Tufted capuchin monkeys (*Sapajus sp*) learning how to crack nuts: does variability decline throughout development?

Briseida Dogo Resende, Mariana Baldy Nagy-Reis, Fernanda Neves Lacerda, Murillo Pagnotta, Carine Savalli

Abstract

We investigated the process of nut-cracking acquisition in a semi-free population of tufted capuchin monkeys (*Sapajus sp*) in São Paulo, Brazil. We analyzed the cracking episodes from monkeys of different ages and found that variability of actions related to cracking declined. Inept movements were more frequent in juveniles, which also showed an improvement on efficient striking. The most effective behavioral sequence for cracking was more frequently used by the most experienced monkeys, which also used non-optimal sequences. The nature of the elements that compose the nut cracking task channels development, comprising some variation in behavior sequences and actions.

Keywords: primates; tool use; ontogenesis

Tufted capuchins from different populations spontaneously crack nuts using tools (Fragaszy, Izar, Visalberghi, Ottoni, & Oliveira, 2004; Moura & Lee, 2004; Ottoni & Mannu, 2001). They usually place the nut on a horizontal surface (usually a stone, called anvil) and strike it with a second stone (called hammer) using one or both hands. This is a complex behavior, shared with chimpanzees, in which several elements and actions must be coordinated, and it takes combinatorial manipulation of objects to develop (Inoue-Nakamura & Matsuzawa, 1997; Resende, Ottoni, & Fragaszy, 2008). Similarly, wild chimpanzees at Mahale Mountains National Park process the fruit of *Saba florida* to eat its pulp. This complex task requires manual dexterity and the process involves several stages. Corp & Byrne (2002) investigated the variation in the manual processing techniques used by different individuals and across age. When compared with adults, infants used a wider variety of actions. They usually co-fed with their mothers, and paid them close attention. The authors attributed some aspects of the development of processing skills to physical maturation (leading to increased manual abilities) and trial and error learning, but they argued that the social environment could also scaffold the learning process.

Insert Figure 1: Adult capuchin is cracking nuts, while a juvenile explores the site at Tietê Ecological Park, SP, Brazil. Some *Syagrus* nuts are on the anvil. Photo: Mariana B. Nagy-Reis.

Longitudinal studies of the development of manipulative behavior in free-living non-human primates are rare (e.g. Corp & Byrne, 2002, Inoue-Nakamura & Matsuazawa, 1997; Resende et al., 2008.) Accordingly, while several studies of the nut-cracking behavior in capuchin monkeys have focused on aspects such as biomechanics and selectivity (e.g. Fragaszy et al., 2010; Liu et al., 2009; Visalberghi et al., 2009), few of them focus on developmental aspects. Resende et al. (2008)

conducted a longitudinal study of the emergence of tool using skills of capuchins living at Tietê Ecological Park, São Paulo State, Brazil (hereafter TEP), where the monkeys spontaneously crack nuts of *Syagrus romanzoffiana* (Figure 1). Adults frequently succeed with one or two strikes (Resende, Hirata, Nagy, & Ottoni, 2011). Resende et al. (2008) found that manipulation of nuts and stones and percussive actions with these objects emerged when the monkeys were as young as six months old. Moreover, in order to fully succeed in cracking nuts, they had to learn the correct action sequence: (1) take the nut, (2) place it on the anvil, (3) take the hammer stone and (4) hit it against the nut. The monkeys initially performed the elements of the action sequence in variable order before producing the correct one consistently. This is similar to nut-cracking behavior of wild chimpanzees (Inoue-Nakamura & Matsuzawa, 1997).

In this study, we investigated the process of nut-cracking acquisition using a dynamic systems view of development. This view predicts high variability in configuration during exploration stage and progressive stability (Smith & Thelen, 2003). We first compared efficiency across different age classes, and then used longitudinal analysis and behavior sequence analysis to check if variability declined over time. We predicted that actions not associated with efficient nut-cracking would tend to disappear, as behavior stabilizes, and that effective behavioral sequence would be used more frequently by the most experienced monkeys.

