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The Evolution of Dominance Hierarchy in Cercopithecines: a meta-analysis and research proposal

By

Yijun Yang

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Faculty Advisor: Jill Mateo
Preceptor: Resney Gugwor

Introduction

Socioecology- a broad discipline that encompasses diverse social, ecological, and environmental phenomenon- has never ceased to be explored. Observations in this field can be independently explained by the theory of evolution (Darwin, 1859) and theories of kin selection (Hamilton, 1964, 1964), and sexual selection (Darwin, 1871, 1876), which make the association between socioecological factors with the advantage of survival and reproduction opaque. Hypothetically, for instance, the bonds between female cercopithecines can be either interpreted as a manifestation of nepotism, for the female is the philopatric sex in all cercopithecines. On the other hand, the philopatric females can assess the males' quality based on the outcome of competition for group membership and their social status, through observing the dynamic shift of group composition brought by the immigrant and emigrant males. Although the sexual selection and kin selection can individually account for the observation of female philopatry, by individually assessing the power of the specific mechanisms that influence the group composition, the role of group composition- a directly observable trait- in affecting the reproductive outcome of ingroup individuals is underestimated. With this, the present proposal attempts to identify the role group composition, which is shaped by various socioecological factors, as a meta-trait, and to bridge the relationship between it with the individuals' fitness output in the groups.

Cercopithecines are selected for illustrating this relationship, because of operational convenience. In detail, all cercopithecines live in groups with a sex ratio that in favor of females who are the philopatric sex, and this feature has been theoretically categorized as female-bonded primate groups or FB groups (Wrangham, 1980). FB groups provide temporal and spatial convenience for males to control the access to females by rivals, and the differentiated access among males is the key to predict the differences in fitness (Emlen & Oring, 1977). The Queuing and queue-jumping model (Altmann, 1962; Alberts, Watts, &

Altmann, 2003) illustrates the relationship between dominance hierarchy and difference of fitness between males by pooling data from rhesus macaques (*Macaca mulatta*) and savannah baboons (*Papio cynocephalus*), and it predicts that as the availability of females increases, the highest rank of males to mate with a female decrease, because of his energetic constrain of mate-guarding in dyadic antagonistic interaction and the collective challenge by more than one lower-ranking males. Though FB-group model, the model of male distribution, and the queue and queue-jumping model all imply that dominance hierarchy in FB primate groups is essential for predicting the difference of fitness between males, this relationship is moderated by various factors other than the number of females in a group.

Cowlishaw and Dunbar (1991) point out a male's difficulty of preventing his rivals' access to females is in a positive relationship with the number of females in the group and the females' seasonality of breeding or their degree of synchrony of estrus. From males' perspective, when females are cycling temporarily adjacent to one another, selectively to mate-guard some females may leave mating and breeding opportunities to other males. From females' perspective, this provides the chance of mating with multiple males, and their availability of mating or breeding with multiple males (no long-lasting breeding pair bond) increases the potential for the group to have more adult males whose fitness may be exclusively gained from the reproducing directly in FB groups.

As group size increases by the immigration of outgroup males, the relationship between dominance hierarchy and fitness difference between males is further complicated by the occurrence of a male-male coalition (Cowlishaw & Dunbar, 1991). In FB primate groups, the coalition between lower-ranking males may pose energetic challenges to the mate-guarding of higher-ranking males, and the collective action may force higher-ranking males to be excluded from the ongoing mate-guarding without permanently altering their dominance rank. A coalition may occur more frequently when the age differences between higher and lower-ranking males are large, at least in savannah baboons (Alberts, Watts, & Altmann, 2003), in which condition the fitness difference between them is smaller in comparison with groups with the large age difference between males on distinct dominance ranks.

Taken together, the fitness output between two males on two adjacent dominance rank in a given breeding season (one male has recently won a dyadic antagonist fight against the other) is positively predicted by the number of available females (not pregnant and in estrus) that he can maximumly monopolize in a given mating season by excluding the access of other males (Equation 1, sensu Emlen & Oring, 1977; Wrangham, 1980; Cowlishaw & Dunbar, 1991):

$$\mathrm{F} \propto \mathrm{N}.$$

Equation-1
F: the number of offspring that is sired by a male in a given breeding season
N: the number of available females (not pregnant and in estrus) that a male can maximumly monopolize in a given mating season by excluding the access of other males

The number of females that a male can monopolize is complicated by several socioecological factors (Cowlishaw & Dunbar, 1991; Alberts, Watts, & Altmann, 2003): the number of males relative to available females in a given breeding season, the age difference between males in a group, and the occurrence of coalition for replacing a male from mate-guarding. Taken together, in FB groups where the membership and bonds among females are relatively stable, the difference of fitness output between males, as approximated by the number of mating opportunities or the genetic relation between males and potential offspring, is likely mathematically predicted by the features of the composition of males in a group. The variables may include the number of males, their ages, and the stratification of males based on their ages or the duration of their residency (seniority):

$$\mathrm{D} \propto \frac{\mathrm{N}}{M_1 * T_1 + M_2 * (T_2 - T_1) + M_3 * (T_3 - T_2) + \cdots + M_x * (T_x - T_{x-1})}.$$

Equation-2:
D: the difference of fitness output between the members on two adjacent dominance ranks in a given breeding season
N: the number of available females (not pregnant and in estrus) that a male can maximumly monopolize in the given mating season
M_x: the adult male (labeled 'x') that joined the group as an immigrant ($M_x = 1$)
T_x: the age or seniority of M_x

To account for the age difference between males, a younger male who joined the group recently would have a lower number of T_x in comparison with a male who has remained his residency in the group. '$\int_1^x M_x * T_x$' (equals T_x quantitatively) captures the complexity of the group composition, because group complexity can be approximated by the number of adult males and the coalition in antagonistic interactions among them. Given the findings by Cowlishaw and Dunbar (1991), and Alberts, Watts and Altmann(2003). coalition in antagonistic interaction is more likely to occur when the age difference between males is greater than in groups with a smaller age difference (Hypothesis 1).

While controlling the number of available females in a group, for a FB primate group with 3 adult males (A, B, and C) in a given breeding season, the 3 males would be more likely to challenge one another individually without other males' help in an antagonistic interaction for replacing the male who is mate-guarding a female than a conspecific group contains 3 adult males (D, E, and F) who have larger age differences between them. This is because '$M_A * T_A + M_B * (T_B - T_{B-A}) + M_c * (T_C - T_{C-B})$' (the group contains male A, B, and C) is smaller than '$M_D * T_D + M_E * (T_E - T_{E-D}) + M_F * (T_F - T_{F-E})$' (the group contains male D, E, and F). Then, FB primate groups with greater potential for the occurrence of antagonistic support may exhibit a smaller difference of fitness output (Alberts, Watts, & Altmann, 2003) between males in two adjacent dominance ranks (Hypothesis 3), though younger adult males, especially those at their prime age of reproduction and combat, who are presumably more competitive in dyadic antagonistic interaction may often have a higher fitness output than older resident males of the group (Altmann, 1962; Alberts, Watts, & Altmann, 2003) (Hypothesis 2).

If the complexity of group composition (‘$\int_1^x M_x * T_x$’) is approximated by male members’ seniority, then the structural complexity increases with the increase of the number of males while controlling the age difference among them especially when there are multiple males join into the group simultaneously. I predict that the difference of fitness output between two males on two adjacent dominance ranks decreases (Hypothesis 4). In short, the mate access and fitness output are under the direct influence of the structural complexity of male composition, in which complexity is modulated by the number of adult males in a group and the age or seniority difference among them. Finally, though dominance rank directly exhibits the difference of combat ability between adult males (Altmann, 1962; Alberts, Watts, & Altmann, 2003), group complexity modulates the strength of this relationship because it exhibits the group’s stratification of male members and their differences in behavioral strategies for gaining mate access (Hypothesis 5).

Taken together, in the present model, the number of males and the age or seniority difference between them are two predictors for estimating the asymmetry of fitness output between adjacent dominance ranks. And the dynamic shift of the two predictors may favor different behavior strategies in different ecologies and at different points of life history. Previous studies have found that males are more collaborative in antagonistic interaction when the age difference among males is large (Alberts, Watts, & Altmann, 2003) and are more persistent in mate-guarding a smaller number of available females for a longer time in a breeding season when there is a large number of rival males (Wrangham, 1980; Alberts, Watts, & Altmann, 2003). The evolution of social behaviors may be seen as the key to promote group cohesiveness from males’ perspective by directly benefit their fitness, but also enhance the functioning of a group against threats from predation and intergroup competition.

Dimorphism, dispersal, group composition, and mating system

Naturalistic observations show cercopithecines are potentially a rich source for investigating the proposed relationship between mate-access with the structural complexity of the group in response to male immigration. Across different cercopithecine genera, males are generally larger in size than females, and the body mass ratio between males and females ranges from 1.2 to 2.9 (Smith & Jungers, 1997; Setchell et al., 2001). All cercopithecines live in a group, the typical group size ranges from 10 to 100 individuals, except extreme cases found in DeBrazza's monkey (mean group size is 6.6; Mugambi et al., 1997), gelada baboon (100-170; Swedell, 2010) and mandrills (340- 845 animals; Abernethy et al., 2006).

Male is the sex of dispersal in all known cercopithecines. The mating systems of cercopithecines overall have a sex ratio in favor of females (Altmann, 2000), ranged from monogamous groups, one-male multi-female groups to multi-male multi-female groups (Andelman, 1986). In a one-male multi-female unit, like in hamadryas baboon, the resident alpha is constantly challenged by outgroup rivals (Swedell et al., 2011). In multi-male multi-female groups, like in rhesus macaques, within-group competition among ingroup males over mate-access through the regulation of dominance hierarchy is found, in addition to the threat from outgroup rivals (Maestripieri & Hoffman, 2011).

