From learning 'who monkeys support', we infer 'What they know'

Yijun Yang[1, *]

[1]Division of Social Sciences, University of Chicago, Chicago, Illinois, the United States of America

*Corresponding author: yijunyang@uchicago.edu

Abstract. Though understanding what monkeys see and know without inferring anthropomorphically is virtually impossible, the more detail and concrete the ground of this inference we have, the more promising our surmise would be. A closer look into the male-male relation in cercopithecines, a genus of old world monkeys, confirms what scientists have theorized: in the absence of inclusive fitness advantage, the males cooperate closely with nonkins following the norm of reciprocity, resulting in a stratified rather than linear, continuous dominance hierarchy, as a function of seniority and age. This feature is ubiquitous and found in 3 species of macaques and yellow baboons; and it is reliably robust across 4 continents, 5 study sites, 17 troops, and 297 monkeys. In other words, although new members of a group are often at the prime age of belligerence, because senior males share a longer history of cohabitation and reciprocal relation with one another, they intervene in each other's fight and outcompete the new members who are often not supported. This implies that, in cercopithecines, the support to nonkins may be guided by a mental scorebook, which enforces them to reciprocate in the future when their reciprocal partners are in need.

Keywords: Cognition; Cooperation; Evolution; Comparative Approach.

1. Introduction

Cooperation combines individual forces in a contest, making the outnumbered party disadvantageous. As competition grows fiercer, game theory predicts that natural selection would favor more sophisticated forms of cooperation [1]. For example, on the primeval stage, the union of multiple functionally complementary replicators outcompetes the union that is composed by a smaller number of functionally homogeneous replicators [2]. And for a single-cellular organism, teaming-up with a mitochondrion facilitates energy conversion and is metabolic advantageous [3]. As cells join and become specialized, multi-cellular organisms emerge, and many of them combine forces and form groups. In short, cooperation marks every milestone of the evolution of natural selection [1].

The evolution of human cognition is of no exception to this trend: advanced cognitive ability is the key to solve the problems occurred or may occur in complex forms of cooperation, especially when the cooperators are not genetically related [4, 5]. Thus, evolutionary psychology that investigates how human cognition evolved becomes increasingly important. As we cannot directly ask what nonhuman animals know, analyzing their behavior is currently the only source for us to understand to what extend their cognition is similar or different from human beings, making evolutionary psychology and its comparative method increasingly valuable [6].

Compared with other mammalian species living in groups composed mainly by close kins who are the primary cooperators and even cobreeders, social primates who live and cooperate closely with nonkins show several unique cognitive adaptations that had been thought belonging uniquely to humans [7]. For instance, behavioral contagion, a manifestation of empathy has been found in capuchin monkeys, chimpanzees, and humans [8-10]. In addition, disadvantageous inequity aversion has also been consistently found in capuchin monkeys and chimpanzees, who reject the reward and protest the experimenter when their peers get a more desirable reward than themselves [11, 12]. Like humans, in ultimatum game, chimpanzees tend to play fairly, especially when the final reward assignment is dependent on whether the partner accepts their offer [13]. Finally, chimpanzees are found to hunt and patrol strategically and in group, use tools to forage and extract food, observe others' tool-using closely, and more likely to pick up the tool that has been used and discarded by others, suggesting that they possess the cognitive ability to monitor and incorporate what others do and know

[14]. Together, although sex, dominance hierarchy, and tolerance have been found influencing social decision-making [15], monkeys and great apes show a wide repertoire of adaptations that facilitate their cooperation with nonkins.

Ontogenetically, in chimpanzees and humans, the maturation of social contagion and inequity aversion are two millstones of developing full-fledged social cognition. Few weeks after birth, the infants of the two species engage in neonatal imitation or protoconversation with their caregivers [16-18]. Later, they become increasingly sensitive to the attention, intention, and belief of other as the skills of individual and shared intentionality mature [5].

However, little attention has paid on studying the above adaptations in monkeys, and this paucity of research prevents us from identifying the starting point of the evolution of complex mechanisms used in cooperation, like intention reading and sharing. Thus, although monkeys are like humans and chimpanzees as they form, recognize, and exploit social relations, little is known about how they achieve this understanding and what they know about others and themselves [19]. The answer to these questions may help us clarify in what ways are monkeys similar and different from great apes and humans, thereby drawing a continuity of cognitive adaptations that have sequentially and additively appeared in the evolution and are the composing infrastructures of the full-fledged human cognition. Hence, it would be fruitful to know how monkeys cohabitate and cooperate with one another. As an initial step, we should focus on identifying the socioecological structures of their groups and explain them with the cognitive ability manifested by the social behaviors of monkeys.