Methods

Subjects and Study Area

Our subjects were tufted capuchin monkeys living in a semi-free group in Tiete Ecological Park (TEP). We identify them as *Sapajus sp*, given that the present population descended from released animals likely representing what are now considered separate species (*Sapajus apella*, *Sapajus nigritus*, and *Sapajus libidinosus*) (for a taxonomic review, see Lynch-Alfaro, Silva Jr., & Rylands, 2012). This group has been studied since 1995 (Otonni & Mannu, 2001) and was already habituated to researchers and equipment when this study began.

The animals were provisioned but also foraged on naturally available food items such as fruits, leaves and small birds and mammals (Ferreira, Resende, Mannu, Ottoni, & Izar, 2002). The palm tree *Syagrus romanzoffiana* grows in the park and produces nuts, which the monkeys could collect from the ground to crack open and eat the kernel (Ottoni & Mannu, 2001). The group consisted of 28 monkeys, but 11 of them were excluded from our analysis because they were rarely present at the filming site. Table 1 shows the subjects included in our different analyses.

Insert Table 1

Data Collection and Transcription

We collected data using four video cameras (Sony HC90), with the frequency of acquisition = 60Hz. The cameras were placed inside plexiglass boxes for protection and were positioned from orthogonal directions, covering an area of approximately 1 m^2 of the nut-cracking site (Figure 2). To ensure the capture of the best angle for analysis, we used the images of the camera in which the sagittal plane of the monkey was perpendicular to the camera. As soon as any monkey approached the site, we started filming using remote controls. Researchers stayed at the nut-cracking site five days a week, usually from 8h30 am to 4h00 pm. The monkeys used the site for cracking nuts in 48 days distributed from April/2006 to February/2007.

Insert Figure 2: Scheme of the nut-cracking site (at the center) and the relative positions of the four video cameras (C1-C4).

Following Resende et al. (2008), a cracking episode started when one or more monkeys, simultaneously or sequentially, struck an object (usually a stone) against an anvil, whether or not another object had been placed on the anvil beforehand. The episode ended when the last subject visiting the site stopped pounding, did not look for other nuts and started performing activities unrelated to nut-cracking. Brief interruptions associated with moving and searching for nuts, or observing other monkeys cracking nuts were included within an ongoing episode.

We transcribed the behaviors in each episode using the categories defined in Table 2. For the longitudinal analysis, we transcribed the data using EthoLog 2.25 software (Ottoni, 2000). For each episode, we recorded the absolute frequencies of adequate placement and effective striking, inept movements and successful cracking of nuts (see Table 2 for detailed descriptions). The software built first order matrices with antecedent and subsequent behaviors, which we used in the behavior sequence analysis.

Insert Table 2

Analysis

1) Comparing the cracking behavior across different age classes

We measured the proficiency of each subject (n=17) using the three following variables: 1) Efficiency (EF), defined as the number of strikes needed to open a nut. To calculate this we divided the total number of strikes performed by each monkey by the total number of nuts it opened. Values closer to 1 indicate higher efficiency. When the subject did not open any nut, we arbitrarily considered EF = 100. Those who had EF ≤ 2 were considered more efficient monkeys; those with

EF>2 were considered less efficient. 2) Index of Nut-placement Adequacy, a measure of the perceptual-motor skills necessary to place a nut on the anvil. To calculate this, we divided the number of adequate nut placement by the total number of nut placements on any surface available to the monkey. We considered nut placement to be adequate if a nut was placed on the anvil before the strike and if it did not fall off. 3) Index of Efficient Strikes, a measure of the perceptual-motor skills necessary to strike a nut and open it. To calculate this, we divided the total number of efficient strikes by the total number of strikes performed by each subject. Efficient strikes happened when the hammer hit the nut that was on the anvil.

We used Mann-Whitney tests to determine if Efficiency, Index of Nut-Placement Adequacy, Index of Efficient Strikes, and Number of Strikes, were different between adults and juveniles. To determine if efficiency increased with age, we correlated Age with a) Efficiency; b) the Index of Nut-placement Adequacy; and c) the Index of Efficient Strikes using Spearman Rank Correlation.