Female philopatry and male dispersal

Males' access to females is complicated by the evolutionary history and socioecological factors of cercopithecines. First, different from cercopithecines, colobines, the other subfamily of the Old-World monkeys, present a heterogeneous pattern of dispersal among species, and in most species of colobine, both sexes disperse. This can be assumed that the exclusive male-dispersal pattern in cercopithecines is recently evolved from a common ancestor of cercopithecines and colobines. The only exception to this pattern in cercopithecines is hamadryas baboon (Swedell et al., 2011), where females are also found to leave their natal one-male unit to other units within a band or clan. But the observed dispersal by females largely occurs in response to the recent replacement of the alpha male in the one-male unit. Taken together, male cercopithecines are found to map themselves geographically to the distribution of females and are observed to compete against each other for mate-access, as theoretically predicted by Emlen and Oring (1977).

As predicted by the model (Emlen & Oring, 1977), access to reliable and high-quality food sources is the key to females' reproductive success. Physiologically, check pouches, an adaptation for food storage in cercopithecines, has been hypothesized and observed to enhance individuals' efficiency of foraging under intense scramble or contest competitions within a group (e.g. blue monkeys; Smith et al., 2008). Evolutionarily, this adaptation can potentially be a result of the opportunistic and yet selective food choice of cercopithecines (Chapman et al., 2002). Under an intense competition over food, a strong, nepotistic alliance between females from the same matriline may play an important role in the turnout of the competition over food (Wrangham, 1980), and kin-selection theory predicts females to preferentially cooperate with close relatives than nonrelated individuals (Hamilton, 1964, 1964). In short, within-group scramble and contest competitions over food resources may have evolutionarily favored individuals with nepotistic alliances, which may account for the predominant female philopatric pattern in cercopithecines.

Apart from the within-group cooperation and tolerance of food access, the risk of predation may be another factor that facilitates the congregation of females. Cercopithecines are preyed upon by predators from a large array, including large cats, snakes, eagles, chimpanzees, and monkeys. An augmentation of group size (Lehmann et al., 2007) helps to dilute the risk of predation and enhances the ability to detect predators (van Schaik et al., 1983). The ability of the large group to detect approaching predators is granted by giving and being attentive to alarm calls in some species of cercopithecines. For instance, in Diana monkeys (Zuberbühler, 2000a, 2000b), experimental manipulations show Diana monkeys make different alarm calls in response to different predators. And Zuberbühler (2000b) also found Diana monkeys can distinguish the alarm calls made by other Diana monkeys and chimpanzees in response to leopards. And when hearing the alarm call by chimpanzees in response to leopards, Diana monkeys also produce leopard alarm calls even though they are made known about the presence of chimpanzees.

Evidence collected from free-ranging rhesus macaques reveals a kin-biased response toward the experimental playback of vocalization. Rendall, Rodman & Emond (1996) habituates female rhesus macaques with the vocalization of one member of the same matriline, but she presents a significant rebound of response towards the vocalization of another member in the subsequent playback while remaining less responsive to the already habituated vocalization. Taken together, some species of cercopithecines present the ability to distinguish alarm calls by different species, to understand the causal and temporal relationship of the predation risk and alarm calls, and to differentially respond to alarm calls by ingroup peers with different degree of relatedness.

The role of males in the female congregation

Naturalistic observation, experimental manipulation, and theoretical models reviewed above provide insights on the mechanisms of adapting to the group living and the evolutionary significance of living in bonded relationships with other females, especially with the members in the same matriline. Thus, it would not be surprising to find the shift of males' geographic distribution as a temporal reaction to the shift of females' distribution (Emlen & Oring, 1977; Altmann, 1990; Nunn, 1999), because the number of offspring sired by a male is found to be predicted by the number of available females that he can access to (Emlen & Oring, 1977; Cowlishaw & Dunbar, 1991).

From the perspective of females, for reproducing, sperms from males are required. Besides, group augmentation by male immigration dilutes the risk of predation faced by group members (van Schaik et al., 1983; Lehmann et al., 2007) and enhances the ability to detect predators at a longer distance (van Schaik et al., 1983). With a closer look at the role of male long-tailed macaques (*Macaca fascicularis*) in predator detection, van Schaik et al. (1983) found that, at the peripheral region of the group, males' occupation in the high altitude of a canopy enhances the group's ability to detect a predator in a long distance.

Apart from prevention of predation, another benefit that can be gained from the long-term affiliation with males is the prevention of infanticide by the males who are not related with the offspring of the females (e.g., Japanese macaques; Soltis et al., 2000), especially when the immigrant male takes over the alpha position (Swedell et al., 2011; Kerhoas et al., 2014). To obscure the paternity of offspring, especially in multi-male multi-female groups, resident females are commonly observed to mate with multiple males (promiscuous mating), because this may reduce the risk of infanticide (Soltis et al., 2000).

The tendency to mate promiscuously is found even in one-male groups, where the alpha male is presumed to have exclusive access to all the females in the group. Genetic tests show that the resident male does not monopolize the paternity of all the offspring by resident females statistically (e.g., patas monkey; Ohsawa et al., 1993). These findings indicate that males in a one-male unit may not always be more reproductively successful compared with males in groups with a complex composition. And this opens the possibility of male-male cooperation for guarding the mate-access to ingroup females from outgroup males while sharing the chances of mating with ingroup males through the modulation of dominance hierarchy (see Hypothesis 1 to 5 above).

Female cercopithecines exploit a wide range of physiological and behavioral traits for promiscuous mating. The traits include the alternation of skin color (Dubuc et al., 2009), the exhibition of sexual swellings (Brauch et al., 2007) and copulatory calls (Semple, 1998; Maestripieri & Roney, 2005), and the tendency of being synchronously receptive with other ingroup females (Altmann, 1962; Ostner et. Al., 2008). These traits are hypothesized to facilitate the advertisement of females' fertility, which may intensify the competition for mate access, sperm competition, and may result in confused paternity. Still, high-ranking males on average achieve greater reproductive success in comparison with subordinates (Soltis et al., 2001). Identified by previous findings, male cercopithecines preferably mate with females who are at the peak of their fertility, through tracking the ovulatory circle and parity (e.g., barbary macaques; Semple & McComb, 2000), as well as the ranking (e.g., Japanese macaques; Perloe, 1992).

In short, the winners of dyadic male-male competitions, often having a higher dominant hierarchy, are expected to have a better reproductive output. While situated lower in the hierarchy, these males may take advantage of the synchronous availability of females and the energetic constrain of the dominant males and gain some chances of mating (Altmann, 1962; Wrangham, 1980; Cowlishaw & Dunbar, 199), but also expel dominant males from a consortship by challenging them collaboratively with other low-ranking males (Alberts, Watts, & Altmann, 2003).

Males do not territorially guard high-quality food sources

Cercopithecines exhibit a flexible and diverse food choice, ranging from fruits, nuts, hard seeds, roots, leaves, and even grasses, and the dietary composition between and within species are both considerably large (Chapman, et al., 2002). Within the same species, the difference in the dietary composition may be contributed by the geographic variation of groups' home range. For example, blue monkeys live at the edge of the forest consume more gums than the other groups that live in the center of the forest, whereas the other group has a dietary composition with a greater proportion of young leaves during the same period of the year (Rudran, 1978).

Across different habitats or geographic locations, moustached guenons who live in larger forests have a greater proportion of diet composed by fruit, but in fragmented smaller forests, insect and flower feeding are most frequently observed feeding behavior (Tutin, et al., 1997). Although arboreal cercopithecines largely rely on fruits as the staple of their dietary composition (see review in Chapman, et al., 2002), annual variability of fruit is found associated with the length of the dry season, in which season flowers are found as the fallback food (Tutin, et al., 1997).

Reviewed by Swedell et al. (2011), African papionins occupy a large array of geographic distribution and consequently present a heterogenous yet continuous variation of dietary composition. Semi-arboreal cercopithecines (e.g., mandrills) inhabit and forage at lower strata of forest, and they rely primarily on fruits, nuts, and insects that are commonly found on the forest ground. A similar dietary reliance on fruits, seeds, and insects by chacma baboons (*Papio ursinus*) and mangabeys (*Cercocebus atys*) who also live on heavily forested mountains. Outside of the forest, savannah baboons (yellow, olive, and chacma baboons) that occupy savannah-woodlands rely less on fruits that are not commonly available outside of forests, but they are adaptive to a large array of food sources including berries, seeds, leaves, and invertebrate preys. Interestingly, savannah baboons who live near human-inhabited sites are observed to scavenge from garbage, and female scavengers present a surprisingly higher body fat and body mass index (BMI) than non-scavenging counterparts (Altmann, et al., 1993). The most restricted and yet specialized food choice is found in gelada, they are found inhabiting on grasslands and having digestive adaptations for their granivorous feeding habit (Swedell et al., 2011).

The dietary diversity of arboreal and semi-arboreal cercopithecines are rarely found in terrestrial cercopithecines, partially due to the scattering distribution of various food resources and their habit of not relying on a single source of food across different seasons of a year. Exceptions known include vervet monkeys (Cheney, 1981), blue monkeys (Butynski, 1990), and Diana monkeys (Hill, 1994). Interestingly, the territory guarding in Diana monkeys is primarily played by females. Reviewed by Swedell et al. (2011), territorial cercopithecines are often found in large groups, group size ranges from more than 100 (gelada herds) to less than 20 (mangabey groups), even though the geladas heavily rely on grasses as their primary food source, which food source is categorized as low in quality and evenly distributed across a large geographic range.

Taken together, most cercopithecines live in social groups with a biased sex ratio that favors females and a mixed degree of territoriality that is predicted by group size, but not by the resources that the group is defending, because the dietary composition of most cercopithecines is heterogeneous and varies across seasons. Thus, I tentatively hypothesize, from females' perspective, that the congregation of conspecifics and associated intergroup aggressions are primarily over food sources that are not territorially defendable but are accessed through foraging across a large range of space. From the males' perspective, however, their role in the intergroup aggression towards outgroup males is primarily orientated toward mate-guarding or female-herding. For example, in mandrills, males' influx into groups, that are composed only of females, enlarge the group size consequently, during the breeding season when females are synchronously reproductively available (Abernethy, Wickings & White, 2002).