Based on the impression from previous studies, it is suspected that male monkeys may form reciprocal relations to support one another in antagonistic interactions [20, 21]. This brings three predictions: first, if reciprocal support in antagonistic interactions is common, it would bring structural changes to the dominance hierarchy that is a ranking of status based on the turnouts of dyadic antagonistic interactions [22]; second, the structural change would be found in the sex that cooperate with nonkins, for example male cercopithecoid monkeys, because their societies are characterized as female-bonded groups (hereafter FB groups) where females maintain a lifelong cohabitation with their kins while males migrate and live with nonkins [23, 24]; finally, because reciprocal relations are established gradually after repeated prosocial dyadic interaction (e.g., you scratch my back and I scratch yours) [25], seniority and age would thus influence the frequency and strength of antagonistic support, thereby indirectly influencing the shape of the dominance hierarchy.

To test these predictions, the present study proposes two hypotheses: First, the senior males who share a long history of cohabitation are on stable, adjacent, and ambiguously divided dominance ranks (*Hypothesis 1*); Second, the dominance rank of the senior males may differ from that of less senior and younger ones (*Hypothesis 2*) because they may preferentially and reciprocally support the members of the same cohort of seniority in antagonistic interactions.

2. Method

As predicted by the hypotheses, the relation between seniority and dominance hierarchy is expected to exist ubiquitously across groups of different geographic regions and even distinct monkey species. To meet this demand, a focus on the lineage of cercopithecines was chosen given the great heterogeneity of the species and their ecology and the prosperity of previous research. To minimize the impact of kin selection, only males and their dominance hierarchy were investigated. Given the above considerations, macaques (*Macaca*) and baboons (*Papio*) were chosen as the subjects of our study.

2.1 Material and Subject

To gather data, an archive screening was done using the following key words: “Dominance Rank”, “Age”, and “Macaques”. In this exact order, they were connected by ‘AND’ function and searched in academic search engines. The search engines included Web of Science and PubMed, which were provided by the University of Chicago, Chicago, Illinois, where the study was conducted. And this

choice exclusively represents all the accessible engines that adhere the convention of natural sciences, especially psychology, ecology, and anthropology. All searching and screening were conducted independently by Yijun Yang.

The initial searching yielded 226 results from Web of Science and 107 from PubMed. Then, the first round of manual screening was conducted and found 41 results among them (22 from Web of Science and 19 from PubMed) relevant to our study, while other results were excluded because they do not study macaques. In the second round of screening, the abstract and method of each relevant result were carefully read and evaluated, and 3 results (2 reviews and 1 primary study) were found having a good fit to the scope of our hypotheses. Using the exact protocol above, the references cited by two reviews were subsequently screened, and relevant studies were retrieved. Specifically, in Baker and Eaton's review [26], 2 published datasets [27, 28] were retrieved, and in Sprague's review [29], the four studies were retrieved while three other ones were excluded for not studying macaques.

Together, the present study eventually had a sample of macaques from 7 primary studies [27, 28, 30-34], and they together provide the description of 217 macaques of 12 troops (one troop was assessed twice in two mating seasons). The macaques in the sample are in three species: Rhesus macaques (*Macaca mulatta*; N = 118, in 8 troops), Japanese macaques (*Macaca fuscata*; N = 52, in 2 troops), and barbary macaques (*Macaca sylvanus*; N = 47, in 2 troops), and they were studied independently in 4 different sites in Europe, Asia, and South America. In addition, they all live in a semi-free ranging lifestyle where human feed them only occasionally during the time when food is scarce (see Table 2 for a summary).

2.2 Statistical Analysis

2.1.1 Analysis 1 – Macaques

A meta-analysis was chosen to investigate whether the relationship between seniority and dominance hierarchy exist universally because: first, no previous study has a sample that is large, wide-ranging, and heterogenous enough for concluding the relation between seniority and dominance hierarchy is species universal; second, although most of the sampled studies include individuals' dominance rank, age or seniority as background demographic information, little attention has paid on their relationship; finally, these information given by each sampled study can be easily converted into Pearson's correlation between dominance hierarchy and seniority, which can be used for detecting whether there exists a general and universal trend after analyzing them in the framework of meta-analysis.

