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Evolution of Human-Like Social Grooming Strategies Regarding Richness and Group Size

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Human social strategies have evolved as an adaption to behave in complex societies. In such societies, humans intensively tend to cooperate with their closer friends, because they have to distribute their limited resources through cooperation (e.g., time, food, etc.). It also makes the situation difficult to have uniform social relationships (social grooming) with all friends. Thus, the social relationship strengths often show a much skewed distribution (a power law distribution). Here we aim to show adaptivity of such social grooming strategies in order to explore the evolution of human social intelligence. We use a model in the framework of evolutionary games where the social grooming strategies evolve via building social relationships with cooperators. Simulation results demonstrate four evolutionary trends. One of the trends is similar to the strategy that humans use. We find that these trends depend on three parameters; individuals' richness, group sizes, and the amount of social grooming. The human-like strategy evolves in large poor groups. Moreover, the increase of the amount of social grooming makes the group size larger. Conversely, this implies that the same strategy evolves when the amount of social grooming is properly adjusted even if the group sizes are different. Our results are important in the sense that, between human and non-human primates, the differences of the group size and the amount of social grooming are significant.

Keywords: social grooming, evolutionary game, social structure, Yule–Simon process, cooperation

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1. INTRODUCTION

Cooperation is common among humans and it is fundamental to our society (Smith and Szathmáry, 2000; Fehr and Fischbacher, 2003). The amount of cooperation by other people is limited because they have to pay costs (e.g., money, time, opportunities, food, etc.) (Santos et al., 2006; Xu and Wang, 2015). Therefore, people carefully choose their friends in order to receive intensive cooperation (Rand et al., 2011; Grujić et al., 2012; Wang et al., 2012).

Actually, people tend to cooperate with close friends. An experimental study using the Donation Game shows that participants tend to cooperate more with closer friends (Harrison et al., 2011). Another study using the Public Goods Game shows that friend groups are more cooperative with each other than with other groups (Haan et al., 2006). Additionally, in a data analysis study dealing with the data set of a social network game, people's frequent communication increases their cooperative behavior (Takano et al., 2016a,b).

Thus, it is important that humans have stronger social relationships in greater numbers with cooperators than with others. We define social grooming as the behavior that constructs social relationships. Primarily, social grooming is the act of cleaning or maintaining the body of a social partner in primates (Dunbar, 2000, 2004; Nakamura, 2003). Social bonding is part of the functional aspect of social grooming. Therefore, human social bonding behavior is also called social grooming (Dunbar, 2000, 2004), as a hypothetical extrapolation of the findings in non-human animals.

The behavior constructing social relationships is not limited to humans but widely observed in primates (Kobayashi and Kohshima, 1997; Dunbar, 2000, 2004; Nakamura, 2003; Kobayashi and Hashiya, 2011; Takano et al., 2016a,b; Takano and Fukuda, 2017). In doing so, they face cognitive constraints (Dunbar, R. I. 2012) (e.g., memory and processing capacity) and time constraints (i.e., time costs) in constructing and maintaining social relationships. These time constraints are not negligible, as people spend a fifth of their day in social grooming (Dunbar, 1998) for maintaining the relationship (Hill and Dunbar, 2003; Roberts and Dunbar, 2011). Therefore, the strength of existing social relationships exhibits a negative correlation with the total number of social relationships (Roberts et al., 2009; Miritello et al., 2013b).