Males' adaptation of mate-accessing

The review of the socioecological observations of cercopithecines provides the confidence for hypothesizing the cercopithecine males may possess adaptations that allow them to compete against each other for access to females. Evolution would differentially favor the traits that optimize male cercopithecines' strategy for herding females in different socioecological conditions, which strategy may range from herding females solitarily to collectively. Across different species of cercopithecines, indeed, species variation of males' strategies is found. For example, in Papios, hamadryas baboons (*Papio hamadryas*) (Swedell et al., 2011) live in one-male multi-female groups, but olive baboons (*Papio Anubis*) and yellow baboons (*Papio cynocephalus*) typically have few males and multiple females in a group (Buchan et al., 2003).

Within a species, Sinha et al. (2005b) have found that a heterogenous number of males in different groups of wild bonnet macaques (*Macaca radiata*) ranging from 1 male to 6 males, and they note that the different compositions of groups are associated with the different types of male-male relationship. In a one-male group, male bonnet macaques are found to be aggressive to outgroup males and even to resident males who have not yet dispersed from the natal group. However, in multi-male groups, male bonnet macaques are tolerant towards other ingroup males, where a complex web of cooperative relations is built upon not kinship but reciprocity (Silk, 1992, 1994).

Similarly, in captivity, stumptail macaques (*Macaca arctoides*) can be held in all-male groups in a tolerant atmosphere, when having no exposure to females (Butovskaya & Kozintsev, 1996). The tolerance between males is potentially an adaptation for avoiding costly conflicts and promoting group solidarity. In a more extreme case, mandrills, arguably present the greatest sexual dimorphism of body size (Setchell, Lee, Wickings & Dixson, 2001) and coloration (Setchell & Wickings, 2005) in cercopithecines, show fierce competition only during the time of breeding seasons, during which period a seasonal influx of males into female-bonded (FB) groups is observed (Abernethy, White & Wickings, 2002; Setchell, Smith, Wickings & Knapp, 2008).

Behaviorally, male cercopithecines face the difficulty of mate-guarding and harem-defending when there is a synchrony of estrus among females (Ostner, et al., 2008), because males may not be available to inseminate all the females at the timing when the chance of conception is at the peak, which allows subordinates or outgroup males to claim some paternity of the offspring in the group (Ohsawa et al., 1993). Strategically, due to a lack of solidarity, the failure of the ingroup males of preventing the intrusion of outgroup males may further complicate the competition over mate-access.

Within a group, dominance hierarchy among male members in a group may function as a queue for differentiating the priority of mate-access (Cowlishaw & Dunbar, 1991; Alberts, Watts & Altmann, 2003), while this relationship is mediated by the age difference between male members because of the role of coalition in antagonistic interaction (Alberts, Watts & Altmann, 2003). Though established through ranking the asymmetric outcome of dyadic antagonistic interaction, a dominance hierarchy signals the relative combat ability of each constituent member and helps avoid costly contest among ingroup males (Wrangham, 1980).

Thus, dominance hierarchy may potentially facilitate the long-term association and reciprocal social interaction between male members, which may account for the observation where coalition for replacing a male from consortship is more likely found among males who are in the same age cohort and sharing a longer duration of cohabitating (Alberts, Watts & Altmann, 2003). And this long-term association through the presence of dominance hierarchy may serve to facilitate males’ aggression, either acted solitarily or collectively, towards outgroup males (Maestripieri and Hoffman, 2011; Georgiev et al., 2016).

Predictions

To test the role of dominance hierarchy on the male-male relationship within a group and its role on the cohesiveness of the group as a whole while facing the influx of outgroup males, I categorize the hypotheses made above into two clusters. First, a dominance hierarchy serves as the queue that predicts the priority of mate-access (Emlen & Oring, 1977; Wrangham, 1980; Cowlishaw & Dunbar, 1991; Alberts, Watts & Altmann, 2003), but also predicts the differential strategies of males for accessing a mate (Category 1: *The Queue;* see *Table 1* in Appendix-1). This category involves two hypotheses proposed above: (i) younger adult males, especially those at their prime age, are more competitive in antagonistic interaction and therefore ranks higher on dominance hierarchy than older adult males (Hypothesis 2); (ii) older and lower-ranking males are strategically different from younger and higher-ranking males for mate-accessing by engaging in a more collaborative antagonistic challenge for replacing a male from his current consortship (Hypothesis 5).

In category 2 (*The Solidarity;* see *Table 1* in Appendix-1), I tentatively assume the observed association between having a larger age or seniority difference with observing a greater occurrence of collaborative antagonistic challenge (Alberts, Watts & Altmann, 2003) is contributed by the facet of group cohesiveness of dominance hierarchy, because the failure of preventing the influx of young adult males into the group may transform the strategy of the original residents from being collaboratively aggressive towards potential immigrants to contesting against new group members cooperatively. This category includes: (i) an influx of outgroup males may decrease the difference of fitness output of any two males who occupy adjacent dominance ranks (Hypothesis 4); (ii) the influx of males increases the age or seniority difference among ingroup males and thereby shows a greater incidence of collaborative antagonistic support (Hypothesis 1); (iii) the increase of collaborative antagonistic support decreases the difference of fitness output between any two males on two adjacent dominance ranks without permanently alternating the dominance hierarchy (Hypothesis 3).

From category 1, Hypothesis 2, I predict (*prediction 1*) that in multi-male multi-female groups, naturalistic observation and long-term record on the dyadic antagonistic interactions may reveal that the alpha male in each group of this kind is likely to be the prime-aged adult male who is young and not natal to the group, and he may have the greatest opportunities of mating (e.g., wild savannah baboons: Alberts, Watts & Altmann, 2003). Then, Hypothesis 5 can be tested by identifying whether the age of males predicts a greater occurrence of a coalition in antagonistic interaction for replacing a male from his ongoing consortship. And I predict (*prediction 2*) that older and lower-ranking males with a greater seniority are more likely to be observed to form a collaborative party in an antagonistic challenge and the male who replaces the one originally in a consortship may reciprocally help others in the party without gaining the access to mate (Strum, 1982; Noë & Sluijter, 1995).

To test the role of dominance hierarchy on promoting group cohesiveness (category 2), Hypothesis 4 can be tested (*prediction 3*) by measuring the relationship between the intergroup difference of fitness output (i.e., the number of mating opportunities or genetic testing) with the number of males across different groups, while controlling the number of available females. And previous studies by Cowlishaw and Dunbar (1991, 1992) have found a decrease of difference in mating opportunities when the number of adult males in a group increase. An increase of group size by an influx of outgroup males may bring changes to a dominance hierarchy, especially when immigrant males are prime aged young adults who recently dispersed from their natal group. And this brings an increase in the age difference of the group after immigration.

Thus, Hypothesis 1 (under category 2) yields a prediction (*prediction 4*) that the occurrence of coalition increases with the increase of age difference across different groups of a species. And age difference is defined as the average age difference (the sum of the age difference between every two males who are the closest in their ages divided by the number of males minus one: $\frac{\sum_{1}^{N-1} Age_{male\,x+1} - Age_{male\,x}}{N-1}$). This is different from the calculation by Alberts, Watts, and Altmann (2003), because I try to include all the male members instead of just the three with the highest dominance rank. As an innovation, the increase of coalition may be equally or better accounted by the increase of male members' differences on seniority (i.e., $\frac{\sum_{1}^{N-1} Seniority_{male\,x+1} - Seniority_{male\,x}}{N-1}, prediction$ 5). Table 1 (see Appendix-1) offers a comprehensive review of the categories, hypotheses, and predictions above.

Interpretation of possible outcomes

Predictions 1 and *2* investigate the role of a dominance hierarchy in predicting the intragroup structural composition and strategic difference of individual male members on different ranks (category 1). Hypothetically, when the group is geographically isolated from the contact with other groups, intergroup dispersal of males may be obstructed. Then, a young adult male in the group may not achieve a dominant rank that corresponds with his combat ability. Ideally, in a geographic location where the foraging range between multiple groups overlaps, young males are expected to evaluate the cost and benefit of dispersing to a new group or staying in their natal group (Emlen, 1995).

The expected greater occurrence of a coalition in antagonistic interaction in groups with a larger age difference (*prediction 2*) can also be complicated by nepotistic cooperative choice by resident males. In groups where a new immigrant male has closely related resident male relatives, kin selection theory would predict a cooperative act favors the genetic kin rather than other group mates, when the cost of losing direct mating opportunities and weakening the relationship strength that built upon reciprocal antagonistic support are controlled (Hamilton, 1964, 1964).

Cowlishaw and Dunbar's review (1991, 1992) suggests a negative association between the number of ingroup males and mate-access in rhesus macaques and baboons. However, this pattern may only exist in rhesus macaques and baboons, but not in other species of cercopithecines. Then, *prediction 3* may still fail to be observed in species where groups contain a variably small number of males, for example, 1 to 3 male members. Due to the pressure of extra group copulation by females, a male may not be more reproductively monopolizing (e.g., mating access or the reproductive output of all the ingroup females) in a one-male group than in a multi-male group. For instance, according to the genetic data from rhesus macaques in Cayo Santiago, the extra-group paternity is as high as 24.7% (Widdig et al., 2015).

The females may also influence the mate-access by males by selectively prefering certain males who have had strong ‘friendship’ with them (Smuts, 1985). And the female’s mating choice then gives an alternative strategy for resident males to gain mating opportunities instead of solely cooperating with other males in the group. Thus, in cercopithecines species where males form long cohabitation with females, prediction 4 may be mediated by the strength of the relationship between sexes.