To meet this demand, Hunter and Schmidt's meta-analysis [35] was adopted because it allows a survey of the scattered effects across samples, permits the use of Pearson's correlation as the effect size [36], and is sensitive to detecting the general trend across samples. In practice, the effect size of each sampled study was weighted, then used for calculating a single weighted average effect size ($\bar{r}$). Because only one of the sampled studies reports both age and seniority while others report only age, for consistency, age was to compute coefficient and feed the meta-analysis as inputs. This decision is justified because seniority and age are two mutually substitutional socioecological variables and were found highly correlated [26-34]: monkeys' seniority increases as they grow older -- a characteristic of the social animals whose group affiliation is often consistent since their full maturity.

Then, to investigate what causes the general and universal correlation between dominance hierarchy and seniority, a follow-up study was conducted using the following logic. If the high ranking and lower ranking males differ not in seniority (H_0), *Hypothesis 2* is rejected because the dominance hierarchy is not linearly continuous nor resembles a queue of either decreasing or increasing seniority. On contrary, if the high ranking and lower ranking males differ in seniority (reject H_0), it can be concluded that the dominance hierarchy is skewed to two ends and thus stratified, in which the two strata are occupied by the members of the two seniority cohorts.

To repeat, the question in interest is whether there exists a stratification of dominance hierarchy and whether it is resulted from the preference of the senior males to support the members of the same cohort in antagonistic interactions. Given the impression from naturalistic observation [21, 25], if the

dominance hierarchy is skewed and stratified, the cause is attributed to the antagonistic support of the senior rather than the new immigrants because they were rarely observed providing help nor being supported in fights.

To conduct the follow-up study, the raw data of seniority and rank were extracted from the study by Hill [28] and the 1st to 9th ranks were defined as high ranks while the 10th to the 18th lower ranks. This decision was justified by two reasons: First, although seniority can be substituted by and is found strongly correlated with age, only Hill [28] reports it, meeting the criteria of not using age as the proxy of it; Second, a careful look into the raw data revealed that, due to the difference of immigrational history, the 9 highest ranking males are of the same seniority cohort whereas the 9 lower ranking ones represent a more recent wave of immigration.

2.1.2 Analysis 2 - Yellow Baboons

Due to a paucity of data, a similar meta-analysis on baboons could not be conducted. Following the same protocol except a new combination of keywords ("Dominance rank" AND "Age" AND "Baboons"), only 2 reviews [20, 37] and one primary study [38] out of 259 results were found relevant, and the two reviews were subsequently excluded because they do not provide relevant data as the sampled studies above. Thus, the raw data of the remaining study were retrieved from DRYAD - an open online database of natural science research, which offered a dataset that describes the age and dominance rank of 80 yellow baboons (*Papio cynocephalus*) from 6 troops studied in Amboseli Baboon Research Center (Amboseli, Kenya). Among the subjects, a careful analysis revealed that 63 subjects of them are free ranging while the rest 17 are from the troop that is routinely fed by humans.

The 17 subjects were excluded because it has been found that human feeding may influence baboons' natural behavior and physical condition (e.g., body mass index) [39] that directly links to combat ability [20]. Though a meta-analysis is meaningless and illegitimate given the limited sample size and its restricted geographic representativeness, the five troops together yield a relatively large sample that is sufficient to investigate whether there is a stratification of dominance hierarchy in Amboseli yellow baboons. To test this, age and dominance hierarchy was also extracted and quantified using the exact same protocol as above, except with a different high- versus lower-ranking definition. Given the finding that, in Amboseli yellow baboons, the three highest ranking males (the 1st – the 3rd) are often prime-aged new immigrants who just joined the group and thus are much less senior than other males [20], the males of the three highest ones (the 1st – the 3rd) are defined as high ranking males while the rest are of lower ranks.

2.3 Apparatus

Together, a meta-analysis was conducted to see whether the correlation between age and dominance hierarchy is consistently found across the 12 macaque samples. A Pearson's correlation analysis was conducted to test whether this correlation also exist in Amboseli yellow baboons. Finally, to test whether dominance hierarchy is stratified because of seniority, three Welch's t-tests on two samples of resus macaques [28] and a collapsed sample of five yellow baboon troops study [38] were conducted. The raw data, coefficients, and demographic information of the samples can be found in the sampled works [27, 28, 30-34, 38]. The meta-analysis was conducted using Microsoft Excel software (version 16.52). All t-tests and correlations were done in R [40]. The present study reports no intervention involving animals or humans, and thus no ethical approval is required nor assigned. The University of Chicago, Chicago, Illinois permitted this study.