2) Longitudinal analysis

We followed the longitudinal changes in the cracking behavior of only the subjects that were filmed throughout the whole period of data-collection (n = 7). Following the dynamic systems view, we expected to find an optimization of actions throughout the learning processes, with an increase in the rates of Adequate Placement and Efficient Strikes, followed by stabilization.

To characterize the changes in the frequency of the different nut-cracking behavioral categories throughout development, we calculated the following rates for each subject: Adequate Placement (number of adequate placements / time), Efficient Strikes (number of efficient strikes / time), Non-adequate Strikes (number of non-adequate strikes / time) and Inept Movements (number of inept movements / time). “Time” was defined as the total duration of filmed episodes of cracking per month.

For the longitudinal analysis of Efficiency, Efficient Strikes, Non-efficient Strikes, Inept Movements and Adequate Placement, we used a two-month-period data: April/May, June/July, August/September, October/November, December/January, and the month of February. Friedman non-parametric test was used to determine whether these frequencies changed throughout the months.

All the non-parametric tests were done using the software BioEstat 3.0 (Ayres, Ayres Jr., Ayres, & Santos, 2007).

3) Behavioral Sequences Analysis

We used all nut-cracking episodes from subjects (N=13) that were successful in opening nuts (Average number of episodes/subject=15.1, SD = 11.1). We considered that there is an optimal sequence of behavior for cracking nuts: Take nut – Place nut – Take hammer – Strike. Here “optimal” is used in terms of the highest benefit-cost ratio, since this is the shortest sequence that can be used to open a nut. We hypothesized that the more efficient the monkey was, the more it would use the optimal sequence. To test this, we analyzed the behavioral sequences considering only the behavioral categories involved in the sequence (Take nut; Place nut; Take hammer; Strike). The other categories were collapsed into the label “Others”. We then built a symmetric matrix with antecedent and subsequent behavior, and, for each nut-cracking episode, we divided the number of optimal pairs of behavioral sequences (i.e. Take nut / Place nut; Place nut / Take hammer; Take hammer / Strike) by the total number of possible pairs. This represented the proportion of optimal sequences used in each episode of each individual. This proportion was then averaged by episodes, so that, for each monkey we calculated an Index of Optimal Sequence that ranges from 0 to 1 (optimal sequences = 1). We used Spearman test to correlate their Efficiency to the Index of Optimal Sequence, predicting a positive correlation. We also predicted that the least efficient monkeys would frequently use several sequences of behavior, and the most efficient monkeys would preferably use the most efficient sequence for cracking the nut, indicating a decline in variability. We used Mann-Whitney test to compare the most efficient (EF≤2) subjects with the least efficient ones (EF>2) to test this.

This study is in agreement with ASP Principles for the Ethical Treatment of Non Human Primates and it was approved by institutional animal care committees. All research reported in this manuscript adhered to the Brazilian legal requirements.

Results

1) Comparing the cracking behavior across different age classes

Adults showed the majority of strikes (85%) and their Number of Strikes was different from the juveniles' (Mann-Whitney test: Z(U)=20.10, N=17, p<0.05). There was a strong correlation between Age and Efficiency (Spearman Rank Correlation: r_S=0.80, p<0.01, N=16), and adults were more efficient than juveniles (Mann-Whitney test: Z(U)=3.12, N=17, p<0.01). Adults and juveniles also differed on the Index of Efficient Strikes (Mann-Whitney test: Z(U)=3.01, N=17, p<0.01). Adult males showed the highest scores (61%) followed by adult females (34%), juvenile females (23%) and juvenile males (11%). The Index of Efficient Strikes was positively correlated with Age (Spearman Rank Correlation: r_S=0.71, p<0.01, N=16). Considering that a previous study showed that the animal's weight can predict its success in nut-cracking (Fragaszy et al., 2010), we wondered if these findings were a consequence of adults being heavier than juveniles. We thus compared adult females (lighter) to adult males (heavier), and found that they did not differ on Efficient Strikes (Mann-Whitney test: Z(U)=1.46, N=11, p=0.14), nor on Efficiency (Mann-Whitney test: Z(U)=1.28, N=11, p=0.20).