Finally, *prediction 5* does not stand in conflict with *prediction 2* in conditions where the age difference between males does not correspond with the difference of their residency length. In particular, male immigrants may not always be young adults with high capacity in combats, and they may not rank high in dominance hierarchy but still face collective and aggressive challenges from the original resident males. As in *prediction 2*, the coalition in antagonistic interaction against new immigrants (predicted by *prediction 5*) may also be compromised by the nepotistic biases of cooperation.

Method

Meta-analysis: age, rank, and macaques

A meta-analysis is conducted for testing whether the highest-ranking adult males in groups of cercopithecines are at their prime age when combat ability, physics, and reproductive potential are the strongest, as predicted by *prediction 1*. Respectively, key words: “dominance rank, age, and macaques” that are logically connected by the “AND” function are entered into the search engine powered by the Web of Science and PubMed, for the convenience of free access provided by the University of Chicago. Web of Science yields 226 results, and PubMed gives 107 results. Then a manual screening on the title of each result is conducted, and 41 results ($N_{\text{Web of Science}} = 22$, $N_{\text{PubMed}} = 19$) that are shown relevant to the research question are elected. Two results from PubMed are first excluded for avoiding repetition of sampling. The criterion of a crude screening excludes results that have a focus on species other than macaques and studies that investigate the socioecological conditions of females.

After the initial screening, the abstract and method sections of each elected article are manually checked. Studies use the categorical divisions of age (e.g., adolescents, young adults, and adults) and the ones that do not include primary data or correlation coefficient between age with dominance hierarchy are subsequently excluded. Then 2 reviews and 1 primary study are elected for a thorough review, and the references cited by each of the 3 studies are also manually screened based on the same criterion. The review by Baker and Eaton (1992) includes the original data retrieved from Norikoshi & Koyama (1975) and Hill (1986) with consent, and the correlation coefficient between age and dominance hierarchy of males from two Japanese macaque groups and one rhesus macaque group are presented. Another review is done by Sprague (1992), 7 primary studies are included without presenting the original data. Then, by screening the reference of this review, each one of the reviewed studies is retrieved from the library system of the University of Chicago. By repeating the same criterion of screening, 1 study is excluded, and the studies by Norikoshi & Koyama (1975) and Hill (1986) are also excluded for they have already been included in the present analysis.

All screening and reviewing are conducted by Yijun Yang. Table 2 in Appendix-2 presents a comprehensive overview of all the studies included in the present analysis. Finally, 6 studies that present original data or Pearson’s correlation coefficient are included. For operational convenience, the Pearson’s correlation coefficient between ages and dominance are calculated in R (version 4.0.1, 2020) from the original data presented by studies and reviews, because all other primary studies included in the present analysis use Pearson's correlation coefficient as a report of the effect size (Pearson, 1904). To investigate the true effect size among independent reports of correlation coefficients, the present study elects the Hunter and Schmidt's method (Hunter & Schmidt, 2000) of meta-analysis for computing the weighted average effect size ($\bar{r}$). This method of meta-analysis is designed specifically for reviewing studies that use correlation coefficient as a report of effect size, and it describes the general pattern of previous observations combined while controlling the heterogeneity of sample sizes and not assuming an equal variance across different samples.

To understand the weighted average effect size of the meta-analysis, a follow-up descriptive statistic is done by averaging the age of the three highest-ranking males from 4 studies (8 troops) individually and combined. This analysis answers the question that is partially derived from *prediction 1* about what age is the highest-ranking male in a group on average, in addition to directly testing the predicted positive correlation between age and dominance rank (see, *prediction 1* in Table 1) by the meta-analysis.

The original data are also used to test whether dominance rank in macaques is stratified by the seniority of group members (the duration of residency in a given group), as predicted by *prediction 5*. The Welch's t-test is done by using the original data from two Japanese macaque troops that are reviewed by Baker and Eaton (1992), because their study is the only one, among the studies included in the present analysis, that specifically focuses on the predictive power of seniority versus age on males' dominance rank. The t-test is used for comparing the mean difference of seniority between a senior subgroup of males ($N_{seniority} \geq 4$ y) that occupy the highest 9 ranks of the hierarchy with a subgroup of males ($N_{seniority} \leqslant 3$ y) that occupy the middle 9 ranks of the hierarchy (10th - 18th). The Welch's t-test is used for the present study does not assume the two subgroups have an equal variance of seniority, but also qualifies the effect size by limiting the degree of freedom of the sample.

Pearson's Correlation: age, rank, and baboons

The same procedure of searching and screening is also conducted on baboons, except the key words: "dominance rank, age, and baboons" that are logically connected by the "AND" function are entered into the search engine powered by the Web of Science and PubMed, respectively. 13 studies are found relevant from the initial and subsequent screening 259 results ($N_{\text{Web of Science}} = 214$, $N_{\text{PubMed}} = 45$). Among the 13 studies, 2 are reviews of the longitudinal research done in Amboseli Baboon Research Center (Amboseli, Kenya), and only 1 (Galbany, et al., 2015) provides raw data that allow a calculation of effect size (r). The rest relevant studies adopt a heterogenous research methods and statistic approaches, which provides no consistent evaluation of the effect size across the studies.

Considering the publicly availability of data from research in Amboseli, Galbany, et al. (2015)'s raw data are retrieved from DRYAD, after a through screening on the 303 studies that were conducted in Amboseli. In this sample ($N_{\text{male}} = 80$), yellow baboon (*Papio cynocephalus*) males that are not wild-feeding and adults are excluded from the studies, and this leaves 63 subjects from 5 social groups. Following a similar procedure above, the Pearson's correlation between males' rank and age is conducted, and descriptive statics of means and standard deviations are calculated. Different from the method above, the stratification of dominance rank is analyzed by comparing the age of the males ($N_{\text{high}} = 28$) who are ranked on the highest place (rank =1), the second highest, and the third highest with the age of the rest subjects in the Welch's t-test, given subjects' seniority and group affiliation are not available. Again, the Welch's t-test is used for not assuming an equal variance between the subgroup of high-ranking males and non-high-ranking males.

Results

Macaques: meta-analysis, descriptive statistics, and Welch's t-test

The reviewed 6 studies in the meta-analysis present original data or correlation coefficient from 12 troops that have been studied from 1973 to 1989. 217 male macaques, including 148 rhesus macaques (*Macaca mulatta*), 52 Japanese macaques (*Macaca fuscata*), and 17 barbary macaques (*Macaca sylvanus*), are sampled. All subjects have reached sexual maturity or adulthood (age equals or greater than 3 y) before the point of sampling. The studies show a disagreement on the reported statistical significance of the correlation between age and dominance rank, 6 studies found the correlation statistically significant and 4 do not, and the p-value is missing in two of the studies. However, the Hunter and Schmidt's method focuses on the weighted average effect size of all those studies combined, the disagreement of the significance of the correlation does not prevent the meta-analysis for concluding a large (0.5-1.0), medium (0.3-0.5), or small (0.1-0.3) effect size by collapsing all the reported correlation coefficients.

The result of the meta-analysis yields a strong positive effect of the correlation between age and dominance rank ($\bar{r} = 0.699$, $\hat{\sigma}_{\mathrm{p}} = 0.048$, $\hat{\sigma}_{\mathrm{e}} = 0.015$, ~~df = 195,~~ $CI_{\mathrm{lower}} = 0.270$, $CI_{\mathrm{upper}} = 1.128$), which indicates the increase of age is strongly correlated with the advance on dominance hierarchy). The follow-up descriptive statistic indicates that the average age of the three highest-ranking males from 8 troops is 9.6 years old. The four troops of rhesus macaque studied by Drickamer and Vessey (1973) show the lowest average age of the three highest-ranking males (6 years old after rounding), whereas the two Japanese macaque troops present the highest one (15 years old after rounding).

The Welch Two Sample t-test reveals the significant difference of seniority between 9 top ranking males with 9 middle ranking males from troop A in Baker and Eaton (1992)'s review ($p < 0.001$, $t = 12.786$, $df = 17.989$, $\mathrm{Mean}_{\mathrm{top}} = 5.300$ y, $\mathrm{Mean}_{\mathrm{middle}} = 2.309$ y), and the difference is also significant when comparing the seniority between 9 top ranking males with

9 middle ranking males from troop B ($p < 0.001$, $t = 12.248$, $df = 6.7681$, $Mean_{top} = 5.257$ y, $Mean_{middle} = 2.375$ y).

Baboons: Pearson's correlation, descriptive statistics, and Welch's t-test

Baboons' age and rank exhibit a significant positive correlation ($r = 0.577$, $t(61) = 5.512$, $p < 0.001$***), indicates there is a large effect size of age. The observed correlation is further explicated by the comparison of means between the age of high-ranking males with non-high-ranking males. High-ranking males ($N_{high} = 28$, $Age_{mean} = 9.3$ y) have a significantly lower mean age ($t(38.474) = -4.826$, $p < 0.001$***) than non-high-ranking males ($N_{non} = 35$, $Age_{mean} = 12.8$ y). The distribution of age in relation to rank is presented on *Graph 2* (Appendix-2).

Discussion

As predicted by *prediction 1,* age is significantly correlated with the dominance rank among male macaques in 6 out of 10 studies that present p-values. Then the meta-analysis indicates the effect of this correlation is strong and positive, which offers a conclusion that dominance hierarchy in macaques is associated with the age of males. The follow-up descriptive statistic specifies this correlation, it indicates that male macaques on average achieve their highest dominance rank (top three) around the age of 9.6, which age is found as the prime age of combat and reproduction (e.g., rhesus macaques; Maestripieri, 2019).