3. Results

Overall, the results of both meta-analysis and correlation support *Hypotheses 1* (see Table 1), dominance hierarchy and age are strongly correlated ($r > 0.5^{***}$). Given this strong correlation and the tendency that older monkeys are often senior residents of a group, it can be argued that the correlation between seniority and dominance hierarchy found by Hill [28] is universal in the genus of *Macaca*.

The three independent t-tests on three samples of two rhesus macaque troops and one yellow baboon sample all revealed significant and robust difference of seniority between high ranking and lower ranking males (all $p < 0.001$***). These findings support *Hypothesis 2* and supplement the meta-analysis and correlation analysis: dominance hierarchy is correlated with age and sonority because the males from the more senior cohort either monopolize the highest 9 ranks as in rhesus macaques or are dominated by the three highest ranking males as in yellow baboons. See detailed and separated description in the next two sections.

Table 1. Results Summarized

Hypothesis	Age-Rank Coefficient (N)	Seniority: High- vs. Low-Ranking	Supported ?
H1	0.699***(218)		
	0.577***(63)		Yes
H2		t(17.989) = 12.786, p < 0.001***	
		t(6.7681) = 12.248, p < 0.001***	
		t(38.474) = -4.826, p < 0.001***	Yes

H1: *Hypothesis 1*
H2: *Hypothesis 2*
Coefficient***: large effect size
p < 0.05*, p < 0.01**, p < 0.001***

3.1 Macaques

The meta-analysis revealed a strong positive correlation between age and dominance rank ($\bar{r}$ = 0.699, $\hat{\sigma}$p = 0.048, $\hat{\sigma}$e = 0.015, df = 195, CI_{lower} = 0.270, CI_{upper} = 1.128). Although, 4 of 12 reported coefficients are not significant, the general trend is otherwise positive and strong, as indicated by a large overall effect size across the samples ($\bar{r} > 0.5$). Though a descriptive statistic suggests a wide age range of high ranking males, this does not compromise the above findings because: first, strong and positive correlation of age and dominance hierarchy is found in the troops where the mean age of high ranking males contributes the two ends of this range; second, this wide range is likely resulted from an adaptation to different local environments, as this sample contains 12 different troops from 4 sties of 3 continents.

Table 2. Summary Meta-analysis

Species	Site	Affiliation	Size	Coefficient
Rhesus Macaques	La Parguera, Puerto Rico	A	15	0.615*
		C	17	0.430
		I	11	0.300
		E	7	0.741
	La Parguera, Puerto Rico		20	0.744***
	Canyo Santiago		14	0.707**
	Canyo Santiago		23	0.185
	Canyo Santiago		11	0.713*
Japanese Macaques	Arashiyama, Japan	A	26	0.925‡
		B	26	0.934‡
Barbary Macaques	Affenberg Salem, Germany	A	17	0.920***
		A†	30	0.862***

$\bar{r}$ = 0.699, N_{total} = 217
p < 0.05*, p < 0.01**, p < 0.001***
A†: troop A observed in a different breeding season
‡: p-value is not provided by the original study

In addition, as revealed by the two t-tests, in both troops, high ranking males have a significantly greater seniority than that of lower ranking ones (Troop A: $p < 0.001$***, $t = 12.786$, $df = 17.989$, $M_{top} = 5.300$ y, $M_{low} = 2.309$ y, and Troop B: $p < 0.001$***, $t = 12.248$, $df = 6.7681$, $M_{top} = 5.257$ y, $M_{low} = 2.375$ y), with the mean seniority difference of 3.0 and 2.9 years in troop A and B respectively, indicating a stratification of dominance hierarchy as a function of the seniority difference. All the outputs that are mentioned and omitted for brevity can be found in Table 2.