On the other hand, it is important to select cooperative partners in the evolution of cooperation because cooperators tend to be exploited by defectors (Axelrod, 2006). To select appropriate cooperative partners, it is known that reading others' intentions play an important role (Han et al., 2012, 2015; Arechar et al., 2017). Arechar et al. (2017) revealed that sending a message for their intentions (selecting a strategy in repeated games) when subjects play the games promotes cooperation even when an error is incorporated. Han et al. (2012, 2015) showed that, by theoretical models, others' intentions which are formed by past interactions in repeated games enhance cooperation. Moreover, commitments (e.g., prior agreements to cooperate) are other mechanisms to build long-term cooperative relationships, which enable cooperation to evolve by natural selection (Nesse, 2001; Martinez-Vaquero et al., 2015, 2017). Han et al. (2015) emphasized that the balance between intention and commitments is important for cooperative relationships. These are the mechanisms working in direct reciprocity. Spatial reciprocity and network reciprocity also suggest the necessity of fixed relationships (Perc and Szolnoki, 2010; Perc et al., 2017). Therefore, it is reasonable to consider that humans and other social animals tend to cooperate with their close partners (Haan et al., 2006; Harrison et al., 2011; Takano et al., 2016a,b).

Humans must construct and maintain social relationships within the constraints of this trade-off. We expect that strategies are employed to distribute the limited time resources to maximize benefits from their social relationships (Brown and Brown, 2006; Miritello et al., 2013a; Saramaki et al., 2014). As a result of such strategies, social relationship strengths, as measured by frequency of social grooming (Roberts and Dunbar, 2011; Arnaboldi et al., 2012, 2013; Song et al., 2013; Fujihara and Miwa, 2014; Saramaki et al., 2014; Takano and Fukuda, 2017), may often show a skewed distribution (Zhou et al., 2005; Arnaboldi et al., 2013), distributions following a power law (Hossmann et al., 2011; Arnaboldi et al., 2012; Hu et al., 2012; Pachur et al., 2012; Song et al., 2013; Fujihara and Miwa, 2014; Takano and Fukuda, 2017). Moreover, it has been demonstrated that social structures of non-human primates (Kanngiesser et al., 2011; Tung et al., 2015; Levé et al., 2016; Dunbar, R. I. M. 2012) are also skewed.

The skewed distributions of the relationships could be generated by a strategy where individuals select social grooming partners in proportion to the strength of their social relationships (Pachur et al., 2012; Takano and Fukuda, 2017); known as the Yule–Simon process (Yule, 1925; Simon, 1955; Newman, 2005). Individuals should pay time costs to win the competitions with others by strengthening their social relationships with cooperators, assuming that having strong social relationships is to receive cooperation.

Human societies using these strategies are much larger than those of non-human primates. Based on the social brain hypothesis, human intelligence has evolved to adapt to large societies. Therefore, the evolution of human strategies of social relationship construction may explain the origin of human intelligence. However, evolutionary stability of the strategies, i.e., the Yule–Simon process, is still open investigation.

In this paper, we aim to show the adaptivity of the social grooming strategies in order to explore the evolution of human social intelligence predicted by the social brain hypothesis. Especially, we focus on how environments drive the evolution of a social grooming strategy that humans use in their daily life. The evolution should depend on group size and the amount of resources for cooperation. For this purpose, we simulate the evolution of the strategy to receive cooperation from others with different environmental conditions for cooperations. We show that strategies evolve depending on the strength of social relationships.

2. METHODS

We expand the model of Takano and Fukuda (2017) to an evolutionary game. They consider two types of individuals; social groomers and cooperative groomees (**Figure 1** (Takano and Fukuda, 2017). In the real world, individuals are groomers

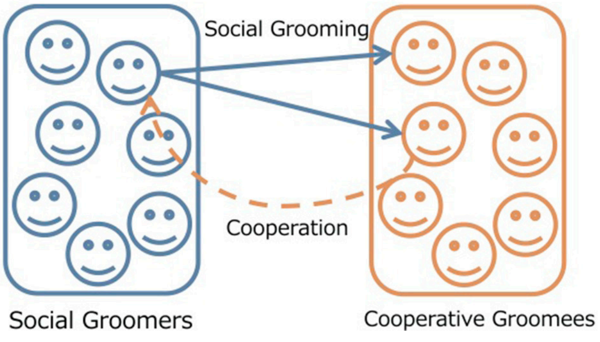


FIGURE 1 | Concept of our model. Social groomers interact with cooperative groomees depending on their social grooming strategies. Cooperative groomees cooperate with social groomers who are top R_C on the strengths of social relationships. Groomer strategies evolve based on their fitness which is the amount of cooperation from groomees.