Adults and juveniles differed upon the Index of Nut-placement Adequacy (Mann-Whitney test: Z(U)=3, N=17, p<0.01), but there was no correlation between the Index of Nut-placement

Adequacy and Age (Spearman Rank Correlation: r_S =0.418, p=0.11, N=16). This index increases with age until around 4 years old and then it seems to stabilize (Figure 3).

Figure 3: Index of Nut-placement increases with age and it stabilizes in adults.

2) Longitudinal analysis

Contrary to what we expected, the overall Efficiency and the Rate of Adequate Placement did not change over time (Efficiency: Fr=2.34; gl=3; p=0.5; Adequate Placement: Fr=2.16, gl=4; p=0.7). However, when only juveniles who started to succeed in the cracking task during this study were considered, there was an improvement in Efficiency (Chu = from 4.9 to 3.6 hits to crack a nut; Jab = from no cracking to 2.7 hits to crack a nut). The Rate of Efficient Strikes differed significantly over the months (Fr=9.32; gl=4; $p<0.05$), increasing (Figure 4). The rate of Non-efficient Strikes did not significantly differ throughout the study as a whole. But when we considered the ratio Efficient Strikes/Non-efficient Strikes, we found a significant difference, indicating that efficient strikes increased and non-efficient strikes declined with experience (Figure 5), as predicted (Fr=0.04; gl=4; $p<0.05$). Inept Movements were more frequent in younger monkeys (Mann-Whitney test: Z(U)=2.738, $p<0.05$), indicating that younger monkeys performed more irrelevant acts for solving the task.

Figure 4: ES (Number of Efficient Strikes/Seconds) throughout 9 months of data collection.

Figure 5: ES/NS (Efficient Strikes/Non-efficient Strikes) throughout 9 months of data collection.

Chu and Jab, the younger monkeys who learned to crack open nuts during this study, behaved as predicted after they started cracking: their rates of Efficiency, Adequate Placement and Efficient Strikes increased, and the rates of Non-efficient Strikes and Inept Movements declined.

3) Behavioral Sequences Analysis

The “More efficient” monkeys (which used up to 2 strikes to open the nut) were Drw, Dav, Edu, Med, Sus, Ze and Vav, and the “Less efficient” (which used more than 2 strikes) were Csc, Chu, Fil, Fri, Jab. Their Index of Optimal Sequence and their Efficiency are shown on Table 1. As we expected, higher Efficiency was strongly correlated with higher use of Optimal Sequence (Spearman rs=-0.82, n=13, $p<0.05$), and, as predicted, the most efficient monkeys differed from the least efficient subjects in their use of the Optimal sequence (Mann-Whitney test: Z(U)=2, n=13, p=0.05). Adults and juveniles also differed in the predicted direction (Mann-Whitney test: Z(U)=2.16, n=13, $p<0.05$). We also found a positive correlation between Age and the Index of Optimal Sequence ($r^2=0.56$; n=12; $p<0.01$).

Discussion

As the monkeys grew older, activities related to cracking nuts first increased, then stabilized and variability declined, according to what we expected. Thelen and Corbetta (2002) stated that variability in behavior is a way of detecting instability: when a system stabilizes, variability declines. Our results corroborated the predictions: the older and the more efficient the monkey was, the more it used the optimal sequence for cracking nuts, and variability declined.

