quantity and certain mate behaviours associated with sexual dimorphism in some species.

In a study concerning swordtail fish, it was shown that in five different tests, females consistently show a mate preference for males with longer tails, and the longer the tail, the greater the strength of this preference. These results not only suggest that the fish were indeed capable of distinguishing between different lengths but also highlight the significant evolutionary role this ability played. Another example can be found in a study regarding the mating preferences of female peacocks, which demonstrate a greater inclination to select males with longer tails. This trait might make them more successful in mating but would incur a substantial disadvantage in terms of survival abilities due to being more visible to predators.

Discriminate quantities can be useful also for protection against predators, some social animals tend to join groups of individuals of the same species; being able to recognize which one is the larger can influence the survival of the singular individual. For example, cohorts of guppies were systematically observed across three distinct quantity discrimination tasks. These tasks encompassed the identification and aggregation with the larger group of conspecifics from a binary choice scenario, a behavioural pattern known to confer increased protection against predation. Furthermore, guppies were engaged in the discrimination between disparate sets of food items, selecting the numerically superior quantity. Additionally, subjects exhibited discernment in selecting food items based on their size, favouring larger items over smaller alternatives (Lucon-Xiccato, Dadda, 2016). It has been demonstrated that those who selected the larger shoal seemed to select the smaller amount of food in the other tests this is not linked to their ability to distinguish quantities but can be related to social contest, they have to optimize food intake and eat faster than other individuals to overcome competition for food.

To summarize, we can state that the cognitive ability to discriminate quantities is a key and adaptable skill in various natural contexts such as: foraging, optimizing food intake, mate selection, predator defence mechanisms, and so on. This ability enhances the animal's chances of survival. Over the years, numerous tests have been reported in the literature for assessing the quantitative discrimination capacity in various animal species. Although the specific skills under examination are not the same for all the species analysed and the methods with which the tests were performed often differ between spontaneous quantitative choices and training procedures.

### 1.2. A review of the discrimination quantity abilities in animals

Cognitive ethologists have primarily investigated mammals, in particular Old-World monkeys, and birds (-pigeons (Diaz, \& Wasserman, 2023), New Zealand robin (Garland, Low, Burns, 2012), and Jungle crows (Bogale, Kamata, Mioko, \& Sugita, 2011). More recently studies have investigated different teleost fish, such as guppies (Lucon-Xiccato, Miletto Petrazzini, Agrillo, Bisazza, 2015), angel-fish (Gómez-Laplaza, Díaz-Sotelo, \& Gerlai, 2018) and mosquito fish (Agrillo, Dadda, \& Bisazza, 2007).

Regarding ungulates, there is interesting research about the giraffes, it has been proven that despite their relatively low encephalization quotient can show either way complex cognitive skills, either probably this is strictly linked to the selective pressures experienced in different socio-ecological conditions. In giraffes, specifically, the discrimination of quantity may lead animals to choose the
location with a greater number of trees, the tree with a higher quantity of leaves or flowers (Berry \& Bercovitch, 2017), or possibly even the area with fewer predators. Moreover, their pattern of separating and coming together dynamically might be crucial for assessing how many members are in the group when deciding whether to split up or join a particular smaller group, based on the current situation. (Aureli et al.2008).

The research conducted on giraffes took place at the zoos of Barcelona and Leipzig, having as protagonists the giraffes housed in these facilities as the main subjects. It's important to note that these animals are in captivity, and the sample size is scarce. Three different types of tests were performed. The first focused on quantity discrimination, considering the numerosity of the presented stimuli. The second type considered both the size and the quantity of the stimuli and the third type examined how these stimuli were distributed (sparse versus dense configuration). The results have shown that giraffes rely on the Analogue Magnitude System to discriminate quantities. In the tests, they demonstrated sensitivity to differences presented in the stimuli, indicating a preference for maximizing their food intake by choosing the food with greater numerosity or volume. This preference takes into consideration cognitive biases. However, giraffes exhibit better discrimination of quantities when food items differ in quantity rather than in size.

Numerous studies have been conducted with Old World primates, including: rhesus monkeys (Beran, 2001, 2007a, b; Brannon and Terrace, 1998; Cantlon and Brannon, 2006; Hauser, Carey and Hauser, 2000); squirrel monkeys (Thomas and Chase, 1980; Terrell and Thomas, 1990), chimpanzees (Beran and Beran, 2004; Beran, Evans and Harris, 2008; Biro and Matsuzawa, 2001; Boysen and Berntson, 1989; Matsuzawa, 1984; Tomanaga,2008), gorillas (Hanus and Call, 2007) and orang-utans (Call, 2000).

A study conducted at the Detroit Zoological Society investigated the quantity judgment abilities of two adult male western lowland gorillas (Gorilla gorilla) by presenting discrimination tasks consisting of a pattern of dots on a touch screen. Both gorillas exhibited performance above chance levels in both congruent and incongruent trials across all tasks, demonstrating their capability to utilize numerical cues. Despite the significant influence of the number-to-area ratio on their responses, it implies that the gorillas did not rely solely on the numerical magnitude, suggesting the involvement of other pertinent dimensions in their decision-making processes. These findings support the conclusion that gorillas, like other primates, use an ANS for discriminating quantities. (Vonk, Torgerson-White, McGuire, Thueme, Thomas \& Beran, 2014). In other tests conducted with Chimpanzees, using different amounts of food stimuli. They select the food sets with the larger amounts of food in the majority of the trials. They were not distracted by the number of items in the
two sets, they didn't utilize numerical abilities as a primary cue in this task. This leads us to conclude that they utilize the amount of food to guide their responses. Also, chimpanzees use AMS to discriminate quantities.

Concerning the less commonly analysed categories we can find reptiles, amphibians, and insects. However, also several mammals have been almost neglected by the literature, for example, the broad category of New World monkeys.