A meta-analysis is not done on previous research that investigates baboons, another well-studied species of cercopithecine, because most published articles do not make their original data publicly available, adopt different protocols of categorizing age and rank, and using a heterogenous statistic method for presenting effect size. However, the studies done in Amboseli provides a rich source for investigating the relationship between age and rank, though the paucity of data from other sources prevent an attempt of conducting meta-analysis. A review of literature shows an agreement on the association between age and dominance rank that is found in the present study, in contrast to a disagreement on this association among studies on macaques. Baboons, similar to macaques, grow to subadults at the age of 4 (e.g., Savanna baboons, Bercovitch, 1986) to 7 (e.g., yellow baboons, Altmann, et al., 1977), and they become full adults and reach their prime stage of physics around the age of 10 (Altmann, et al., 1977). Empirically, yellow baboon (Alberts & Altmann, 1995), olive baboon (Packer et al. 2000), and Savanna baboon (Bercovitch, 1986) groups present a consistent tendency that the highest-ranking males have an age around 10 on average. This line of research finding is consistent with the result shown by the present meta-analysis, where the high-ranking males in macaque groups have an age of 9.8 on average.

This convergence supports *prediction 1*, but it has to be interpreted with caution. The group size of baboons tested and reviewed above is generally larger than macaques', and the descriptive statistics show that there is a larger number of old adult males (older than the three highest-ranking males) in baboons troops than it is in in macaque groups. This discrepancy may be explained by the observed collective revolution by middle-ranking macaques against the highest-ranking macaques (e.g., rhesus macaques; Georgiev, et al., 2016), which consequently expels the previous alpha and causes him to live in solitude outside of his original group. Also, the absence of males older than the highest-ranking ones may be attributed to the heightened mortality of rhesus macaques in the context of breeding season and fluctuation of dominance hierarchy (Maestripieri, 2019).

On the other hand, the sampled studies on macaques report a small number of troops that share an overlapping habitat. The greatest degree of cohabitation is reported by Drickamer and Vessey (1973), in which study site 4 troops of rhesus macaque are found to coexist together. Intriguingly, they also report the lowest average age of the highest-ranking males (6 after rounding) among all studies sampled, which may indicate a violent intragroup rank revolution that potentially contributed by a striking degree of intergroup interaction and male transfer.

Finally, Baker and Eaton (1992) raise an important qualification on the association between age and dominance rank in macaques, for they found seniority (the duration of group residency) serves a better prediction of the dominance rank than age by adding both age and seniority as predictors into a linear regression model. This finding is corroborated by the stratified observation of the dominance hierarchy in relation to different seniority cohorts. Indicated by the t-test, in troop A and B (Baker & Eaton, 1992), the top 9 highest-ranking males all have stayed in the group for more than 4 years, whereas the middle 9 ones have an average seniority of fewer than 3 years (after rounding). The stratification of a dominance hierarchy in relation to the difference of seniority implies the existence of collaboration between male macaques from the same seniority cohort, as predicted by *prediction 5*.

However, in baboons, Cowlishaw & Dunbar (1991) argue the stratification of age, rather than seniority, may predict the likelihood of collaboration in antagonistic support. This argument is supported by two lines of finding. First, the strong positive correlation between rank and age is found in 5 troops of baboons in Amboseli, and the three highest-ranking males are significant younger than the rest of male members, which high-ranking males has an average age (9.3 y) that is close to the prime age reported by previous research (e.g., wild savannah baboons: Alberts, Watts & Altmann, 2003). Second, their argument serves no contradiction with the observation of rank stratification by age, because of the absence of seniority as a predictor in their report and the observed strong positive correlation between age and seniority in both Japanese macaques and rhesus macaques (Baker & Eaton, 1992).

The present meta-analysis, follow-up statistic, Pearson's correlation, and theoretical speculation based on Welch's t-test present empirical support to *prediction 1* and *5* (see Table 1 in Appendix-1), and preliminarily delineate the queue and solidarity facets of the dominance hierarchy, as predicted by *equation 1* and *2* and the literature review. Future studies are needed to specify the role of numerous socioecological factors on the queue and solidarity facets of the dominance hierarchy enlisted by *predictions 2, 3, 4,* and *5*. In short, the present study suggests future studies to use a combination of a linear regression model, naturalistic observation, and controlled experiment for further developing our understanding of the two facets of dominance hierarchy.

Future Direction

Linear Regression

The group size, the averaged difference of mating opportunity (or fitness output provided by genetic data) between two adjacent dominance ranks of all macaque or baboon groups should be treated indiscriminately as independent observations. Then, a linear regression model should be used for investigating how well the group size (predictor variable) linearly predict the averaged difference of mating opportunities (outcome variable), while having the time of observation as a covariate.

Considering the complex nature of the social groups, previous studies have identified the role of extra group copulation (Widdig et al., 2015), male-male coalition (Alberts, Watts & Altmann, 2003), and female-male friendship (Smuts, 1985) on influencing the mating opportunities of ingroup males. Thus, the proposed linear regression model may leave a large proportion of unexplained variance of the outcome variable. However, there may be a difficulty of adding the proposed factors as either covariates or predictors (e.g., in a multivariate regression model), because the reviewed studies that have a focus on the role of dominance do not include observations or data other than dominance ranks, groups sizes, and information about group composition. Then, a simple correlation analysis between group size and the averaged difference of mating opportunities should be conducted, and a significant negative relationship between the two variables is expected (see *predictions 1 & 3*).

Mediation check

Parallelly, linear regression and correlation analysis should also be conducted for investigating the relationship between the average age difference between ingroup males with the averaged difference of mating opportunities. As an innovation, the present study predicts the average age difference may act as a mediator in the relationship between the group size with the averaged difference of mating opportunities, because a group that is larger compared with other groups may be contributed by a greater incidence of immigration. Thus, the mediation check may give a statistical description about whether group size will still be a significant predictor when being isolated from the explanatory power of the averaged age difference while bridging the relationship between group size and averaged age difference of a group.

Naturalistic observation

Prediction 4 can be tested by analyzing the data from longitudinal naturalistic observations on groups of cercopithecines. However, group size and occurrence of a coalition in antagonistic interaction should not be taken into analysis unless they are gathered immediately prior, or after, or during the period of the breeding season. Also, naturalistic observation on coalition behavior is expected to distinguish antagonistic behaviors (e.g., involving physical contact or aggressive display) versus non-antagonistic ones, and breeding context (e.g., replacing a male from his established and ongoing consortship) versus other social encounters, for the present study is only interested in the coalition in antagonistic interaction in a breeding context. Then, similar to the methods proposed above, age difference and the frequency of coalition should be taken as the predictor and the outcome variable, while the group size should be treated as the mediator

Controlled experiment

Adult male cercopithecines from various groups should be recruited, and baboons and rhesus macaques are the most desirable candidate in accordance with the previous studies (Cowlishaw & Dunbar, 1991, 1992; Alberts, Watts & Altmann, 2003) that provide a rich source of naturalistic observations and theoretical inferences. The experiment is composed of two parts: (i) a competition condition, and (ii) two coalition conditions.

In the competition condition, the focal adult male from *group A* will be situated with an adult male who has had cohabitated with the focal for at least 2 breeding seasons successively, an adult male from *group B* who the focal has no prior exposure to, or an adolescent male from *group A* who is natal to that group. Derived from the experimental set-up by Ostner, Wilken, and Schülke (2021), in all three scenarios, the focal has to be situated closely (2 meters) with the stimulus (a cohabiting male, a stranger male, or an adolescent male), while both the focal and the stimulus have to be situated within the range of 5 meters with the exposure (an adult female who is in estrus). All three subjects are physically isolated from other members in either *group A or B*, and they are kept in three isolated cells of a large room for 5 minutes before the start of the experiment, no visual, auditorial, and olfactory exposure to any other subjects are allowed during the habituation period. During the experiment, the focal and stimulus only have visual access to the exposure, as a transparent window is used for obstructing their approaching.

There are two coalition conditions, including a dyadic coalition condition and a triadic coalition condition. Similar to the contest condition, in the dyadic collation condition, the focal male will be situated, habituated, and later observed with a cohabiting male, a stranger male, or an adolescent male across three scenarios. However, the focal and stimulus males are exposed to both an estrus female and a random adult ingroup male who is not taken as a focal or stimulus male across all three scenarios of the experiment. Finally, in the triadic coalition context, a focal male will be simultaneously situated, habituated, and experimented with two stimulus males. Across three scenarios in triadic coalition context, similarly, the focal male still be exposed to an estrus female and a random male member in his group, but he will be observed together with two random ingroup adult males, one ingroup adult male and one stranger male, or one ingroup adolescent male and one stranger male. Still, the approaching of the stimulus and focal to the exposures is obstructed by the transparent window.

During the period of experimenting, behavior coding in naturalistic observation by an experimenter and a blind observer will be conducted, and inter-rater consistency of recording will be calculated. Both experimenter and blind observer need to indicate the presence or absence of antagonistic behaviors between the focal and the stimulus in the competition condition. And they need to distinguish the main receiver of the aggression from either a partner of the focal or a neutral observer in addition to firstly noticing the presence of antagonistic behaviors, in the coalition condition involving two stimuli.

Across all the conditions, antagonistic behaviors including facial threats (e.g., staring open mouth), certain vocalizations (e.g., grunts, barks, and screams), a shortening of distance (e.g., by a lunge or pursuit), fierce biting, and head shaking will be recorded as present on a checklist derived from De Waal and Yoshihara (1983) either they are performed by the stimulus or the focal. And the present protocol also distinguishes antagonistic behaviors into two categories (De Waal, & Yoshihara, 1983): aggression, fierce aggression, judged by whether fierce biting and head shaking is present in the antagonistic interaction. From the perspective of the focal, observers note whether he is helped or not helped by the stimulus in two coalition conditions but not in the competition condition.

Across all conditions and scenarios, observation lasts standardly for 10 minutes. But observation is extended to 15 minutes when antagonistic behaviors are observed and to 20 minutes only if there exists fierce aggression, for conducting a post-conflict (PC) observation on the focal (De Waal, & Yoshihara, 1983). PC behaviors include self-grooming (groom or lick ones' own body), proximity shortening by either party (closer than 2 meters), and contact-sit (continuous sitting and huddling with the stimulus for more than 15 seconds), social grooming (groom or lick the body of stimulus).