3.2 Yellow Baboons

A significant positive correlation between age and dominance hierarchy was also found in the sample of 63 yellow baboons ($r = 0.577$, $t(61) = 5.512$, $p < 0.001$***), similar to the findings in macaques. Although t-test also reveals a stratification of dominance hierarchy, what contributes to this correlation is different from that found in macaques. In the sampled yellow baboons, the high ranking males have a seniority significantly lower than that of the lower ranking ones ($t(38.474) = -4.826$, $p < 0.001$***). This is because the three highest ranking males ($N_{top}= 28$, $M_{age} = 9.3$ y) are significantly younger than the males of lower ranks ($N_{low} = 35$, $M_{age} = 12.8$ y), and their age on average matches exactly with the prime age when the combat ability reaches the peak [20, 41]. This finding is not a surprise because the queue and queue-jumping model suggests that the three highest ranks are often taken by the prime aged new immigrants who despotically monopolize most of the mate-access by outcompeting the senior males in fights [20].

4. Discussion

The results indicate that dominance hierarchy is not only ubiquitous in cercopithecines but also subjected to the influence of age and seniority. As two important but overlooked socioecological factors, age and seniority explain and reveal a stratification of dominance hierarchy, thereby challenging the traditional view that dominance hierarchy resembles a linear and continuous queue resulted only from the turnouts of dyadic agnostic interaction among ingroups [22] (see Figure 1 for illustration).

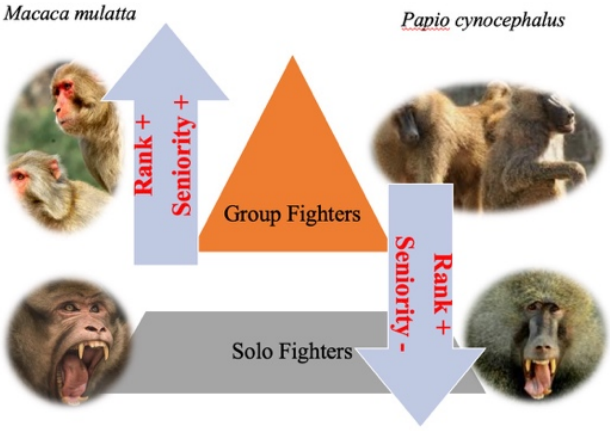


Fig. 1 Stratification and Seniority

This challenge benefits our understanding of the evolution of human cognition in two ways. First, in contrast with the conventional view that engaging in and understanding social roles belong uniquely to humans [7], it is possible that monkeys at least distinguish the nonrelated ingroup males from different seniority cohorts and may preferentially support those of their own cohort. Previous studies corroborate this speculation: the research on macaques, baboons, and capuchin monkeys have shown that monkeys recognize group members' kinship and distinguish ingroups from outgroups [19]. On the other hand, monkeys are also attentive and even understand others' attention, as they are sensitive to others' vocalization and gaze direction, monitor what others are doing and getting, and protest when others are disadvantageously treated [15, 19].

Together, monkeys may be capable of keeping a mental scorebook that tracks what is going on in their social world and guides how they are going respond to the happenings. Importantly, this speculation by no means argue that monkeys can deliberate or think reflectively in a voluntary fashion [4, 5, 7] because the present evidence are not sufficient to prove that they are self-aware, deliberate, or cognitively reflective. However, it is certain that they know things and are motivated by their knowing to act, which are especially important for them to navigate in the complex social world [19].

To know how monkeys see the world is difficult if not impossible, but the comparative method used by evolutionary psychologists is a promising path that may eventually give us the answer [6]. If human cognition evolved step-by-step by accumulating adaptations emerged at different points of the history [43], a comparison between the cognition of monkeys and great apes with that of humans may help delineate the path of the evolution of human cognition.

Together with previous findings, the author argues that it is the evolution of cognition in the primate lineage that allows cooperation to be increasingly more complex and flexible. Specifically, monkeys may cooperate reciprocally driven by the cognitive infrastructure of inequity aversion [11-13], spontaneous prosociality [10], behavioral synchrony [8-10], and mental scorekeeping. Then, after the emergence of individual intentionality, great apes (e.g., chimpanzees) incorporate others' knowing through complex casual inferences [43, 44], resulting in more sophisticated forms of cooperation that demand intention and belief reading. Eventually, after the emergence of recursive thinking and shared intentionality [45], socio-casual inferences reach its peak complexity and flexibility, allowing the bird's eyes view that expand the scope of knowing to not only what self and others know but also what others know about the self [4, 5, 45].