TABLE 1 | Descriptions of model parameters.

Parameter	Description
s	Parameter of social grooming strategies for reinforcing relationships. See also **Figure 2**.
q	Ratio of creating a new social relationship with a stranger.
R_g	Frequency of social grooming in a grooming stage.
w_{ij}	Strength of social relationships between i and j (the number of social grooming from i to j).
d_{ij}	Normalized w_{ij}, i.e., $w_{ij}/max(\{w_{i1}, w_{i2}, \ldots, w_{iM}\})$
R_c	Number of cooperation from groomees to groomers.
M	Number of groomees.
N	Number of groomers.
T	Number of generations.

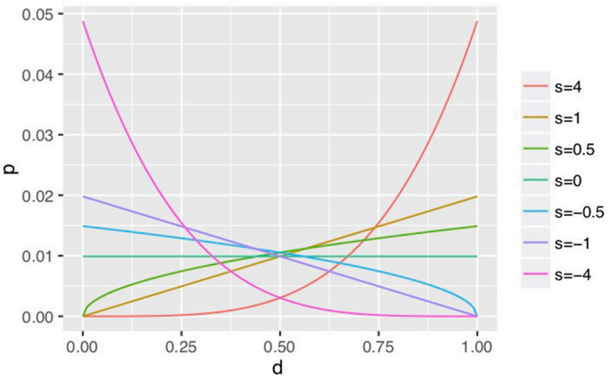


FIGURE 2 | Examples of social grooming strategies. Social groomers with large *s* tend to interact with a groomee in a strong social relationship (large *d*). On the other hand, groomers with small *s* tend to interact with a groomee in a weak social relationship (small *d*). When $s = 0$, groomers interaction is independent from *d*. When $s = 1$, groomers interact in proportion to the strength of social relationships, i.e., the Yule–Simon process.

and groomees, simultaneously. For simplicity, they use this classification to focus on the social grooming strategies for social structures. In this paper, we only focus on the evolution of social grooming strategies while cooperation from gromees' is static. This is because that cooperative behaviors are common in humans and primates (Silk, 2009; Rand and Nowak, 2013). Given that cooperation from groomees' is static, we can consider the evolution of groomers' strategies. While the evolutionary dynamics of cooperation are well-known (Nowak, 2006; Perc and Szolnoki, 2010; Rand and Nowak, 2013; Perc et al., 2017), there are few study on the evolutionary dynamics of social grooming. Groomers construct their social relationships with groomees depending on their social grooming strategies in a "grooming stage." Cooperative groomees cooperate with groomers depending on social relationship strengths in a "cooperation stage." Groomer strategies evolve based on their fitness which is the amount of cooperation from groomees in each generation. Groomees' cooperation strategies are static. **Table 1** shows the parameters of this model.

In a grooming stage, groomer i repeatedly interacts with cooperative groomees R_g times depending on their social grooming strategy (s_i, q_i). q_i is a ratio that i constructs a new social relationship with a stranger, new groomee j, and s_i is a parameter of a probabilistic function $p(d_{ij}; s_i)$ which selects existing social grooming partner j depending on d_{ij} $(d_{ij} > 0)$. We used the following function (**Figure 2**) as a simple function to express various strategies depending on d_{ij} including concentrated investment to strong relationships ($s = 4$), diversified investment to weak relationships ($s = -4$), at random ($s = 0$), and the Yule–Simon process ($s = 1$; i.e., human-like strategy).

$$p(d_{ij}; s_i) = b(d_{ij}; \alpha_i, \beta_i) / \sum_{k=1}^{M} b(d_{ik}; \alpha_i, \beta_i), \tag{1}$$