Cotton-top tamarins (Saguinus oedipus), belonging to New World primates, were subjects of a pilot study. Three experiments were conducted with this species (Stevens et al., 2007). Their performance varied based on the ratio between comparison quantities, indicating the ability of tamarins to assess discrete numbers in both food and non-food contexts. They consistently selected arrays with larger amounts of food, even when the number of food stimuli was constant; the study propose that tamarins can distinguish both number and total amount. Those experiments highlighted those quantitative factors like density or item size influenced representations of total amount. They provide the first systematic investigation showing that tamarins quantify over sets based on the total amount of food rather than the number of items.

Several studies have been conducted on capuchin monkeys; subsequently, I have analysed a subset of these, showing their results. These studies can be useful as a basis for reflection and a benchmark for the pilot study conducted by me. In the first study (VanMarle et al., 2006) the capuchins had to discriminate between two different amounts of food, in terms of numerosity. They selected the major quantities of food more than the minor. The performance was ratio-dependent meaning that the bigger the proportional difference the more prone they were to select the larger amount. The results support the theory that capuchins monkeys use Analogue Magnitudes System sets of discrete objects and continuous substances.

In another study (Beran, 2007) were analysed the capability of capuchins to assess the conservation of discrete quantity. This implies the idea that physical quantities do not change because the arrangement is modified. For this experiment previous training, to teach them to select the more numerous sets of items, was necessary. They were presented with a computerized task, with an array changing in numerosity and spatial conformation. They select correctly the array with the larger number of items and they don't change their selection when the conformational space of the items is modified. The data indicate that capuchins are sensitive to simple arithmetic manipulations that involve the addition of items to arrays and also that they can conserve quantity. (Beran, 2007). Their performance matched that of rhesus monkeys (Beran, 2007), and they also succeeded in a similar test.

Another test (Beran and Parrish, 2015) regarding the discriminative capacities of capuchin monkeys was held, in which small or large sets with the same ratios had to be discriminated. They do not show improved discrimination performance for small sets compared to large sets. From that study, we can notice a difference in the performance between capuchins and humans.

In the last study (Addessi et al., 2007) analysed they investigated the relative numerousness judgments with food compared to tokens. The experiment was held at the Primate Centre of the Institute of Cognitive Sciences and Technologies of CNR in Rome, with groups of capuchin monkeys. Food is utilized as valuable stimuli while tokens are considered non-valuable stimuli that acquire value in the context of the experiment. In addition, they also checked for which one of the two non-verbal mechanisms the capuchins rely on (AMS or OBS). In both tests, they selected the larger number of items although the success rate was higher with the food in comparison to the tokens.

The influence of the ratio between arrays on performance indicates that capuchins relied on the same system for numerical representation, analogue magnitude, regardless of the type of stimuli and across both the small and large number ranges. (Addessi, Crescimbene \& Visalberghi, 2007).

Some of the information derived from these studies will be subject to comparison with the results obtained from my experiments. To enlarge the investigation to New World monkeys in the present thesis I observed the spontaneous preference for the larger amount of food in three species: Panamian White-Throated Capuchin Monkey (Cebus Imitators), Geoffroy's Spider Monkey (Ateles geoffroyi), and Mantled Howler Monkey (Alouatta palliata). With the exception of capuchin monkeys which were investigated a lot for their cognitive abilities comprising quantity discrimination ability, no previous tests were conducted on these species. It is also important to note that the sample of animals I studied is too small to consider the results as conclusive, and therefore, they cannot be representative of the species. However, they may offer an interesting starting point for future investigations and analyses in this field. In this sense, this thesis can be considered as a pilot study for a deeper investigation in the near future.

### 1.3. The species under investigation

The Panamian White-Throated Capuchin, scientifically known as Cebus imitator, was classified by the IUCN Red List of Threatened Species as Vulnerable in the year 2020. Is a species of New World monkey. The geographic range of this species includes Honduras, limited parts of central and eastern Nicaragua, spanning through the northern regions of Costa Rica and extending into western Panama.

While there have been sporadic reports of their presence in southern and western Belize and the far eastern region of Guatemala.

The Panamanian white-throated capuchin exists in varying population densities, ranging from 5 to 60 individuals per square kilometre, in several locations across Central America. They inhabit several forested habitats, from lowland to montane areas reaching elevations of up to 1.500 meters, encompassing topical dry deciduous forests to wet forests and mangroves. As extractive and manipulative foragers, these capuchins demonstrate adaptability to utilize the full spectrum of resources available within their forested environment. Their diet predominantly comprises fruits and assorted insects, although they consume also a wide array of other invertebrates, eggs, and small vertebrate prey. Additionally, they occasionally consume leaves, flowers, stems, and nectar. They seldom descend to the ground to forage, access water sources, or migrate between forest patches.

Regarding their physical characteristics, white-throated capuchins exhibit a head-body length ranging from 34.3 to 42 centimetres, displaying minimal sexual size dimorphism. Their prehensile tail extends between 44 and 46 centimetres while their weight ranges from 3.7 to 3.9 kilograms for males and 2.6 to 2.7 kilograms for females. Reproductive behaviour in White-faced capuchins occurs throughout the year, with a notable birth peak during the late dry/early rainy season within Costa Rican dry forests. The social structure is characterised by a linear dominance hierarchy among both males and females, with the alpha male predominantly siring the offspring, despite all males engaging in mating activities. One of the primary threats to them is the loss and habitat degradation. Additionally, farmers often perceive capuchins as pests due to their crop-raiding behaviour, which has resulted in their persecution. Furthermore, the species faces the additional risk of being hunted for the pet trade and, on occasion, serving as a source of bushmeat.

The second species examined; Geoffroy's Spider Monkey (Ateles Geoffroy) has most recently been assessed for The IUCN Red List of Threatened Species in 2020. Atleles Geoffroyi is a species of New World primate. There are six recognized subspecies.

The monkeys are covered with reddish-dark brown fur that can be darker depending on the zone of origin. Spider monkeys are diurnal and arboreal animals and have prehensile tails that facilitate their movement in the forests. They normally are frugivores but also feed on leaves and flowers. Size and composition of $A$. geoffroyi in the wild, with group sizes varying from 16 to 56 individuals, and a female/male sex ratio of 0.8 to 4.4 (Di Fiore et al. 2010) Average weight for adult males is 8.21 kg , ranging from 7.42 to 9 kg , and for females 7.7 kg , ranging from 6 to 9.4 kg (Ford and Davis, 1992). The social structure is a mixed group characterised by males and females in different proportions with
a social organization in which the members of a large stable group separate daily into small subgroups of changing sizes and composition (Di Fiore et al. 2010).