Adequate Nut-placement increased until up to four years of age, then it stabilized. Most of our juvenile subjects were older than four years. At this age, tufted capuchins are closer to being considered young adults, and this might explain why we found no difference on the Index of

Adequate Nut-placement between juveniles and adults. Efficient Strikes increased for all subjects through time: as predicted, variability declined and tool users channeled their actions toward those that would result in opening up the nut. Juveniles that achieved success in the cracking task also increased Adequate Placement and Efficient Strikes, and declined Inept Movements and Non-efficient Strikes. Our subjects were all above 36 months-old: by this age, capuchins are juveniles able to combine actions and objects of the nut-cracking task in the correct order (Resende et al., 2008). Similarly, Corp and Byrne (2002), studying chimpanzee's development of complex extractive foraging task, noticed that infants showed more variability in actions then adults, including some which were not efficient for processing the fruit and reaching its pulp. This variability declined as they got older and more proficient: procedures present in adult repertoire persisted and increased with age, whereas procedures absent in adult repertoire tended to disappear. They highlighted the importance of physical maturation for understanding the development of the studied technique, followed by trial and error learning. In the present study, physical maturation is less important for explaining the differences we found because we compared older juveniles and adults. Although weight is a strong predictor of efficiency (Fragaszy et al., 2010), the monkeys´ experience needs to be considered to explain our results. None of our subjects reached the highest Index of Optimal Sequence, meaning that non-optimal sequences of behavior persisted even in adults. These "errors" (i.e. deviance from the optimal sequence) might be considered as self-generated opportunities for perceptual learning that can guide subsequent acts (Lockman, 2000). In other words, capuchins from our study might be seeking perceptual variation, using this as a source of information that guides the acquisition of tool use. The monkey's body is constantly changing throughout its development, including its size, weight and strength. This means that, with age, it has to adjust its movements and strategies to maintain proficiency in nut-cracking (or in other tasks). For this reason, even after a certain behavior seems stabilized, it might be beneficial to keep exploring and trying different manipulations periodically. These hypotheses must be further investigated.

The persistence of variability is important for a generalist monkey such as the tufted capuchin, who survives well in different kinds of environments. They are always exploring different forms of doing things, so they must use their actions in flexible ways. On the other hand, some stable and socially transmitted behaviors (traditions) have been described in groups of capuchins (Ottoni & Izar, 2008), and social life might be partially responsible for maintaining them (Fragaszy et al., 2013; Gunst, Boinsky, & Fragaszy, 2008; Ottoni, Resende, & Izar, 2005). If we consider cracking nuts, the nature of the elements that compose the task channels a way of acting, which comprises some variation. Initial variability in manipulative behavior can make way for developmental changes in skills. But social life, the growth and biomechanics of the body and the nature of the task also constrain the possible changes and must be taken in consideration.

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Table 1

Subjects, Age (J=Juvenile; A=Adult), Efficiency = EF = (N strikes/cracked nuts);Sex (M=Male; F= Female), studies they took part in. and IOS = Index of Optimal Sequence (refers to the subjects from Part 3).

Subject	Age	EF	Sex	1	2	3	IOS
Ana	A	2.6	F	X	-	-	-
Ang	J	3.0	F	X	-	-	-
Chu	J	6.5	M	X	X	X	0.42
Csc	A	4.5	F	X	X	X	0.44
Cla	J	100	F	X	-	-	-
Drw	A	2.5	M	X	X	X	0.41
Dav	A	1.7	M	X	-	X	0.42
Edu	A	1.4	M	X	-	X	0.5
Fil	A	5.0	F	X	X	X	0.39
Fri	J	7.0	F	X	-	X	0.25
Jab	J	93	F	X	X	X	0.19
Jan	A	1.3	F	X	-	-	-
Med	A	1.6	M	X	-	X	0.46
Sus	A	2.0	M	X	-	X	0.43
Vav	A	1.9	F	X	-	X	0.41
Vck	J	100	M	X	X	X	0.33
Ze	A	1.8	M	X[1]	X	X	0.44

[1]Removed from analysis where his exact age was required, because it is unknown

Table 2 – Behavioral categories used in the transcription of the cracking episodes.