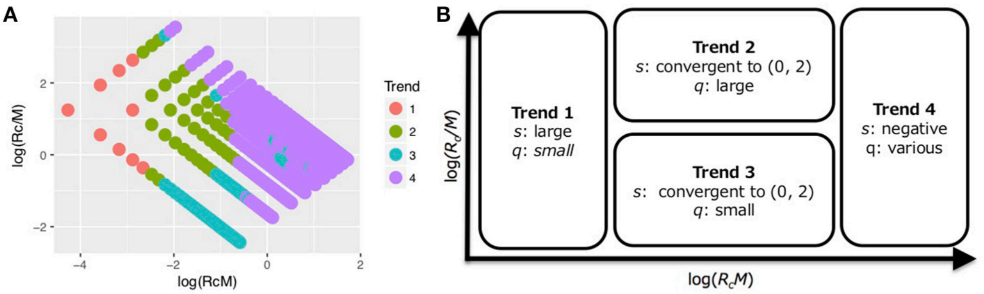
where $\alpha_i = 1 + s_i, \beta_i = 1$ when $s_i \geq 0$ while $\alpha_i = 1, \beta_i = 1 - s_i$ when $s_i < 0$. d_{ij} is $w_{ij}/max(\{w_{i1}, w_{i2}, \ldots, w_{iM}\})$, where w_{ij} shows strength of social relationships, i.e., the number of social grooming from i to j. This function only depends on d_{ij}, because previous studies have revealed that people select their social grooming partners depending on the strength of social relationships (Pachur et al., 2012; Takano and Fukuda, 2017). Therefore, this function can simply represent human-like social grooming strategies. M is the number of groomees. $b(x; \alpha, \beta)$ is a normalized beta distribution $x^{\alpha-1}(1-x)^{\beta-1}/B(\alpha, \beta)$, where $B(\cdot, \cdot)$ is a beta function. While using other functions which have fewer assumptions by using more dimensions is possible (e.g., nonparametric functions), we used Equation (1) because it is simple and is expressive enough to represent various social grooming strategies (**Figure 2**).

In a cooperation stage, groomee j cooperates with groomers in the top R_c as ranked by $\{w_{1j}, w_{2j}, \ldots, w_{Nj}\}$. The total payoff (i.e., fitness) of each groomer is the number of cooperation (i.e., the number of times ranked in the top R_c of each cooperator). That is, cooperators cooperate in their close relationships according to their resources R_c. R_cM shows all resources in the environment (R_c, M), i.e., the total amount of cooperation.

The next generation is generated by sampling with replacement in proportion to the groomers' fitness, i.e., the roulette wheel selection. In each generation, s mutates by the Gaussian distribution $(\mu = 0, \sigma = 0.2)$ and q mutates by the Gaussian distribution $(\mu = 0, \sigma = 0.05)$, where μ is a mean and σ is a standard deviation of the distribution, where $q \in [0, 1]$ (if q is out of range by mutation, then it is set to the nearest value in 0 or 1). Groomers' s and q in an initial generation are set by the Gaussian distribution $(\mu = 0, \sigma = 5.0)$ and by uniform distribution $[0, 1]$, respectively. Cooperators do not evolve.

We conducted evolutionary simulations 30 times on each R_c and M by using this model $(R_c \in \{5, 10, \ldots, 50\}$, $M \in \{5, 10, \ldots 200\})$. The number of groomers N is 100, the number of social grooming actions R_g in each grooming stage is 300 (we also use $R_g = 100$ in experiments shown in Figures S1, S3, and S4), and the number of generation T is 200. The source code is available at "https://doi.org/10.6084/m9.figshare.5526850.v1."

We set the mutation parameters to be small so that evolution converges at the equilibrium point. At the same time, we set those



Parameters and Evolution Results

Concept Diagram

FIGURE 3 | Summary of results of evolutionary simulations. We found four evolutionary trends (s and q of the final populations) depending on total resources R_cM and the ratio of each cooperator's resources to the number of cooperators R_c/M (see details **Figure 4**, Figures S1, S2). **(A)** Shows the results of evolution with parameter R_c and M. Each color shows the most frequent trend in parameters of the point. This was created based on **Figure 4**. **(B)** Is the concept diagram. Trend 1 evolved when R_cM was small. Trend 4 evolved when R_cM was large. Trends 2 and 3 evolved in the intermediate range between trends 1 and 4 where R_c/M determined whether groomers evolved to trend 2 or 3. The behavior of trends 2 and 3 were similar to human strategies, although trend 2 was closer, as described.