The species Ateles Geoffroyi is spread in: Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico (Campeche, Chiapas, Oaxaca, Quintana Roo), Nicaragua, and Panama. They are distributed throughout Central America, including tropical forests, dry deciduous forests, cloud forests and mangrove forests. The population density of Ateles geoffroyi varies considerably among populations and across its distribution range. Their actual population status is decreasing; in nature, they have a life expectancy of 25 years that can be extended to $30 / 35$ in captivity. Among the major threats to this species, we can find intense habitat loss, the decline of their living environment is caused by the targeted cutting down of specific trees that are crucial for their food, and overexploitation for the pet trade (Estrada et al. 2006, Ramos, Fernandez, and Wallace 2008). Due to the spider monkeys delayed sexual maturity, the birthing of one offspring at a time, and extended gaps between births, any danger posed to their habitat or directly to the group affects significantly the overall survival of these wild populations (Ramos-Fernandez and Wallace, 2008). Other treats for their survival are: capture for pet trade and hunting in some regions, as well as for bush meat.

The last species examined, the Mantled Howler Monkey (Alouatta palliata), has been assessed for the IUCN list of threatened species in 2015 as vulnerable. Alouatta palliata is a New World Monkey, of the same family of Ateles geoffroyi (Atelidae). In total 5 subspecies are recognised.

The individuals are distributed in Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico (Campeche, Chiapas, Oaxaca, tabasco, Veracruz), Nicaragua, Panama, and Peru. These monkeys are arboreal and they occupy several types of habitats including mangroves, riparian forests, evergreen forests, deciduous forests, and anthropogenically distributed forests; these forests have distinct vegetation types. Alouatta palliata has a decreasing population trend, is patchily distributed throughout its range, and has a wide density variation.

The howler monkeys primarily feed on fruits and leaves, but the proportions vary across different locations. Some population exhibits a mostly folivorous diet, while others maintain a more balanced food intake. Other food items include flowers, petioles, buds, and so on. Group size differs considerably, with certain areas reporting sizes of 40 or more individuals in a single group (seen in Mexico and Costa Rica), although the average group size tends to be around 15.2 individuals (Dias and Negrin 2015). Groups include both males and females, with a sex ratio of 1.79 females per male (Chapman and Balcomb 1998). The expected life span of a wild Mantled Howler Monkey is around $15 / 20$ years old while in captivity can be extended a little bit more than 20 years. The major threats
for this species include habitat loss and fragmentation, as a close consequence of economic and touristic activities, hunting for bush meat, and illegal pet trade.

## 2. Materials and methods

### 2.1. Subjects

In total 6 adult individuals were tested, 3 white-throated capuchins (captive), 2 spider monkeys (captive), and 1 mantled howler monkey (wild). Those individuals were all accommodated in Alturas Wildlife Sanctuary, a centre dedicated to the rescue, rehabilitation, and release of local wildlife in the Osa Peninsula, Costa Rica. If an animal cannot be released due to life-threatening injuries, significant neurological impairments, or excessive habituation to humans, they are either transferred to nearby sanctuaries or become permanent residents of the Alturas Sanctuary.

The three capuchins were all females and they were named, Coco, Pablo, and Honey, we do not know their age but they were in the adult stage. Coco, the most aggressive one, was kept as a pet on a leash in a mountain locality not so far from the rescue centre, she was first confiscated and transferred to a sanctuary when she was young and then came to Alturas (Fig.1). This individual shows aggressive behaviour towards humans and she gets stressed very easily, showing quite often stereotypic behaviours for that reason she needed a longer habituation phase to be comfortable with me. Pablo, is the female that is at the top of the hierarchy, she was kept as a pet by a drug cartel in Costa Rica, then confiscated, and in 2014 came to Alturas, she is very friendly with people. Honey was also confiscated from a family that kept her as a pet, she is reserved, and took more time to get used to my presence.

They are all housed together in a three-compartment enclosure, that can be closed separately in this way we achieve the division and isolation of the animals, so each time right after the test they were separated; this was done specifically to avoid conflict for the food, due to their strong hierarchy and their temperaments. The holes of the fences were sufficiently large to permit them to put the arm through them.


Figure 1. Coco, capuchin monkey of the sanctuary


Figure 2. Festus, spider monkey of the sanctuary


Figure 3. Bruce, wild howler monkey

The howler monkey is a more peculiar individual, he was not part of the resident animals in the Sanctuary, he is an adult male, we call him Bruce (Fig. 3), he came from a tourist zone near the sanctuary, a person noticed that he was injured and call Alturas. He came to us with serious burns and wounds caused by electrocution (it is a common event for wild animals in Costa Rica because the electrified cables are not isolated) since he needed to stay for a quite long period in the clinic, I decided to test him too. Bruce was housed in the clinic in a transporter for the duration of my experiment; the holes of the transporter permitted him to put only his fingers through them. (Fig.4).


Figure 4. The experimental apparatus with stimuli in front of the transporter of Bruce.

All the subjects followed a personalised and species-specific diet, according to the veterinarian, we decided to remove some grams of banana or beetroot depending on the subject to not create an unbalanced diet.