Categories	Label	Description	
Arrive at the site	-	Subject gets closer to the anvil stone.	
Take nut	-	Subject takes the nut using the hands.	
Position Nut	Adequate	Subject puts the nut on the anvil stone, so it does not fall, and where the hammer stone can hit it.	
	Non-adequate	Subject leaves the nut on the anvil stone in an unstable position, so that it falls off the anvil, or in such a way that it is impossible for the hammer to strike the nut correctly, or places something other than a nut.	
Take the hammer	Adequate hammer	Hard object used to hit against another object or surface, usually stone, weighing between 0,30 and 0,85kg and an area between 10X15 cm and 20X30 cm, and at least one flat side.	
	Non-adequate hammer	Hard or soft object, with no flat side, used to hit against an object or surface.	
Strike	Effective	Positioned nut	Subject strikes the plain side of an adequate hammer against the nut that he placed on the anvil (even if the nut is not cracked open).
		Pre- existent nut	Subject strikes the plain side of an adequate hammer against the nut that was already placed on the anvil (even if the nut is not cracked open).
	Non-effective	Subject strikes the hammer against the nut, which falls or flies away.	
Successful nut-cracking	-	Subject cracks open the nut endocarp.	

Inspect	-	Subject closely examines nuts or other objects on the site's ground, or around.
Ingest	-	Subject eats the cracked nuts or crumbs of nuts.
Inept movements	-	Subject rolls, presses, or throws nuts or stones.
Leave	-	Subject leaves the site.
Other	-	Subject watches, grooms, threatens or attack other monkeys or animals. It may also lick, or play

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Figure1
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Figure2