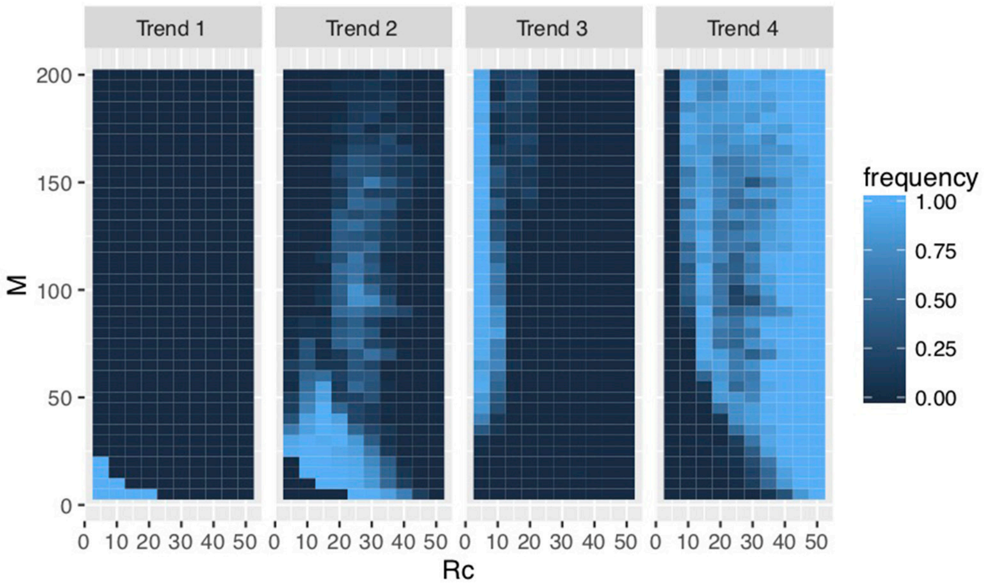


FIGURE 4 | Frequencies of evolution in each trend ($R_g = 300$). Trend 1 evolved when R_cM was small. Trend 4 evolved when R_cM was large. Trends 2 and 3 evolved in the intermediate range between trends 1 and 4 where R_c/M determined whether groomers evolved to trend 2 or 3. Additionally, R_g increased a range of group sizes M in which social grooming strategies evolved to trend 2 or 3, i.e., a large amount of social grooming evolved to trends 2 and 3 in large groups.

parameters to be large so that evolution reaches the equilibrium point within T generations. The initial range of parameters is widely distributed to cover the whole search space. All those values were determined based on the results of preliminary experiments.

3. RESULTS

We found four evolutionary trends in the results of the simulations (**Figure 3**). These trends are explained by total resources R_cM and the ratios of each cooperator's resources to the number of cooperators R_c/M (**Figure 4**, Figure S1).

Groomers evolved to trend 1 when R_cM was small. Their s evolved larger and their q evolved smaller. This strategy concentrates investment into strong social relationships (e.g., $s = 4$ in **Figure 2**). Groomers tended to evolve to trend 4 when R_cM was large with $s < 0$. This strategy widely invests in many weak social relationships (e.g., $s = -4$ in **Figure 2**). These trends' s do not converge, meaning that they do not have characteristic values.