### 2.2. Stimuli \& apparatus

The experimental apparatus consisted of two wooden plates with an inclination of 20 degrees; the inclination was needed to match the animal visual field. Each plate has a circular appearance with a ray of 15 centimetres, and diameters of 30 cm . The two plates were obtained by sectioning a tree trunk and subsequently meticulously levelling the surfaces. One plate underwent a coating process using non-toxic black paint, while the other retained its natural wood hue, characterized by a light chestnut colour. This was necessary to create a visual contrast between the food stimuli and the plate. To the spider and capuchin monkeys were always presented the black one


Figure 5. The apparatus with banana sticks while form the howler monkey was presented the natural one. This was because of the different colours of the selected stimuli: for the howler it was cooked beetroot (dark red/purplish colour) that created a strong contrast with the light chestnut colour of the plate and for the others was banana (light yellow/whitish) that create a strong contrast with black colour. (Fig.5)

On this plate, two food stimuli were simultaneously presented, with a distance of 8 centimetres. The stimuli consist of banana and beetroot sticks. Beetroot was the favourite food of the Howler monkey tested while banana was the favourite food of the other monkeys. The thickness of the sticks was 1 cm while the length varied according to the pattern of the test presented. One stick is of a fixed size of 10 centimetres while the other varied according to one of the following ratios: $1 / 3,1 / 2,2 / 3,3 / 4$ (that in practice means $3.33 \mathrm{~cm} ; 5 \mathrm{~cm} ; 6.7 \mathrm{~cm}$ and 7.5 cm ) (Fig.6).


Figure 6. Graphical representation at a 1:2 scale of the four trial scenarios, highlighting the distinct ratio among stimuli

### 2.3. Procedure

The testing method employed in this study is the free-choice method, in which animals make spontaneous choices without undergoing prior training. The tests were conducted twice a day, every day, with a two-day break per week, in total 8 days of testing. The howler monkey and spider monkey tests were performed on the same days, while the capuchin monkey tests were conducted the following week. Every individual underwent a total of 16 trials, with 4 trials per numerical ratio (four trials with the proportion of the sticks of $1 / 3$ and so on). The presentation order of stimuli to the animals was designated as pseudo-random or controlled random, as perceived by the subjects as random, while we meticulously adhered to predetermined tables to ensure that the stimulus in front of the animal could consistently vary. Additionally, we systematically changed the side on which the longer stick was positioned to prevent habituation, thereby prompting the subjects to make selections without relying exclusively on memory.

Immediately after cleaning the enclosures, the animals were separated, and the tests were presented to them from outside of the enclosure, before food administration, around 7:30 am. The same procedure was replicated in the afternoon shift at approximately 2 pm . Each monkey was individually presented with the apparatus. They were required to choose their preferred stimulus, and once the selection was made, the plate was removed to minimize or eliminate the possibility of them obtaining both sticks. The stimulus touched first by the animal was considered the selected stimulus. During the tests with the capuchins, I was wearing gloves. (Fig.7)


Figure 7. Presentation of one of the experimental trials to Coco

### 2.4. Ethical note

Our experiments consisted of the observations of monkey behaviour without any direct contact or manipulation of the subjects. All the individuals spontaneously participated in the experiments. The experimental area was their normal enclosure and they were not divided from the other individuals for more than the duration of the test. None of the subjects appeared to be stressed during the experiments and no negative social consequences were observed among them. No food deprivation or fastening was done. The water was available for the entire duration of the experiment at libitum. The experimental procedure was chosen according to the operation manager and the keepers of the sanctuary and complied with the law of the country (Costa Rica).

## 3. Results

During the test procedures, specific tables were followed, outlining the sequence for subjecting individuals to tests with varying ratios. Additionally, these tables detailed whether subjects selected the stick located to the right or left within their field vision. The outcomes from these trials were transcribed and organized into tables. Subsequently, a graphical representation explaining the subjects' performance trends was devised and presented below.


Graphic 1. Graphical representation of Chester's performance


Graphic 2. Graphical representation of Festus's performance


Graphic 3. Graphical representation of Coco's performance


Graphic 4. Graphical representation of Honey's performance


Graphic 5. Graphical representation of Pablo's performance


Graphic 6. Graphical representation of Bruce's performance

In these initial six graphics, the individual performances of each animal are described. On the x -axis, we find the four ratios at which stimuli were presented. On the $y$-axis, we noticed the proportion of choices toward the larger quantity exhibited by the subjects during the tests: the closer the value is to one, the more accurately the animal performed the test (selecting the longer stimulus). The values represented on the $y$-axis constitute the total correct trials divided by the total trials conducted for each ratio. The value will equal one when the animal completes four out of four trials correctly.

In the first graphic (Graphic 1), we observe the performance of Chester, one of the two analysed spider monkeys. He maintained a relatively consistent performance with an accuracy rate of $75 \%$, except for 2 out of 3 instances where he achieved $100 \%$ accuracy. As for Festus (Graphic 2) his performance remained steady and consistent throughout, consistently selecting the larger stick in the test scenarios, resulting in a graphical representation as a line parallel to the $x$-axis, showing a $100 \%$ accuracy rate.

The three graphics concerning the performances of the capuchins are markedly different. Neither Coco nor Honey (Graphic 3, Graphic 4) attained the maximum accuracy percentage at any ratios, displaying fluctuating performances without a discernible pattern. Examining Pablo's graphic (Graphic 5), we notice that as the difference between the two stimuli decreases (indicating an increase in difficulty), errors escalate, reaching up to $50 \%$ in the last two ratios ( 0.67 and 0.75 ). Bruce's performance (Graphic 6.), depicted in the final graph, remained consistent except for an error in the $1 / 2$ ratio.

Of course, these are just descriptive data; they do not yield population inferences as they are individual, demonstrating the trends of six tested monkeys for purely demonstrative purposes. Subsequently, we performed a binomial test for each subject to assess whether the frequency of choices toward one direction over another is statistically significant. The binomial test yielded the following results: Chester ( $p$-value $=0.021$ ), Festus ( $p$-value $=0.001$ ), Coco ( $p$-value $=0.210$ ), Honey $(p$-value $=0.210)$, Pablo ( $p$-value $=0.077$ ), and Bruce ( $p$-value $=0.001$ ). Hence, we can assert that the graphics' trends confirm the performances of the spider monkeys and Bruce, the howler monkey, who are effectively capable of distinguishing between the presented quantities. Concerning the capuchins, none of the three has a value lower than 0.05 , indicating that statistically we cannot claim they were able to perceive the difference in quantity during the tests.

Due to the insufficient sample size, it was not feasible to conduct a statistical analysis by grouping the results of the subjects according to the species, it would have rendered it statistically inadequate. However, an alternative analysis followed by a graphical representation was done, depicting the mean
performance of all monkeys. This approach aimed to provide a comprehensive overview of their collective abilities, groping them under the classification of New World monkeys.