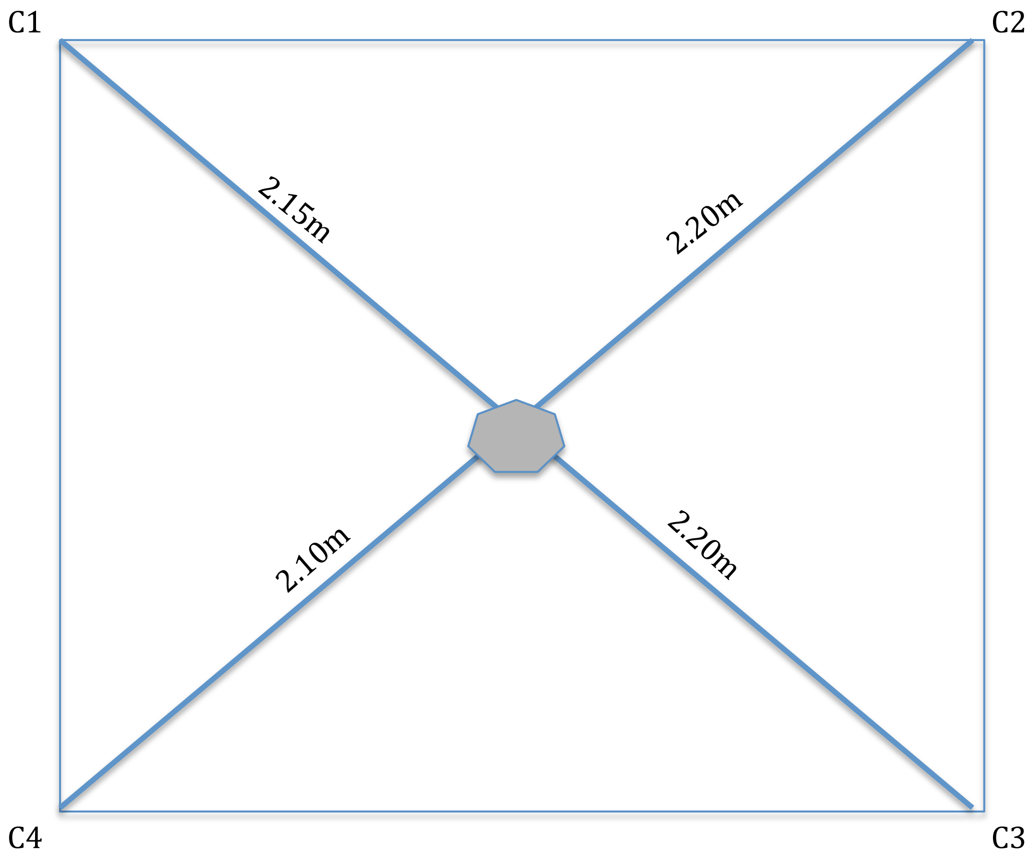

Figure3
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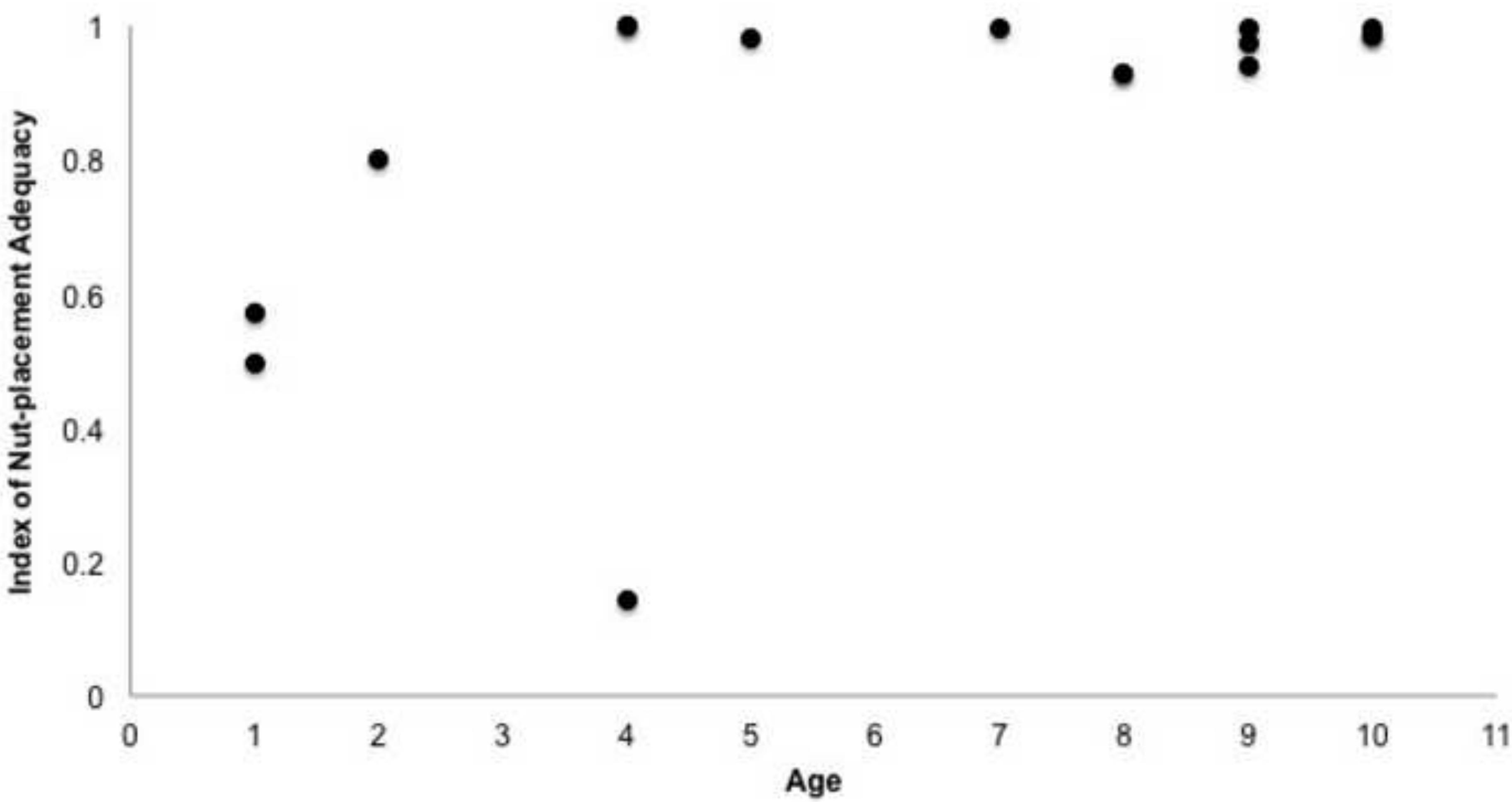