All the exposures (females or female-male pairs) are sampled from the same group with the focal, and they are separated from the rest of the group members once they are observed in a consortship. Males who are observed in consortship is not taken as either focal or stimulus throughout all the scenarios of the experiment, and he will not serve any role except being the exposure in coalition conditions. All subjects' group affiliation, age, duration of group residency, dominance rank, and the degree of relatedness with other subjects in the experiment will be collected and recorded. See the behavior checklist in Appendix-3.

Confounds and Difficulties

The most serious difficulty is brought by the conventional model that defines and measures a dominance hierarchy, which model presents the linear and transitive built upon dominance hierarchy describes the asymmetry of the turnout of antagonistic interactions (e.g., cows, Clutton-Brock et al., 1976; e.g., Macacas; De Waal & Luttrell, 1989)

This linear representation may be problematic in primates, for it intuitively arranges hierarchy through the transmission of the turnout of dyadic antagonistic interaction (Appleby, M. C., 1983), which may oversimplify the reality, where the antagonistic intercourse may take place in a triadic or a more complex form. In the wild, males of different social statuses may face different intensities of male-male competition, and this cannot be faithfully represented by contrasting the males' difference in social status. For example, in rhesus macaques, the alpha male sometimes faces the challenge from a group of cooperative subordinates (Georgiev et al., 2016), and this challenge should be counted differently from a dyadic antagonistic interaction.

Also, the traditional model may have the problem of account the permanent expel of a member from the group, since the expelled member may not be counted as a group member at all. On the other hand, for subordinates, the difference between status may be ambiguous, especially when many members occupy the same social status or when they form cooperative subgroups. And the benefit of the cooperative act by a subgroup is distributed to its members based on the role of reciprocity rather than dominance hierarchy (Alberts, Watts & Altmann, 2003).

Finally, by limiting the role of females (e.g., synchronous receptivity and promiscuity) on influencing the operational sex ratio, the equations above fail to capture the heterogenous mate-choice by females. In reality, females are found to actively assess a male based on a diverse angle, such as the quality of secondary sexual characters (e.g., in mandrills, Setchell et al., 2008; Setchell & Wickings, 2005), male-female relationship (e.g. savannah baboons; Buchan et al., 2003), and his dominance hierarchy (e.g. Japanese macaques; Perloe, 1992; Watson et al., 2012). Besides, female cercopithecines are known to mate promiscuously, so post-insemination selection and sperm competition can also be important factors that influence the fitness output, especially when the fitness output is directly measured by genetic testing rather than approximated by mating opportunities. But this direction has not been thoroughly investigated in cercopithecines nor incorporated in the equations of the present study.

Summary

By assembling diverse factors that influence the group composition of cercopithecines, the socioecology of cercopithecines can be understood through the investigation of the relationship between group composition and members' fitness output. In a favorable socioecological condition, if the number of receptive females that are capable of being monopolized by a single male increase, males would be favored to live in a group where it contains a smaller number of males and is less hierarchically stratified. On contrary, when the monopolization of mating opportunities is threatened by extra group copulation, the influx of adult male immigrants, and overthrown of alpha position, cooperation in antagonistic interaction among the senior resident males may be favored. The equations, hypotheses, and predictions in the present study provide a theoretical framework that suggests a double-facet function of dominance hierarchy: the queue and the solidarity. And the hypothesized two facets are supported by a strong positive correlation between age and dominance rank from a meta-analysis on studies of 11 macaque troops and an independent analysis on 5 baboons troops, and are detailed by the identification of the stratification of dominance rank in relation to the age and seniority of males. Taken together, the highest dominance rank tends to be achieved by macaques and baboons at their prime age (approximately 10 y), and males with a longer cohabitation (seniority) tend to occupy adjacent dominance ranks. A use of naturalistic observation and controlled experimentation in the future may specify whether the stratification of dominance hierarchy in relation to seniority is likely resulted from male-male collation in antagonistic interaction, as predicted by the solidarity facet, and may deepen our understanding the predictive power of dominance rank on males’ mating opportunity and reproductive output.

References

Abernethy, K. A., White, L. J. T. & Wickings, E. J. (2002). Hordes of mandrills (*Mandrillus sphinx*): Extreme group size and seasonal male presence. Journal of Zoology, 258, 131–137.

Alberts, S.C., Watts, H.E., Altmann, J. (2003). Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*, Animal Behaviour, Volume 65, Issue 4, 2003, Pages 821-840, ISSN 0003-3472, https://doi.org/10.1006/anbe.2003.2106.

Altmann, S. A. (1962). A field study of the sociobiology of the rhesus monkey, Macaca mulatta. Ann. N.Y. Acad. Sci., 102,338-435.

Altmann, J., Altmann, S. A., Hausfater, G., & McCuskey, S. A. (1977). Life history of yellow baboons: Physical development, reproductive parameters, and infant mortality. Primates, 18(2), 315. https://doi-org.proxy.uchicago.edu/10.1007/bf02383111

Altmann, J., Altmann, S. A., Schoeller, D., Muruthi, P., & Sapolsky, R. M. (1993). Body size and fatness of free-living baboons reflect food availability and activity levels. American Journal of Primatology, 30(2), 149–161. https://doi-org.proxy.uchicago.edu/10.1002/ajp.1350300207

Alberts, S. C. & Altmann, J. 1995a. Preparation and activation: determinants of age at reproductive maturity in male baboons. Behavioral Ecology and Sociobiology, 36, 397–406.

Appleby, M. C. (1983). The probability of linearity in hierarchies. Animal Behaviour, 31, 600–608.

Andelman, S. J. (1986). Ecological and social determinants of cercopithecine mating patterns. In Ecological Aspects of Social Evolution: Birds and Mammals, 201–216. Princeton, NJ: Princeton University Press.

Baker, P. M., & Eaton, G. G. (1992). Seniority Versus Age as Causes of Dominance in Social Groups: Macaques and Men. Small Group Research, 23(3), 322–343. https://doi.org/10.1177/1046496492233004

Bercovitch, F. B. (1986). Male rank and reproductive activity in Savanna baboons. International Journal of Primatology: The Official Journal of the International Primatological Society, 7(6), 533. https://doi-org.proxy.uchicago.edu/10.1007/bf02736660

Berard, J. D., Nürnberg, P., Epplen, J. T., & Schmidtke, J. (1993). Male rank, reproductive behavior, and reproductive success in free-ranging rhesus macaques. Primates, 34(4), 481–489. https://doi-org.proxy.uchicago.edu/10.1007/BF02382659

Berman, C. M., Lonica, C. & Li, J. (2007). Supportive and tolerant relationships among male Tibetan macaques at Huangshan, China. Behaviour, 144, 631–661.

Berthier J. M. & Semple, S. (2018). Observing grooming promotes affiliation in Barbary macaques. Proc. R. Soc. B 285, 20181964, doi:10.1098/rspb.2018.1964

Brauch, K., Pfefferle, D., Hodges, K., Möhle, U., Fischer, U., Heistermann, M. (2007). Female sexual behavior and sexual swelling size as potential cues for males to discern the female fertile phase in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar, Hormones and Behavior, Volume 52, Issue 3, Pages 375-383, ISSN 0018-506X, https://doi.org/10.1016/j.yhbeh.2007.06.001.

Buchan, J. C., Alberts, S. C., Silk, J. B. & Altmann, J. (2003). True paternal care in a multi-male primate society. Nature, 425, 179–181.

Butovskaya, M.L., & Kozintsev, A.G. (1996). Gender-related factors affecting primate social behavior: Grooming, rank, age, and kinship in heterosexual and all-male groups of stumptail macaques. Am. J. Phys. Anthropol., 101: 39-54.

https://doiorg.proxy.uchicago.edu/10.1002/(SICI)1096-8644(199609)101:1<39::AID-AJPA4>3.0.CO;2-8

Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. Ecol. MOllogr. 60:1-26.

Chapman, C. A., Chapman, L. J., Cords, M., Gathua, J. M., Gautier-Hion, A., Lambert, J. E., Rode, K., Tutin, C. E., & White, L. T. (2002). Variation in the Diets of Cercopithecus Species: Differences within Forests, among Forests, and across Species. The Guenons: Diversity and Adaptation in African Monkeys, 325. https://doi-org.proxy.uchicago.edu/10.1007/0-306-48417-X_22

Cheney, D. L. (1981). Intergroup encounters among free-ranging vervet monkeys. Folia Primatol. 35:124-146.

Clutton-Brock, T. H., Greenwood, P. J. & Rowell, R. P. (1976). Ranks and relationships in highland ponies and highland cows. Z. Tierpsyehol, 41, 202-216.

Cowlishaw, G., & Dunbar, R. I. (1991). Dominance rank and mating success in male primates. Animal Behaviour, 41(6), 1045–1056. https://doi.org/10.1016/S0003-3472(05)80642-6.

Darwin, C. (1859). On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. London: Murray. [1st ed.]

Darwin, C. (1871). ‘‘The Descent of Man and Selection in Relation to Sex.’’ John Murray, London.

Darwin, C. (1876). Sexual selection in relation to monkeys. Nature 15, 18–19.

De Waal, F. B. M., & Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus monkeys. Behaviour, 85, 224–241. https://doiorg.proxy.uchicago.edu/10.1163/156853983X00237

De Waal, F. B. M. & Luttrell, L. M. (1989). Toward a comparative socioecology of the genus Macaca: Different dominance styles in rhesus and stumptail macaques. American Journal of Primatology, 19, 83–109.