Graphic 7. Graphical representation of average performances of the subjects

This graphic (Graphic 7) illustrates the animal's performance across varying collective ratios rather than focusing solely on individual instances. Where individual analyses exhibit substantial randomness, this graphic provides a clearer and more uniform understanding. The values highlighted are the standard error which is the measurement of variability in this comparison indicating the extent of variability in the performance of the animals. It is easier to observe homogeneous results in the case of $100 \%$ accuracy; conversely, as the group's performances become more variable, the bar will be wider and farther from the mean. Examining the graphical representation in detail can be observed precision consistently at the ratio of $1 / 3$ (i.e., 0.33 ), with slightly less precision and more heterogeneity concerning the ratios of $1 / 2,2 / 3$, and $3 / 4$.

| Ratio 0.33 | Ratio 0.50 | Ratio 0.67 | Ratio 0.75 |
| :--- | :--- | :--- | :--- |
| $\mathrm{t}=7.2732$ | $\mathrm{t}=3.2000$ | $\mathrm{t}=2.8366$ | $\mathrm{t}=3.9297$ |
| $\mathrm{df}=5$ | $\mathrm{df}=5$ | $\mathrm{df}=5$ | $\mathrm{df}=5$ |
| $\mathrm{p}<0.001$ | $\mathrm{p}=0.024$ | $\mathrm{p}=0.036$ | $\mathrm{p}=0.011$ |

Tab.1. one-sample t-tests of the performance of the subjects

This table (Tab.1.) provides a more detailed analysis of the specific ratios that the monkeys are capable of distinguishing. It serves as a means to ascertain if their performance is deemed statistically significant, i.e., significantly deviating from random chance. The chance level is represented by 0.5 of the dependent variables. This statistical analysis is known as the one-sample $t$-test. This is a statistical test used to determine whether the mean of a single sample is statistically different from a known or hypothesized population mean considering the variability within the sample.

This test compares each precise point against the chance line. For example, $\mathrm{t}(5)=7.2732, \mathrm{p}<0.001$. the table exhibits four distinct $t$-tests, each corresponding to a ratio $(0.33,0.50,0.67,0.75)$. similarly, these values can be considered statistically significant if the p-value does not exceed 0.05 . in this instance, all values are below 0.05 , confirming that, despite the inherent limitations, subjects generally tended to select the longer stick. This pattern holds across all numerical ratios, allowing us to conclude that, overall, they are indeed capable of distinguishing between all presented ratios.

### 3.1. Analysis of the lateralization bias

Throughout the tests conducted, the side where the stick selected by the subjects was located has been consistently noted. This was prompted by numerous indications in the existing literature (Gil-daCosta et al. 2006, Oleksiak et al., 2011, Boeving et al., 2017, Westergaard et al., 1998) suggesting significant lateralization bias in animals, impacting also motor functions. The term lateralization bias refers to an asymmetry or preference for using a specific side of the body, (usually the left or right side) in cognitive, motor, or sensory functions. It may indicate an asymmetry in functional dominance between the two cerebral hemispheres.

Therefore, our objective is to investigate whether their choices are primarily influenced by this bias or if it has a minimal impact on their performance. To assess this, we will analyse the percentage of times they selected the right stimulus versus the left one. If a notable disparity exists between the two results, we can assert that they possess a motor bias associated with lateralization. The longer banana or beetroot stick was alternately placed to the right and left so that at the conclusion of all the trials,
half of the time the longest stick was positioned to the right and the other half to the left. The stick was not consistently placed on the same side to overcome biases and prevent habituation. The results obtained have been compiled into tables, categorized based on the ratio between the two sticks.

In the first table (Tab. 2) we can see the displacement of the preference of all the monkeys tested regarding the ratio of 0.33 between the sticks, we obtained fairly homogenous results, very similar to those observed in the third table (Tab. 4) where the ratio between the sticks was 0.67 . The second table (Tab. 3) exhibited the most homogeneous results of all, with only Coco showing a slight inconsistency, presenting a stick ratio of 0.50 . However, notably different results were found for the penultimate table (Tab.5) where the ratio was 0.75 . This could be correlated with the sticks appearing very similar to each other, leading the monkeys to be more influenced by the cognitive bias of lateralization due to uncertainty in their choice.

| individuals | ratio 0.33 | ratio 0.33 | ratio 0.33 | ratio 0.33 | left 0.33 tot. | right 0.33 tot. |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| CHESTER | left | left | right | left | 3 | 1 |
| FESTUS | right | left | right | left | 2 | 2 |
| COCO | right | left | left | right | 2 | 2 |
| HONEY | left | right | left | left | 3 | 1 |
| PABLO | left | right | left | right | 2 | 2 |
| BRUCE | left | left | right | right | 2 | 2 |

Tab2. Subjects' preference for left or right, ratio 0.33.

| Individuals | ratio 0.50 | ratio 0.50 | ratio 0.50 | ratio 0.50 | left 0.50 tot. | right 0.50 tot. |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| CHESTER | right | right | left | left | 2 | 2 |
| FESTUS | left | right | right | left | 2 | 2 |
| COCO | left | right | left | left | 3 | 1 |
| HONEY | left | right | left | right | 2 | 2 |
| PABLO | left | right | right | left | 2 | 2 |
| BRUCE | right | left | right | left | 2 | 2 |

Tab 3. Subjects' preference for left and right, ratio 0.50 .

| Individuals | ratio 0.67 | ratio 0.67 | ratio 0.67 | ratio 0.67 | left 0.67 tot. | right 0.67 tot. |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| CHESTER | left | right | left | right | 2 | 2 |
| FESTUS | left | right | left | right | 2 | 2 |
| COCO | right | left | left | right | 2 | 2 |
| HONEY | right | left | left | left | 3 | 1 |
| PABLO | right | left | left | left | 3 | 1 |
| BRUCE | left | left | right | right | 2 | 2 |

Tab 4. Subjects' preference for left and right, ratio 0.67.

| Individuals | ratio 0.75 | ratio 0.75 | ratio 0.75 | ratio 0.75 | left 0.75 tot | right 0.75 tot. |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| CHESTER | right | right | left | right | 1 | 3 |
| FESTUS | left | right | left | right | 2 | 2 |
| COCO | right | left | right | right | 1 | 3 |
| HONEY | left | left | right | left | 3 | 1 |
| PABLO | left | left | left | left | 4 | 0 |
| BRUCE | right | left | right | left | 2 | 2 |

Tab 5. Subjects' preference for left and right, ratio 0.75.