On the other hand, the present finding also reveals a triadic relation of dominance hierarchy, reciprocity, and prosociality. First, given the stratification of dominance hierarchy because of seniority difference, together with previous findings [20-22], it is suspected that senior males reciprocally help each other in fights thus rank adjacently but differently from the males who are less senior. Plus, this preference or bias of reciprocal helping may be a result of keeping a mental scorebook that records the history of reciprocal relations with others. Finally, instead of speculating monkeys are deliberative and cognitively reflective, it is more likely that this mental scorebook influences monkeys' decision-making by enforcing motivational pressure on them, thus turning on or off their expression of prosociality in different social encountering. Although the reciprocity driven by mental scorekeeping may be context-restricted (e.g., grooming and support in fights) and depend on the social history that monkeys share with others, it may mark a key moment of the evolution of cognition in the primate lineage because it solves two problems of cooperation: 'Should I help?' and 'who should I help?'.

5. Conclusion

In evolutionary psychology, the key to understand human cognition is to investigate what monkeys and apes see and know. In the societies of macaques and yellow baboons, the dominance hierarchy is not only resulted from the turnouts of dyadic antagonistic interactions but also correlated with seniority. Surprisingly, seniority is not linearly and positively correlated with dominance hierarchy but skewed and stratified: the males of the two seniority cohorts rank differently on either the higher or lower strata of the hierarchy. Together with previous studies, it is concluded that this stratification is resulted from the senior monkeys' preference to help those with whom they share a long history of cohabitation and reciprocal relation. This finding is essential to understanding what monkeys know about others and how they make the decision to cooperate, because it hints that monkeys may keep a mental scorebook that tracks the happenings in their social world and thus are motivated to respond in certain social encountering when the context dictates, like intervening in antagonistic interaction.

References

[1] Maynard Smith, J., Szathmáry, E. The Origins of Life: From the birth of life to the origin of language. Oxford University Press, 1999.

[2] Dawkins, R. The selfish gene. New York: Oxford University Press, 1989.

[3] Boraas, M., Seale, D., Boxhorn, J. Phagotrophy by a flagellate selects for colonial prey: A possible origin of multicellularity. Evolutionary Ecology, 1998, 12(2): 153–164.

[4] Tomasello, M. Why we cooperate. In C. S. Dweck, J. B. Silk, B. Skyrms, E. S. Spelke (Eds.), Why we cooperate. MIT Press, 2009.

[5] Tomasello, M. A natural history of human thinking. In A natural history of human thinking. Harvard University Press, 2014.

[6] Armstrong, D. Monkeys and consciousness. Behavioral and Brain Sciences, 1992, 15(1): 147-148.

[7] Tomasello, M. The Cultural Origins of Human Cognition. Harvard University Press, 1999.

[8] Demuru, E., Palagi, E. In Bonobos Yawn Contagion Is Higher among Kin and Friends. PLoS ONE, 2012, 7(11): e49613.

[9] Campbell, M., de Waal, F. Chimpanzees empathize with group mates and humans, but not with baboons or unfamiliar chimpanzees. Proceedings of the Royal Society B: Biological Sciences, 2014, 281(1782).

[10] Suchak, M., de Waal, F. Monkeys benefit from reciprocity without the cognitive burden. Proceedings of the National Academy of Sciences, 2012, 109(38): 15191–15196.

[11] Brosnan, S., de Waal, F. Monkeys reject unequal pay. Nature, 2005, 425(6955): 297–299.

[12] Brosnan, S., Schiff, H., de Waal, F. Tolerance for inequity may increase with social closeness in chimpanzees. Proc. Roy. Soc. Lond. B: Biol. Sci. 2005, 272: 253- 258.

[13] Proctor, D., Williamson, R., de Waal, F., Brosnan, S. Chimpanzees play the ultimatum game. Proc. Natl. Acad. Sci. USA, 2013, 110: 2070-2075.

[14] Matsuzawa T. Cognitive development in chimpanzees. Toimonaga M, Tanaka M (eds). Tokyo: Springer, pp 199–276, 2006.

[15] de Waal, F. Natural normativity: The 'is' and 'ought' of animal behavior. Behaviour, 2014, 151: 185-204.

[16] Bard, K. Neonatal imitation in chimpanzees (Pan troglodytes) tested with two paradigms. Animal Cognition, 2007, 10(2): 233–242.

[17] Rochat, P. The infant's world. Cambridge: Harward University Press, 2001.

[18] Woodward, A. The infant origins of intentional understanding. In Advances in Child Development and Behavior, 2005, 33: 229–262.

[19] Cheney, D., Seyfarth, R. How monkeys see the world: Inside the mind of another species. University of Chicago Press, 1990.