On the other hand, s converged to $0 < s < 2$ in trends 2 and 3. Trends 2 and 3 evolved in the intermediate range between trend 1 and 4, and R_c/M determined whether groomers evolved to trend 2 or 3. Groomers evolved to trend 2 when R_c/M was large, where q evolved larger. They evolved to trend 3 when R_c/M

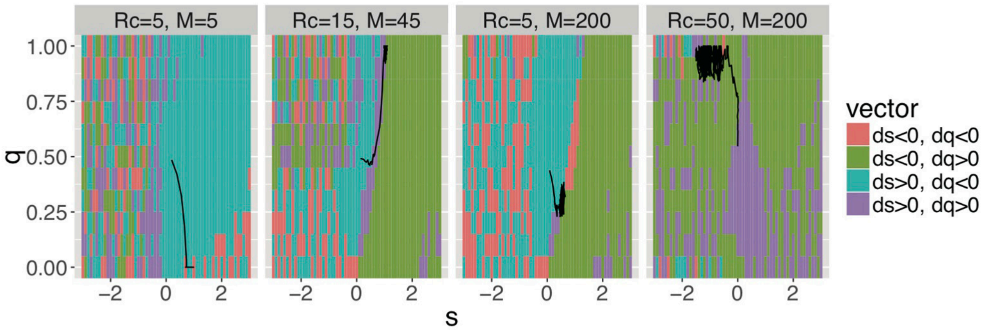


FIGURE 5 | Average selection pressures (ds, dq) in four trends for (s, q) and typical orbits from $(s, q) = (0, 0.5)$ $(R_g = 300)$. These figures show trends 1, 2, 3, and 4 from left. The cell colors show the gradients of s and q (i.e., ds, dq). For example, the figures show s and q decrease when (s, q) is in a cell of $ds < 0$ and $dq < 0$. Areas, where the cell colors are mixed, show little gradients, that is, mutation noises were larger than selection pressures. For example, populations were random walk along the s axis and they were small along the q axis, when $s < -1$ in $R_c = 5$ and $M = 200$. Evolutionary dynamics in $R_g = 100$ showed similar trends (see Figure S3).