Upon observing the table containing the combined results of the monkeys (Tab.6), we can infer that the greatest disparity in the results was obtained from two capuchin monkeys. Although the literature (Westergaard et al,.1998) proves that capuchins have a bias towards lateralization and that it can also interfere with the motor system comparing these tables with the results previously obtained by statistical analysis this bias is not strong enough to overcome the innate instinct to maximize the intake of food, in this case, selecting the major quantity of food (the longer stick). In the performances of the other subjects, it has been demonstrated an equal distribution of choices between right and left. This investigation is made as an additional reasoning within my research and a potential insight for further studies and investigations in the cognitive domain.

| Individuals | tot. left | tot. right | tot. trials |
| :--- | :--- | :--- | :--- |
| CHESTER | 8 | 8 | 16 |
| FESTUS | 8 | 8 | 16 |
| COCO | 8 | 8 | 16 |
| HONEY | 11 | 5 | 16 |
| PABLO | 11 | 5 | 16 |
| BRUCE | 8 | 8 | 16 |

Tab 6. Subjects'preference for left and right results comparison

## 4. Discussion \& Conclusion

The present study aims to investigate whether New World monkeys, specifically capuchin, spider, and howler monkeys, can perceive differences in quantity. The subjects in my tests amount to a total of 6 individuals residing at the Alturas Wildlife Sanctuary in Costa Rica; therefore, they are not laboratory animals and are naïve to cognitive studies. The methodology employed involved the freechoice method, without any prior training. The procedure entailed presenting the subjects with an apparatus consisting of an inclined wooden plate with two food stimuli placed atop it, either banana sticks or beetroot sticks based on the animal's preferences. The wooden plate was either of natural wood colour (for beetroot stimuli) or painted black (for banana stimuli) to create visual contrast, as colours were crucial for differentiation. The stimuli had various ratios ( $1 / 3,1 / 2,2 / 3,3 / 4$ ) and were presented in a pseudo-random order. The animal was required to express its preference by touching and/or grabbing the preferred stimulus, considering that if they perceived a quantity difference, they would select the longer stimulus.

The sequence in which stimuli were presented, the consequent choices of the animal, and even the side on which the chosen stick was located were meticulously recorded on each occasion, and then all data were grouped into tables. Graphs were constructed to illustrate the trends of individual subjects as well as the overall group mean. Furthermore, binomial tests and one-sample tests were conducted to assess the statistical validity of the choices made by the subjects.

The results portray the individual performances of the six tested monkeys across varying ratios of presented stimuli. Notably, Chester and Festus, the spider monkeys, showed consistent and accurate performances, maintaining rates of $75 \%$ and $100 \%$ accuracy, respectively. Conversely, the performances of the capuchins exhibited fluctuating patterns without discernible consistency. Notably, Pablo's errors escalated as the ratio differences diminished, peaking at $50 \%$ in the more challenging ratios ( 0.67 and 0.75 ). Bruce, the howler monkey, presented a consistent performance, barring a single error in the $1 / 2$ ratio. The obtained $p$-values, namely Chester ( $p=0.021$ ), Festus ( $p=0.001$ ), Coco ( $p=0.210$ ), Honey ( $p=0.210$ ), Pablo ( $p=0.077$ ), and Bruce ( $p=0.001$ ), indicated that spider monkeys and Bruce indeed exhibited a statistically significant ability to distinguish between presented quantities. However, statistical significance wasn't observed for the capuchins, implying an inability to perceive the quantity difference during the tests.

Considering the sample size limitations, a statistical analysis based on species classification was not feasible. Yet, an alternative approach was adopted to depict the mean performance of all monkeys collectively, presenting an overview of their collective abilities as New World monkeys. From that general one, you can notice an overall accuracy with the 0.33 ratio, indicative of the fact that bigger is the difference between the two stimuli and better can be perceived by them. Additionally, the onesample $t$-test was performed comparing each precise point against the chance line. With all p values below 0.05 , despite all limitations, the monkeys generally showcased a tendency to select the longer stick across all presented ratios.

### 4.1. Limitations to the study

All of my tests were conducted within the Alturas Wildlife Sanctuary in Costa Rica, using subjects that were naïve to cognitive tests. Consequently, several factors might have influenced the course and outcomes of our trials. The vast majority of similar experiments concerning animals' cognitive abilities are conducted in laboratories where there is the possibility of meticulously controlling all variables that could influence the animal's choices. Furthermore, there is almost always the potential for experiment standardization, which involves replicating the experiment using the same stimuli, apparatus, environments, etc., enabling useful comparison among experiments conducted by different ethologists. Among the factors that we cannot either modify or control, we find any auditory or olfactory stimuli, or environmental factors such as temperature, humidity, and general atmospheric conditions.

Additionally, larger sample sizes of subjects are typically employed, which was one of the biggest limitations indeed, in performing the statistical analyses, we chose to conduct them on the entire group of subjects without species division, as their numbers were too low to permit such categorization. Frequently, when working in a contest different from a laboratory, you must adapt to available resources and utilize the available materials; hence, the apparatus for example, was not manufactured but created by me. Moreover, there were adjustments made during the tests since experimental testing with inexperienced animals necessitated certain modifications. It is important to emphasize that my study is a pilot study, providing valuable insights into species that have not been thoroughly investigated and serving as a foundational platform for further research and in-depth exploration within the field.