[20] Alberts, S., Watts, H., Altmann, J. Queuing and queue-jumping: Long-term patterns of reproductive skew in male savannah baboons, Papio cynocephalus. Animal Behaviour, 2003, 65(4): 821-840.

[21] Georgiev, A., Christie, D., Rosenfield, K., Ruiz-Lambides, A., Maldonado, E., Emery Thompson, M., Maestripieri, D. Breaking the succession rule: the costs and benefits of an alpha-status take-over by an immigrant rhesus macaque on Cayo Santiago. Behaviour, 2016, 153(3): 325–351.

[22] de Vries, H. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour, 1998, 55(4): 827–843.

[23] Wrangham, R. An Ecological Model of Female-Bonded Primate Groups. Behaviour, 1980, 75(3/4): 262–300.

[24] Emlen, S. An Evolutionary Theory of the Family. Proceedings of the National Academy of Sciences of the United States of America, 1995, 92(18): 8092–8099.

[25] Schino, G., Aureli, F. Reciprocal Altruism in Primates: Partner Choice, Cognition, and Emotions, 2009.

[26] Baker, P., Eaton, G. Seniority Versus Age as Causes of Dominance in Social Groups: Macaques and Men. Small Group Research, 1992, 23(3): 322–343.

[27] Norikoshi, K., Koyama, N. Group shifting and social organization among Japanese monkeys. Proceedings from the Symposium of the Fifth Congress of the International Primatological Society, Tokyo: Japan Science Press, pp. 43-61, 1975.

[28] Hill, D. Social relationships between adult male and immature rhesus macaques. Primates, 1986, 27(4): 425.

[29] Sprague, D. Life history and male intertroop mobility among Japanese macaques (Macaca fuscata). International Journal of Primatology, 1992, 13(4): 437–454.

[30] Drickamer, L., Vessey, S. Group changing in free-ranging male rhesus monkeys. Primates, 1973, 14(4): 359.

[31] Tilford, B. Seasonal rank changes for adolescent and sub-adult natal males in a free-ranging group of rhesus monkeys. Int. J. Primatol, 1982, 3: 484–490.

[32] Mcmillan, C. Male age, dominance, and mating success among rhesus macaques. American Journal of Physical Anthropology, 1989, 80(1): 83-89.

[33] Paul, A. Determinants of male mating success in a large group of Barbary macaques (Macaca sylvanus) at Affenberg Salem. Primates, 1989, 30: 461–476.

[34] Berard, J., Nürnberg, P., Epplen, J., Schmidtke, J. Male rank, reproductive behavior, and reproductive success in free-ranging rhesus macaques. Primates, 1993, 34(4): 481–489.

[35] Hunter, J., Schmidt, F. Fixed Effects vs. Random Effects Meta-Analysis Models: Implications for Cumulative Research Knowledge. International Journal of Selection & Assessment, 2000, 8(4): 275.

[36] Pearson, K. On the theory of contingency and its relation to association and normal correlation. London: Dulau and Co. 1904.

[37] Altmann, J., Altmann, S., Hausfater, G., McCuskey, S. Life history of yellow baboons: Physical development, reproductive parameters, and infant mortality. Primates, 1977, 18(2): 315.

[38] Galbany J., Tung J., Altmann J., Alberts S. Canine size in wild male baboons from Amboseli: maturation, aging and social dominance rank. PLoS ONE, 2015, 10: e0126415

[39] Altmann, J., Altmann, S., Schoeller, D., Muruthi, P., Sapolsky, R. Body size and fatness of free-living baboons reflect food availability and activity levels. 1993.

[40] R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. 2020.

[41] Cowlishaw, G., Dunbar, R. Dominance rank and mating success in male primates. Animal Behaviour, 1991, 41(6): 1045–1056.

[42] Dawkins, R. The Blind Watchmaker. Penguin Book. 2006.

[43] Hare, B., Call, J., Agnetta, B., Tomasello, M. Chimpanzees know what conspecifics do and do not see. Animal Behaviour, 2000, 59(4): 771–785.

[44] Hare, B., Call, J., Tomasello, M. Do chimpanzees know what conspecifics know? Animal Behaviour, 2001, 61(1): 139–151.

[45] Tomasello, M., Carpenter, M., Call, J., Behne, T., Moll, H. Understanding and sharing intentions: The origins of cultural cognition. Behavioral and Brain Sciences, 2005, 28(5): 675–691.