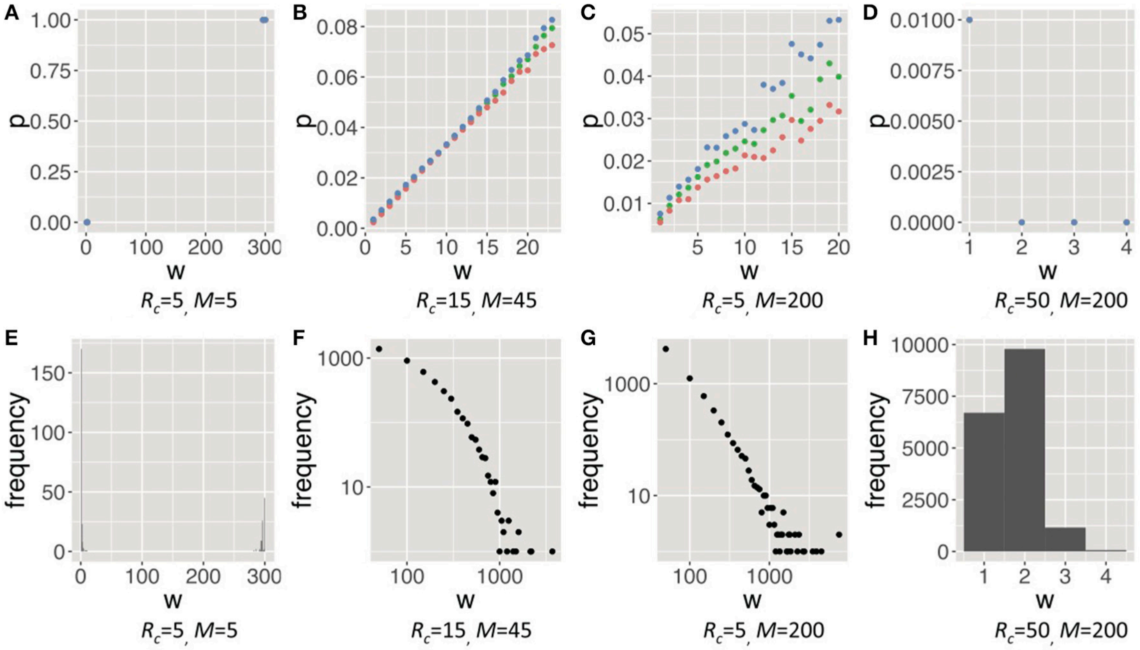


FIGURE 6 | Strategies of social grooming **(A–D)**, i.e., probability p of social grooming after each strength of social relationship w, and social structures of each trend **(E–H)**, i.e., distribution of w in each trend $(R_g = 300)$. These figures show trend 1, 2, 3, and 4 from left. These trends in $R_g = 100$ are similar to them (see Figure S4). In **(A–D)**, the orange points are the 25th percentile, the green points are the 50th percentile and the blue points are the 75th percentile. In the **(A–D)**, we drew w when the number of samples was more than 20. The figures of trend 2 and 3 of the **(F,G)** are shown by using a logarithmic scale in both axes. In the social structure of trend 1 **(E)**, many weak relationships were caused by mutation noises of q.

was small, where q evolved smaller. s in trend 2 tends to be larger than s in trend 3. Both strategies are diversified investments (e.g., $s = 1$ and $s = 0.5$ in **Figure 2**), where groomers intensively invest in strong social relationships while also widely investing in weak social relationships. Additionally, M, where groomers evolved to trends 2 and 3 is larger, when R_g is large (see **Figure 4**, Figure S1).

Next, we demonstrate how the four trends emerged throughout the evolution and how groomers constructed social structures in each trend. Regarding the former, **Figure 5**, Figure S3 shows the evolutionary pressures (ds, dq) of each combination of s and q, and the typical orbits of evolution. Evolutionary pressures were calculated using the method of the average gradient of selection (AGoS) (Pinheiro et al., 2012). That is, we calculated the mean difference of s and q of the next generation of a population in which individuals' s and q obeyed the Gaussian distribution $[(\mu = s, \sigma = 0.2)$ and $(\mu = q, \sigma = 0.2)]$ on each cell (s, q). These orbits were drawn based on the average selection pressures and noises which are a normal distribution with $\mu = 0$

and $\sigma = 0.01$. Incidentally, there is no cell in $(ds, dq) = (0, 0)$. For the latter, **Figure 6**, Figure S4 shows strategies of social grooming, i.e. probability p of social grooming after each strength of social relationship w (**Figures 6A–D**) and social structures of each trend, i.e., distributions of w (**Figures 6E–H**).

Trend 1 evolved in environments with small R_cM. Groomers are in intense competition for receiving cooperation from groomees in the environments. Therefore, they evolved to concentrate investments to a few poor groomees, i.e., large s and small q [$(R_c, M) = (5, 5)$ in **Figures 5**, **6A**]. The results show that they only had very strong social relationships in environments with small R_cM (**Figure 6E**). That is, most w were very large and the number of relationships was low.

Trend 4 evolved in environments with large R_cM. Groomers easily receive cooperation from groomees in these environments. Thus, they constructed many weak social relationships with many rich cooperators [$(R_c, M) = (50, 200)$ in **Figures 5**, **6D,H**]. That is, most w were very small and the number of relationships was high.

Trends 2 and 3 evolved between trend 1 and trend 4. Their s converge to $(0, 2)$, this means groomers with these strategies intensively invest in strong social relationships while they also widely invest in weak social relationships [$(R_c, M) = (15, 45)$ and $(5, 200)$ in **Figure 5**]. Their social grooming probability is in proportion to each strength of the social relationships (**Figures 6B,C**), so their construction processes of social relationships are similar to the Yule–Simon process. As a result, their social structures were similar to power law distributions (**Figures 6F,G**).