The subject that showed one of the best results was Bruce, the Howler monkey. However, we have reason to believe that this outcome is not purely indicative of its cognitive ability to distinguish quantities, but rather that there are other secondary factors contributing. He succeeded in 15 tests out of 16. So apparently, considering the previous studies on the New World monkeys (VanMarle et al., 2006, Ferrigno et al., 2016, Beran \& Parrish, 2016), we can hypnotize that Bruce can perceive this difference. However, we cannot extend this belief to all the Howler species, since the sample utilized comprises a single individual, it cannot, therefore, provide insights into the abilities of an entire species. Typically, individuals who participate in these types of experiments are either born and raised in captivity or have been in captivity for an extended period. However, Bruce is wild and was experiencing an urbanized environment for the first time.

When I started with the first trial Bruce used to receive a once-daily intramuscular injection of 2 ml of amoxicillin, as well as an oral administration of 1 ml of amoxicillin-clavulanate twice a day. He was gentle and probably was because he was in pain. For the first time, he was presented with the apparatus, and he took about 6 minutes to make the decision, probably because he was not so used to me, I decided to sit on the ground to make him more comfortable watching him by distance.

After 3 days he started to select the stimulus almost immediately, I supposed that he was recovering from the injuries and he also stopped all the therapies. The following days he selected the stimulus faster and correctly (apart from one), but from the tenth test onward he showed aggressive behaviour; the vet told me that was aggressive also toward her so probably was because he was almost fully recovered and he did not want to stay longer inside a transporter. This behaviour led me to make some modifications, solely in his case, to the test procedure. Twice, under the advice of the veterinarian. I administered him half a ration of food before subjecting him to the trial, aiming for a less aggressive response, and it seemed to have worked.

In nature, the animal almost always tends to select, where able to discern, the largest piece of food, which consistently provides the greatest advantage (Andersson, 1982, Basolo, 1990, Lucon-Xiccato \& Dadda, 2017). Meanwhile, the fact that once the mechanism was understood, the choice was made swiftly and almost impulsively, could be attributed to a concern that the food might be taken before him by a possible conspecific or another competing species.

Also, the spider monkeys showed a very good performance. For the first four sequences, I presented the tests without including the removal of the plate, so I decided, once all the trials were completed, to take 4 more trials, to be equally among the tests. I excluded from my results the first four; considering all the others. Chester selected the longer stimulus 15 times out of 16 and Festus 16 times out of 16 .

I observed that Festus was less impulsive than Chester, Festus approached the trials and observed both stimuli before deciding while Chester looked quickly and impatiently grabbed one of them. Chester once I removed for the first time the apparatus displayed aggressive behaviour and vocalized. In the tests before the removal, he consistently took both sticks. I have also noticed that they were particularly distracted in the presence of tourists so all the tests were taken avoiding groups of tourists.

Regarding the capuchins, I have more remarks to make. They obtained different results: Coco succeeded in 11 tests out of 16, Pablo 12, and Honey 11. Looking at the trials, as the difference between the sticks decreased, the percentage of errors increased. For instance, in the ratio of $1 / 3$, out of 16 tests conducted, only two were incorrect, whereas in the ratio of $3 / 4$, there were four errors, those results were confirmed and analysed from a statistical point of view However, the errors for individuals were distributed almost randomly across the various trials. Therefore, we cannot assert for sure that they perceive the ratio of $1 / 3$ better than the ratio of $3 / 4$. Several factors influenced the outcome of their tests. Excessive heat, for instance, posed a challenge; I observed their behaviours both during the test administration and throughout the day. When temperatures were high and there had been no rain for several days, they exhibited reduced concentration and increased agitation. Conversely, on days following rainfall, they appeared calmer and undertook the test without displaying signs of aggression. Then, I had to be certain that no tourists were passed near their enclosures in the minutes before the test otherwise they would be stressed.

I had also to increase the distance between one stimulus and another because every time they tried to grab both of the items, they knew that they could have both of them and they did not make a choice anymore, it was not important to take firstly the longer one. There is also the consideration that capuchins may not effectively perceive the quantity difference with the stimuli I used because, in their usual diet, fruits, vegetables, and meat are cut into large chunks. The sizes of the banana sticks
for spider monkeys, for example, were ideal because they were commonly fed with fruits and vegetables cut into strips. Further studies with different types of stimuli would be necessary to better understand this peculiarity.

A common outcome from the previous studies involving capuchins (VanMarle et al., 2006) was that they could rely on the ABS (Analogue Magnitudes System). In the previous tests, capuchin monkeys exhibited the capacity to measure and contrast varying quantities of a continuous substance with a level of proficiency comparable to their assessment of equivalent proportions (i.e., ratios) of distinct objects. Consistently, in all ratio comparisons, capuchins numerous times favoured the larger quantity of the substance, significantly surpassing random chance. Their performance displayed a reliance on the ratio involved: the greater the proportional difference, the higher the inclination of participants to select the larger quantity. All those results are in contrast with the ones that I've obtained. Based on my results, I cannot assert that they effectively perceive the difference in quantity nor if they use the ABS. The best result was achieved by Pablo, scoring 12 out of 16 with a p value $=0.07$ which, nonetheless, is relatively low and not sufficient to be considered statistically significant. The accuracy with which they distinguish 0.33 appears very similar to their accuracy in distinguishing 0.75 . In light of this, there are two possible explanations: the first is that they are highly precise, to the extent that only when presented with a very close ratio, for instance, $17 / 1$, they fail to perceive the difference, so we cannot exclude that with an increase in trials, the correct choices would proportionally rise, thereby minimizing the error rate. The second possibility is that the errors do not follow a specific pattern determined by the ratios; errors seem to occur randomly.

In conclusion, while the individual performances varied, the spider monkeys and the howler monkeys exhibited statistical significance in perceiving quantity differences, contrasting with the capuchins' inconsistent performances, indicating a lack of statistical significance in their ability to differentiate between presented quantities. In the meanwhile, if you look at the average, you can see that the monkeys are quite accurate in all tasks, in particular, if you perform a one-sample $t$-test for each ratio you notice that monkeys can statistically distinguish $1 / 3$ ratio, $1 / 2$ ratio, $2 / 3$ ratio, and $3 / 4$ ratio. Despite this being a pilot study and notwithstanding the various limitations encountered during the tests, the overall obtained results indicate that the tested monkeys are capable of discerning differences in quantity. I hope that this study can be further explored and examined again for future investigations within the realm of cognitive science concerning New World primate species.