Drickamer, L. C., & Vessey, S. H. (1973). Group changing in free-ranging male rhesus monkeys. Primates, 14(4), 359. https://doi-org.proxy.uchicago.edu/10.1007/bf01731357

Dubuc, C., Brent, L.J.N., Accamando, A.K., Gerald, M.S., MacLarnon, A., Semple S., Heistermann, M., & Engelhardt, A. (2009). Sexual Skin Color Contains Information About the Timing of the Fertile Phase in Free-ranging *Macaca mulatta*. Int J Primatol 30, 777–789. https://doi.org/10.1007/s10764-009-9369-7

Emlen, S. T., & Oring, L. W. (1977). Ecology, Sexual Selection, and Evolution of Mating Systems. Science, 197(4300), 215–223. https://doi-org.proxy.uchicago.edu/10.1126/science.327542

Emlen, S. T. (1995). An evolutionary theory of the family. Proceedings of the National Academy of Science 92:8092-8099.

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

Georgiev, A. V., Christie, D., Rosenfield, K. A., Ruiz-Lambides, A. V., Maldonado, E., Thompson, M. E., & Maestripieri, D. (2016). Breaking the succession rule: the costs and benefits of an alpha-status take-over by an immigrant rhesus macaque on Cayo Santiago. Behaviour, 153(3), 325–351. https://doi-org.proxy.uchicago.edu/10.1163/1568539X-00003344

Girard-Buttoz, C., Heistermann, M., Rahmi, E., Marzec, A., Agil, M., Fauzan, P. A., & Engelhardt, A. (2014). Mate-guarding constrains feeding activity but not energetic status of wild male long-tailed macaques (*Macaca fascicularis*). Behav Ecol Sociobiol 68, 583–595. https://doi.org/10.1007/s00265-013-1673-8

Hamilton, W.D. (1964). The genetical evolution of social behaviour. I, Journal of Theoretical Biology, Volume 7, Issue 1, 1964, Pages 1-16, ISSN 0022-5193, https://doi.org/10.1016/0022-5193(64)90038-4.

Hamilton, W.D. (1964). The genetical evolution of social behaviour. II, Journal of Theoretical Biology, Volume 7, Issue 1, 1964, Pages 17-52, ISSN 0022-5193, https://doi.org/10.1016/0022-5193(64)90039-6.

Hill, D. A. (1986). Social relationships between adult male and immature rhesus macaques. Primates, 27(4), 425. https://doi-org.proxy.uchicago.edu/10.1007/bf02381888

Higham, J.P., Pfefferle, D., Heistermann, M., Maestripieri, D., Stevens, M. (2013). Signaling in multiple modalities in male rhesus macaques: Sex skin coloration and barks in relation to androgen levels, social status, and mating behavior. Behavioral Ecology and Sociobiology 67, 1457–1469.

Hunter, J. E., & Schmidt, F. L. (2000). Fixed Effects vs. Random Effects Meta-Analysis Models: Implications for Cumulative Research Knowledge. International Journal of Selection & Assessment, 8(4), 275. https://doi-org.proxy.uchicago.edu/10.1111/1468-2389.00156

Lehmann, J., Korstjens, A.H., Dunbar, R.I.M. (2007). Group size, grooming and social cohesion in primates, Animal Behaviour, Volume 74, Issue 6, 2007, Pages 1617-1629, ISSN 0003-3472, https://doi.org/10.1016/j.anbehav.2006.10.025.

Maestripieri, D. & Roney, J. R. (2005). Primate copulation calls and postcopulatory female choice. Behavioral Ecology, 16, 106–113.

Maestripieri, D., Hoffman, C.L. (2011). Behavior and social dynamics of rhesus macaques on Cayo Santiago. In: Wang, Q. (Ed.), Bones, Genetics, and Behavior of Rhesus Macaques. Springer, Berlin, pp. 247–262.

Maestripieri, D. (2019). Rhesus Macaques, Choe, J. C. (eds), Encyclopedia of Animal Behavior (Second Edition), Academic Press, 2019, Pages 167-172, ISBN 9780128132524, https://doi.org/10.1016/B978-0-12-809633-8.20748-6.

Matsubara, M. (2003). Costs of Mate Guarding and Opportunistic Mating Among Wild Male Japanese Macaques. International Journal of Primatology 24, 1057–1075. https://doi.org/10.1023/A:1026228312706

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

Mugambi, K.G., Butynski, T.M., Suleman, M.A., Ottichilo, W. (1997). The Vanishing De Brazza's Monkey (Cercopithecus neglectus Schlegel) in Kenya. International Journal of Primatology 18, 995–1004 (1997). https://doi.org/10.1023/A:1026352331577

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

Noë, R. & Sluijter, A. A. (1995). Which adult male savanna baboons form coalitions? International Journal of Primatology, 16, 77–105.

Nunn, C. L. (1999). The Number of Males in Primate Social Groups: A Comparative Test of the Socioecological Model. Behavioral Ecology and Sociobiology, 46(1), 1–13.

Ohsawa, H., Inoue, M., & Takenaka, O. (1993). Mating strategy and reproductive success of male patas monkeys (*Erythrocebus patas*). Primates, 34(4), 533–544. https://doi-org.proxy.uchicago.edu/10.1007/BF02382664

Ostner, J., Nunn, C. L. & Schülke, O. (2008). Female reproductive synchrony predicts skewed paternity across primates. Behavioral Ecology 19, 1150–58.

Ostner, J., Wilken, J., & Schülke, O. (2021). Social contagion of affiliation in female macaques. Royal Society Open Science, 8(1), 201538. https://doi-org.proxy.uchicago.edu/10.1098/rsos.201538

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

Packer, C., Collins, D. A. & Eberly, L. E. 2000. Problems with primate sex ratios. Philosophical Transactions of the Royal Society of London, 355, 1627–1635.

Pearson, K. (1904). On the theory of contingency and its relation to association and normal correlation. London, Dulau and Co.

Perloe, S.I. (1992). Male mating competition, female choice and dominance in a free ranging group of Japanese macaques. Primates 33, 289–30. https://doi.org/10.1007/BF02381191

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rendall, D., Rodman, P. S., & Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. Animal Behaviour, 51, 1007-1015.

Rudran, R. (1978). Intergroup dietary comparisons and folivorous tendencies of two groups of blue monkeys (*Cercopithecus mitis stuhlmanniii*). In: G. G. Montgomery (ed.), The Ecology of Arboreal Folivores, pp. 483–503. Smithsonian Institution Press, Washington.

Semple, S. (1998). The Function of Barbary Macaque Copulation Calls. Proceedings: Biological Sciences, 265(1393), 287-291. Retrieved November 29, 2020, from http://www.jstor.org/stable/50833

Semple, S., and McComb, K. (2000). Perception of female reproductive stale from vocal cues in a mammal species. Proc. R. Soc. Lond. B 267, 707–712.

Setchell, J. M., Lee, P. C., Wickings, E. J. & Dixson, A. F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). American Journal of Physical Anthropology, 115, 349–360

Setchell, J. M. & Wickings, E. J. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). Ethology, 111, 25–50.

Setchell, J. M., Smith, T., Wickings, E. J. & Knapp, L. A. (2008). Social correlates of testosterone and ornamentation in male mandrills. Hormones and Behavior, 54, 365–372.

Silk, J. B. (1992). The patterning of intervention among male bonnet macaques: Reciprocity, revenge and loyalty. Current Anthropology, 33, 318–325.

Silk, J. B. (1994). Social relationships of male bonnet macaques: Male bonding in a matrilineal society. Behaviour, 130, 271–291.

Sinha, A., Mukhopadhyay, K., Datta-Roy, A. & Ram, S. (2005b). Ecology proposes, behaviour disposes: Ecological variability in social organization and male behavioural strategies among wild bonnet macaques. Current Science, 89, 1166–1179.

Smith, R. J. & Jungers, W. L. (1997). Body mass in comparative primatology. Journal of Human Evolution, 32, 523–559.

Smith, L. W., Link, A. & Cords, M. (2008). Cheek pouch use, predation risk, and feeding competition in blue monkeys (*Cercopithecus mitis stuhlmanni*). American Journal of Physical Anthropology, 137, 334–341.

Smuts, B. B. (1985). Sex and Friendship in Baboons. New York: Aldine.

Soltis, J., Thomsen, R., Matsubayashi, K. Takenata, O. (2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). Behav Ecol Sociobiol 48, 195–202 (2000). https://doi.org/10.1007/s002650000224

Sprague, D. S. (1992). Life history and male intertroop mobility among Japanese macaques (*Macaca fuscata*). International Journal of Primatology, 13(4), 437–454. https://doi-org.proxy.uchicago.edu/10.1007/BF02547827

Strum, S. C. (1982). Agonistic dominance in male baboons: an alternative view. International Journal of Primatology, 3, 175–202.

Swedell, L. (2010). African papionins: Diversity of social organization and ecological flexibility. In Primates in Perspective, 241–277. New York: Oxford University Press.

Swedell, L., Saunders, J., Schreier, A., Davis, B., Tesfaye, T. and Pines, M. (2011), Female “dispersal” in hamadryas baboons: Transfer among social units in a multilevel society. Am. J. Phys. Anthropol., 145: 360-370. https://doi-org.proxy.uchicago.edu/10.1002/ajpa.21504

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

Tutin, C. E. G., Ham, R. M., White, L. J. T., and Harrison, M. J. S. (1997). The primate community of the Lopé Reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. Am. J. Primatol. 42:1–24.

Watson, K.K., Ghodasra, J.H., Furlong, M.A., & Platt, M.L. (2012). Visual preferences for sex and status in female rhesus macaques. Anim Cogn 15, 401–407. https://doi.org/10.1007/s10071-011-0467-5

Widdig, A., Kessler, M. J., Bercovitch, F. B., Berard, J. D., Duggleby, C., Nuernberg, P., Rawlins, R. G., Sauermann, U., Wang, Q., Krawczak, M., & Schmidtke, J. (2016). Genetic Studies on the Cayo Santiago Rhesus Macaques: A Review of 40 Years Of

Research. AMERICAN JOURNAL OF PRIMATOLOGY, 78(1), 44–62. https://doi-org.proxy.uchicago.edu/10.1002/ajp.22424 Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. Behaviour, 75, 262–300.