The main difference between trends 2 and 3 is how q is affected by R_c/M. When R_c/M is small, groomers have to confine the number of social relationships with groomees to construct strong social relationships, because they compete intensively in each social relationship (i.e., small R_c). Therefore, they evolved to small q with small R_c/M [trend 3; $(R_c, M) = (5, 200)$ in **Figure 5**]. In contrast, when R_c/M is large, they do not have to restrict the number of social relationships with groomees, because their competition is not intense in each social relationship (i.e., large R_c) and the maximum number of their social relationships is small (i.e., small M). Thus, they evolved to large q with large R_c/M [trend 2; $(R_c, M) = (15, 45)$ in **Figure 5**]. Interestingly, these trends of evolution show non-continuous transition (see Figure S5).

4. DISCUSSION

We analyzed the evolutionary dynamics of social grooming strategies and social structures. As a result, we find that the evolutionary dynamics depend on total resources (i.e., R_cM) and the ratios of each cooperator's resources to the number of cooperators (i.e., R_c/M). In the poor small groups, individuals' strategies evolved to concentrate investment among strong social relationships. In the rich large groups, their strategies evolved to wide investment among many weak social relationships. In the middle groups, their strategies evolved according to the Yule–Simon process. These strategies invest intensively in strong social relationships while also investing widely in weak social relationships. As a result of these strategies, skewed distributions of social relationship strengths were generated.

There are two trend strategies which are similar to the Yule–Simon process (Pachur et al., 2012; Takano and Fukuda, 2017). One evolved in relatively rich and small groups in the middle groups. Individuals with this strategy constructed social relationships with all group members, and reinforced their relationships in proportion to the strength of social relationships. The other one evolved in relatively poor and large groups in the middle groups. Individuals with this strategy constructed social relationships with parts of their groups, and reinforced their relationships. In primitive human groups, individuals belong to large groups and interact in small cliques within them (Dunbar, R. I. M. 2012). Hence, humans' social grooming strategy may have evolved in the latter group. Non-human primates may also have similar strategies, because they also construct skewed social structures even though their group sizes are different from humans (Kanngiesser et al., 2011; Tung et al., 2015; Levé et al., 2016; Dunbar, R. I. M. 2012). Their strategies' similarity may be explained by the difference of the amount of social grooming R_g. Our experiments show the increase in the amount of social grooming R_g results in the increase of group sizes M, in which social grooming strategies evolve according to the Yule–Simon process (see **Figure 4**). The same social grooming strategies are stable in different group sizes. Actually, there is a positive correlation between group sizes and the amount of social grooming in primates (Dunbar, 1993, 2016).

If a social grooming strategy based on the Yule–Simon process is universal in primates not limited to humans, and group sizes depend on external factors (e.g., predators, food, etc.), then social grooming strategies of humans and non-human primates evolved to the same strategies by automatically adjusting their amount of social grooming. This relationship between group sizes and strategies may be clearly demonstrated by comparison among humans, non-human primates, and other social animals. This will contribute toward an explanation of the evolution of humans' large social groups.

It is also important how cooperators select other cooperators as their interaction partners (Hauert et al., 2002). For example, if cooperators maintain relationships with other cooperators and break relationships with exploiters, their reciprocal relationships will be maintained and their inegalitarian relationships will be broken (Perc and Szolnoki, 2010; Perc et al., 2017). This mechanism to keep cooperation is known as network reciprocity. Social grooming strategies are network construction strategies. Actually, social grooming has a beneficial effect on the construction of reciprocal relationships (Takano et al., 2016a,b). Our results suggest that the evolution of human-like strategies for network construction depends on the resources of environments and their group size. In this paper, we focused on the evolutionary dynamics of social grooming with stable cooperative behavior. The co-evolutionary dynamics of both behaviors is an issue to be addressed in the future.

Comparison among various species' data sets will be needed in order to clear the relationships between environments and the four evolutionary scenarios of social grooming strategies.

AUTHOR CONTRIBUTIONS

MT: Designed the research, Constructed the model and Performed the simulation; MT and GI: Discussed and analyzed the results and Wrote the main manuscript text; All authors reviewed the manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00008/full#supplementary-material

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The other author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.