## 5. Reference List

- Addessi, E., Crescimbene, L., \& Visalberghi, E. (2008). Food and token quantity discrimination in capuchin monkeys (Cebus apella). Animal Cognition, 11, 275-282.
- Agrillo, C., Dadda, M., \& Bisazza, A. (2007). Quantity discrimination in female mosquitofish. Animal cognition, 10, 63-70.
- Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. Nature, 299(5886), 818-820.
- Basolo, A. L. (1990). Female preference for male sword length in the green swordtail, Xiphophorus helleri (Pisces: Poeciliidae). Animal Behaviour, 40(2), 332-338.
- Beran, M. J., Evans, T. A., \& Harris, E. H. (2008). Perception of food amounts by chimpanzees based on the number, size, contour length and visibility of items. Animal behaviour, 75(5), 1793-1802.
- Beran, M. J., Parrish, A. E., \& Evans, T. A. (2015). Numerical cognition and quantitative abilities in nonhuman primates. In Mathematical cognition and learning (Vol. 1, pp. 91-119). Elsevier.
- Boeving, E. R., Belnap, S. C., \& Nelson, E. L. (2017). Embraces are lateralized in spider monkeys (Ateles fusciceps rufiventris). American Journal of primatology, 79(6), e22654.
- Bogale, B. A., Kamata, N., Mioko, K., \& Sugita, S. (2011). Quantity discrimination in jungle crows, Corvus macrorhynchos. Animal Behaviour, 82(4), 635-641.
- Brannon, E. M. (2005). What animals know about numbers. Handbook of mathematical cognition, 381, 85-107.
- Caicoya, A. L., Colell, M., Holland, R., Ensenyat, C., \& Amici, F. (2021). Giraffes go for more: a quantity discrimination study in giraffes (Giraffa camelopardalis). Animal Cognition, 24, 483-495.
- Cortes-Ortíz, L., Rosales-Meda, M., Williams-Guillén, K., Solano-Rojas, D., MéndezCarvajal, P.G., de la Torre, S., Moscoso, P., Rodríguez, V., Palacios, E., Canales-Espinosa, D., Link, A., Guzman-Caro, D. \& Cornejo, F.M. 2021. Alouatta palliata (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2021: e.T39960A190425583.
- Cortes-Ortíz, L., Solano-Rojas, D., Rosales-Meda, M., Williams-Guillén, K., MéndezCarvajal, P.G., Marsh, L.K., Canales-Espinosa, D. \& Mittermeier, R.A. (2021). Ateles

Geoffroyi (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2021: e.T2279A191688782.

- Diaz, F., \& Wasserman, E. A. (2023). The role of numerical and nonnumerical magnitudes in pigeons' conditional discrimination behavior. Journal of Experimental Psychology: Animal Learning and Cognition, 49(4), 253.
- Ferrigno, S., Hughes, K. D., \& Cantlon, J. F. (2016). Precocious quantitative cognition in monkeys. Psychonomic Bulletin \& Review, 23, 141-147.
- Garland, A., Low, J., \& Burns, K. C. (2012). Large quantity discrimination by North Island robins (Petroica longipes). Animal cognition, 15, 1129-1140.
- Gil-da-Costa, R., \& Hauser, M. D. (2006). Vervet monkeys and humans show brain asymmetries for processing conspecific vocalizations, but with opposite patterns of laterality. Proceedings of the Royal Society B: Biological Sciences, 273(1599), 2313-2318.
- Gómez-Laplaza, L. M., Díaz-Sotelo, E., \& Gerlai, R. (2018). Quantity discrimination in angelfish, Pterophyllum scalare: a novel approach with food as the discriminant. Animal behaviour, 142, 19-30.
- Jones, S. M., \& Brannon, E. M. (2012). Prosimian primates show ratio dependence in spontaneous quantity discriminations. Frontiers in Psychology, 3, 550.
- Kelly, E. M. (2016). Counting on your friends: The role of social environment on quantity discrimination. Behavioural processes, 128, 9-16.
- Lin, F. C., Whiting, M. J., Hsieh, M. Y., Shaner, P. J. L., \& Lin, S. M. (2021). Superior continuous quantity discrimination in a freshwater turtle. Frontiers in Zoology, 18, 1-11.
- Lucon-Xiccato, T., \& Dadda, M. (2017). Individual guppies differ in quantity discrimination performance across antipredator and foraging contexts. Behavioral ecology and sociobiology, 71, 1-9.
- Oleksiak, A., Postma, A., van der Ham, I. J., Klink, P. C., \& van Wezel, R. J. (2011). A review of lateralization of spatial functioning in nonhuman primates. Brain research reviews, 67(12), 56-72.
- Stancher, G., Rugani, R., Regolin, L., \& Vallortigara, G. (2015). Numerical discrimination by frogs (Bombina orientalis). Animal Cognition, 18, 219-229.
- Stevens, J. R., Wood, J. N., \& Hauser, M. D. (2007). When quantity trumps number: discrimination experiments in cotton-top tamarins (Saguinus oedipus) and common marmosets (Callithrix jacchus). Animal Cognition, 10, 429-437.
- VanMarle, K., Aw, J., McCrink, K., \& Santos, L. R. (2006). How capuchin monkeys (Cebus apella) quantify objects and substances. Journal of Comparative Psychology, 120(4), 416.
- Vonk, J., Torgerson-White, L., McGuire, M., Thueme, M., Thomas, J., \& Beran, M. J. (2014). Quantity estimation and comparison in western lowland gorillas (Gorilla gorilla gorilla). Animal cognition, 17, 755-765.
- Westergaard, G. C., Byrne, G., \& Suomi, S. J. (1998). Early lateral bias in tufted capuchins (Cebus apella). Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology, 32(1), 45-50.
- Williams-Guillén, K., Rosales-Meda, M., Méndez-Carvajal, P.G., Solano-Rojas, D., Urbani, B. \& Lynch Alfaro, J.W. 2021. Cebus imitator (amended version of 2020 assessment). The IUCN Red List of Threatened Species 2021: e.T81265980A191708420.