Van Schaik, C.P., van Noordwijk, M.A., Warsono, B. Sutriono, E. (1983). Party size and early detection of predators in sumatran forest primates. Primates 24, 211–221 (1983). https://doi.org/10.1007/BF02381083

Zuberbühler, K. (2000a). Causal knowledge of predators' behaviour in wild Diana monkeys, Animal Behaviour, Volume 59, Issue 1, 2000, Pages 209-220, ISSN 0003-3472, https://doi.org/10.1006/anbe.1999.1296.

Zuberbühler, K. (2000b). Causal cognition in a non-human primate: field playback experiments with Diana monkeys, Cognition, Volume 76, Issue 3, 2000, Pages 195-207, ISSN 0010-0277, https://doi.org/10.1016/S0010-0277(00)00079-2.

Appendix-1

Table 1: The Double Facets of Dominance Hierarchy

Role	Hypothesis	Prediction
Category 1: The Queue	younger adult males who are presumably more competitive in dyadic antagonistic interaction may often have a higher fitness output than older resident males of the group *(Hypothesis 2*)	the alpha male in each group of multi-male multi-female cercopithecine groups is likely to be the youngest adult male, and the alpha may have the greatest opportunities of mating (*prediction 1*)
	males with different dominance ranks and ages behave differently for mate-accessing (*Hypothesis 5*)	older and lower ranking males are more likely be observed to form collaborative party in antagonistic challenge and the male who replaces the one originally in consortship may reciprocally help others in the party without gaining the access to mate (*prediction 2*)
Category 2: The Solidarity	the difference of fitness output between two males on two adjacent dominance ranks decreases as the number of ingroup males increases (*Hypothesis 4*)	the difference of mate-access or fitness output between the males on two adjacent dominance ranks is smaller in groups with a greater number of males (*prediction 3*)
	collation in antagonistic interaction is more likely to occur when the age difference between males is greater than in groups with a smaller age difference (*Hypothesis 1*)	the occurrence of coalition increases in relation to the increase of age difference across different groups of a species (*prediction 4)*
	FB primate groups with greater potential for the occurrence of antagonistic support may exhibit a smaller difference of fitness output between males is greater than in groups with a smaller age difference (*Hypothesis 3)*	coalition may more frequently be observed among males with longer duration of cohabitation in a same group (seniority) than among new immigrants (*prediction 5*)

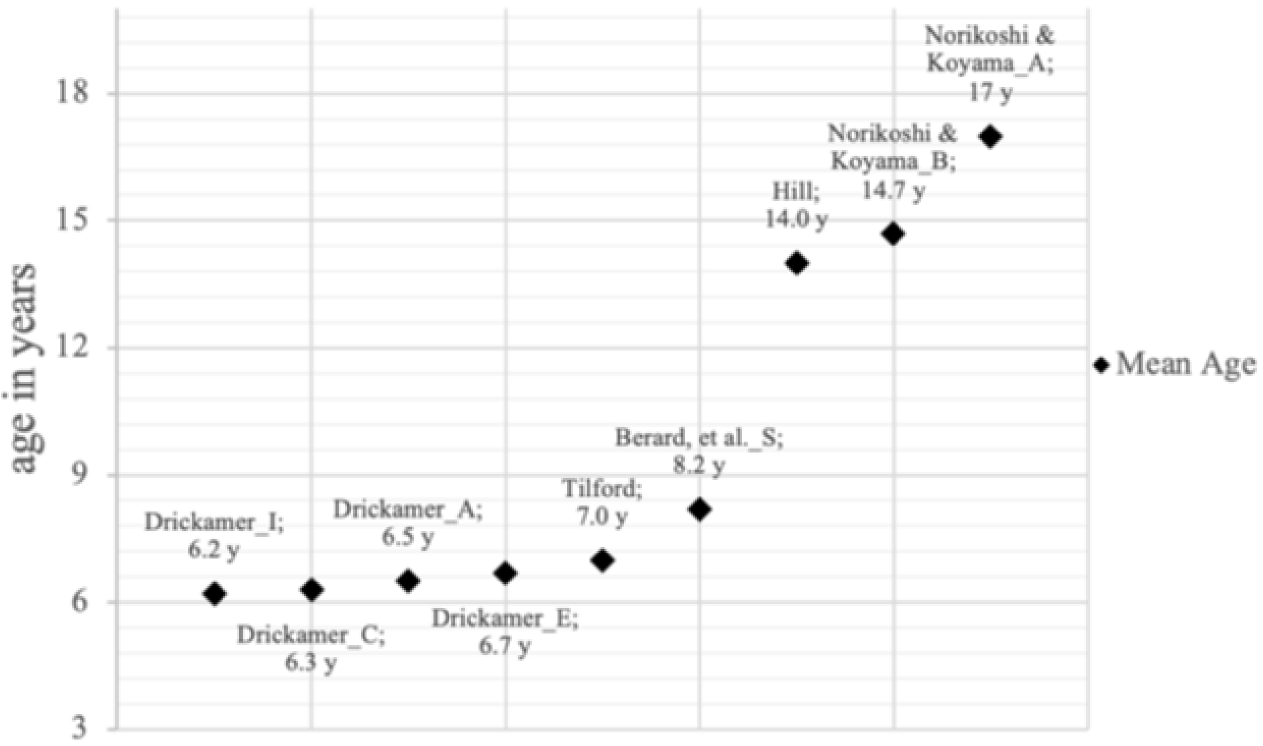
Appendix-2

Table 2: Studies in the Meta-analysis

Study	Species	Site	Troop	N	r	p-value
Drickamer, L. C., & Vessey, S. H. (1973)	rhesus macaqyes	La Parguera, Puerto Rico	A	15	0.615	0.0145*
			C	17	0.43	0.085
			I	11	0.3	0.374
			E	7	0.741	0.056
Norikoshi, K., & Koyama, N. (1975)	Japanese macaques	Arashiyama, Japan	A	26	0.925	NA
			B	26	0.934	NA
Tilford, B. L. (1982)	rhesus macaqyes	La Parguera, Puerto Rico		20	0.744	<.001***
Hill, D. A. (1986)	rhesus macaqyes	Cayo Santiago		14	0.707	<.01**
Paul, A. (1989)	Barbary macaques	Affenberg Salem, Germany	A	17	0.92	<.001***
			A†	30	0.862	<.001***
McMillan, C. A. (1989)	rhesus macaques	Cayo Santiago		23	0.185	>.05
Berard, et al. (1993)	rhesus macaques	Cayo Santiago	S	11	0.713	<.05*
Total				217		

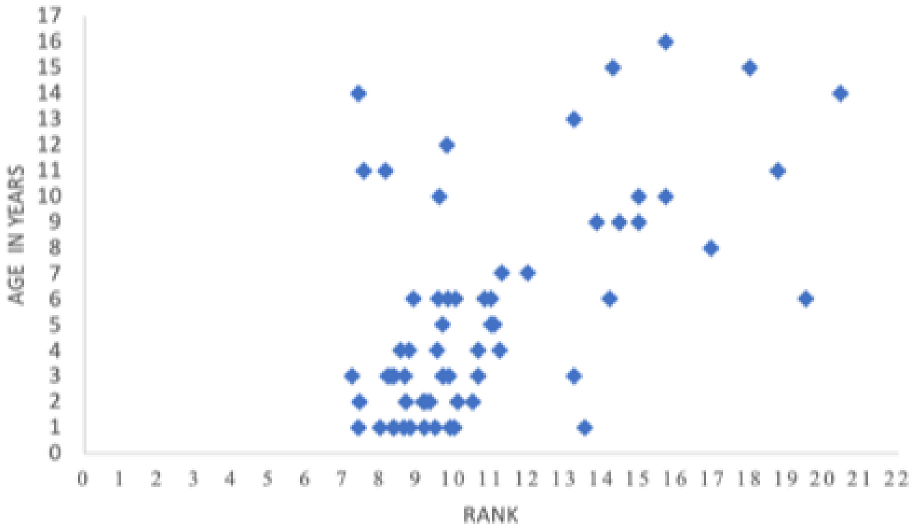
N: the number of subjects
r: the Pearson’s correlation coefficient
p: p value (<0.05, <0.01**, <0.001***)*
A†: the same troop observed in a different breeding season
NA: r value is not presented by the original article

Graph 1: the mean age of the three highest ranking males



Note: each dot represents the average age of three highest-ranking males in groups sampled by each study on macaques

Graph 2: the distribution of males' age in relation to rank



Note: each dot represents the age and dominance rank of an individual male in 5 baboon groups sampled by Galbany, et al. (2015)

Appendix-3

Behavior Checklist

Observer: ___________
Date: _____/_____/_____
Time: _____ • A.M. / • P.M.
Duration: ______
Interrater Consistency: _______

Subjects:
Focal: ________
Affiliation: • A, • B; Age ___; Residency Duration ___; Rank ___
Stimulus:
(i)________
Affiliation: • A, • B; Age ___; Residency Duration ___; Rank ___
(ii)________
Affiliation: • A, • B; Age ___; Residency Duration ___; Rank ___
(ii)________
Affiliation: • A, • B; Age ___; Residency Duration ___; Rank ___
Exposure:
(i) ________
Affiliation: • A, • B; Age ___; Residency Duration ___; Rank ___
(ii) ________
Affiliation: • A, • B; Age ___; Residency Duration ___; Rank ___

Antagonistic Behavior • present, • absent
Starter: ________
Receiver: ________
Facial threatening: • present, • absent
Vocal threatening: • present, • absent
Distance-shortening: • present, • absent
Fierce biting: • present, • absent
Head shaking • present, • absent

Coalition in Aggression: • present, • absent
Helper: ________

Post-conflict Behavior: • present, • absent
Self-grooming: • present, • absent
Proximity-shortening: • present, • absent
Contact-sit: • present, • absent
Social grooming: • present, • absent