Figure4
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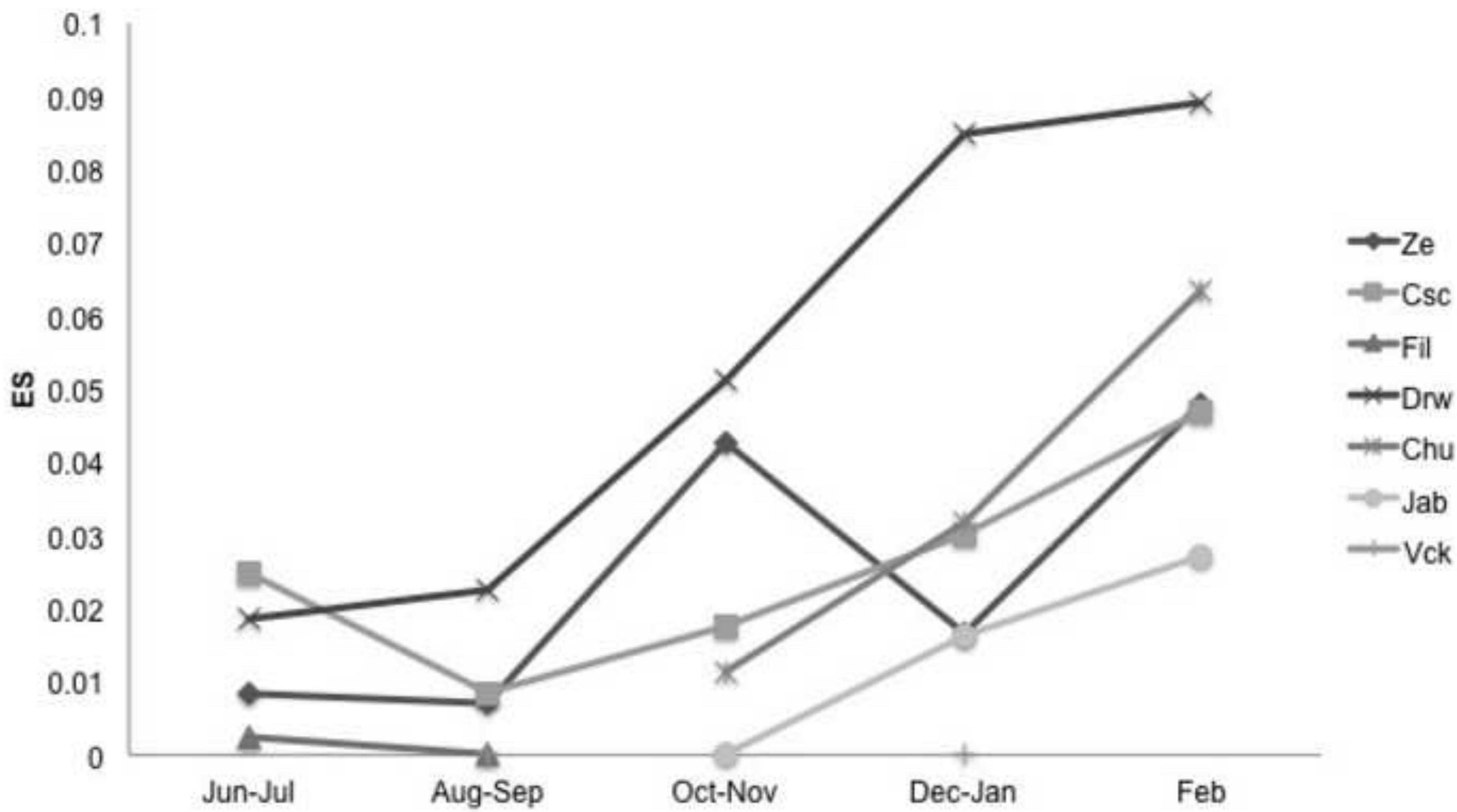

Figure5
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