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Primates as living links to our past: variations in hierarchy steepness but not real egalitarianism¹

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Abstract. Recent decades have been marked by intensive studies of nonhuman primates social behavior, particularly in wild settings, and the accumulation of these data enable some new light to be shed on the evolution of early stages of human social evolution, as well as on the role of cognitive abilities in this process. Practically all multi-male/multi-female non-human primate societies are organized on the bases of social dominance hierarchies with different degrees of steepness. The latter are largely depended on the strength of contest competition for various resources. It is currently demonstrated that dominance patterns in bonobo, with some minor variations are similar to those of chimpanzees. Initial beliefs about peaceful and egalitarian pigmy chimpanzees appear incorrect. The field data on woolly monkeys (*Lagothrix*) revealed that they are highly promiscuous and males are hardly even trying to compete for mating. In this case social relations, close to egalitarian, are the result of a scramble-like competition. The exceptions

Бутовская М. Л. Приматы как модель эволюционного прошлого человека: вариации степени выраженности социальной иерархии и отсутствия истинного эгалитаризма. В последние десятилетия накоплен значительный массив данных о социальном поведении обезьян. Эти данные позволяют по-новому взглянуть на ранние этапы социальной эволюции человека, а также указывают на роль когнитивных факторов в этом процессе. Практически все сложно организованные сообщества обезьян, включающие мультисамцовые и мультисамковые объединения, формируются по иерархическому принципу. Жёсткость иерархических отношений зависит от выраженности конкуренции за монополизируемые ресурсы. В последние годы было показано, что модель отношений доминирования у бонобо, за небольшими отличиями, идентична таковой у шимпанзе. Представления об эгалитарности бонобо оказались несостоятельными. Полевые данные

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are *Callitrichids*, but in this case the social structure is more simple and not represented by multi-male/multi-female units. To conclude, no multi-male/multi-female egalitarian primate societies exist, except for our own species. Egalitarianism in humans has been inextricably linked with moral attitudes encouraging sharing, cooperation, and equality, and discouraging status seeking, conflict, and authoritarianism.

Keywords: egalitarianism, social dominance hierarchies, contest and scramble competition, non-human primates, hunters-gatherers.

о социальной организации шерстистых обезьян (*Lagothrix*) свидетельствуют о высоком уровне промискуитета и отсутствии выраженной конкуренции за доступ к половому партнеру. Однако, по мнению специалистов, социальные отношения, близкие к эгалитарным, у этого таксона возникли по причине невозможности монополизировать пищевые ресурсы в окружающей среде. Реально эгалитарными можно считать лишь игрунок *Callitrichids*. В этом случае, однако, имеет место крайне упрощённая социальная структура, в которой отсутствуют мультисамцовые и мультисамковые объединения. Таким образом, на сегодняшний день у приматов не выявлено ни одного вида со сложной мультисамцовой / мультисамковой организацией, практикующего по-настоящему эгалитарные отношения, за исключением человека. Эгалитаризм в человеческих обществах неразрывно связан с развитием моральных установок, стимулирующих делёж, кооперацию и равенство, и пресекающих доминирование, конфликты и авторитаризм.

Ключевые слова: эгалитаризм, иерархии доминирования, конкуренция за монополизируемые и не монополизируемые ресурсы, обезьяны, охотники-собиратели.

Introduction

The origin of egalitarianism in humans is a hot point of long-lasting disputes in the field of evolution of human societies and politogenesis (Ames 2010; Artemova 2000; Charlton 1997; Boehm 1999; 2000; 2009; Bondarenko, Korotaev 2000; Butovskaya 2000; Fehr *et al.* 2008; Gavrilets *et al.* 2008; Gintis, van Scahik 2013; Mellars, Gibson 1996; Summers 2005; Von Rueden 2014; Whiten, Erdal 2012). Traditionally, one of two models of human political behavior are in the orbit of discussion on the subject: the self-interest (*Homo economicus*) model or the social hegemony model. While the first model describes human individuals as rational self-regarding maximizers, and has been rooted in biology and political sciences (Alexander 1987; Mas-Colell *et al.* 1995), the second model presents individuals as the passive internalizers of the culture, and proclaims cultural hegemony based on indoctrination (Mead 1963; Parsons 1967). Real life, as well as countless examples from human history, reveal the obvious limitations of the cultural hegemony model. For decades ethologists and evolutionary psychologists have provided behavioral ecology alternatives to the cultural hegemony model (Lorenz 1963; Wilson 1975), supported by empirical evidence in favor of the self-interest model. However, with time, their reasoning has been questioned by numerous recent findings from the fields of biological and economic theory (Gintis *et al.* 2005; Henrich *et al.* 2005).

The unique evolutionary passage of hominins, marked with radical morpho-physiological transformations (bipedalism, brain development, cooperative breeding, changes in diet, to mention but a few), along with unique cultural innovations such as fire, cooking, and lethal weapons stimulated the rapid evolution of cognitive abilities, as well as morality. The gene-culture coevolution model has provided certain explanatory priorities in this debate (Lumsden, Wilson 1981; Cavalli-Sforza, Feldman 1981; Richerson, Boyd 1985). According to Gintis and co-authors: “These forces added a unique political dimension to human social life which, through gene-culture coevolution, became *Homo ludens* — Man, the game player — with the power to conserve and transform the social order” (Gintis *et al.* 2019: 17). It was primarily “strong social interdependence plus the availability of lethal weapons in early hominine society”, that “undermined the standard social dominance hierarchy, based on pure physical prowess, of multi-male/multi-female primate groups, characteristic” (*Ibid.*).

Currently most anthropologists agree that humans share a common ape ancestor with chimpanzees, as the Homo-Pan split occurred 7–13 million years ago (Langergraber *et al.* 2012; de Manuel *et al.* 2016). “We did not evolve from a living great ape, but the earliest human species anatomically resembled living great apes” (Begun 2016: 8). In turn, our closest living relatives, bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*) diverged approximately 1.5–2.6 million years ago. Obviously, humans and chimpanzees evolved differently from that same ancestor, but the main question “Why we have changed so much and apes so little” until now has remained “the biggest puzzle in paleoanthropology” (*Ibid.*).

The goal of this paper is to demonstrate that: a real egalitarian political system in which the group controlled its leaders is an essential adaptation, which evolved in the passage of hominin evolution; egalitarian systems are not observed in primate species with multi-male/multi-female societies (the *Macaca* species will be used to confirm this statement); to a certain extent egalitarianism is a human innovation, but not a social quality, inherited from the chimpanzee–human last common ancestor equally shared by *Homo* (human) and *Pan* (chimpanzee and bonobo) genera of *Hominini*.

Hierarchy steepness, affiliation and social constraint model in *Macaca* genus

Recent decades have been marked by intensive studies of non-human primate social behavior, particularly in wild settings, and the accumulation of these data enables some new light to be shed on the early stages of human social evolution, as well as on the role of cognitive abilities in this process. Practically all multi-male/multi-female non-human primate societies are organized on the basis of social dominance hierarchies, with different degrees of hierarchical steepness. The latter are largely dependent on the degree of competition for various resources. These statements may best be illustrated by data from the *Macaca* genus, as modern macaque species demonstrate a wide range of variation along the egalitarian — non-egalitarian scale, probably associated with their shared evolutionary history, as well as current ecological adaptations (Butovskaya *et al.* 2000a; Thierry 2004).

Our comparative study of social behavior, social structure and phylogenetic relatedness in species from the *Macaca* genus, revealed strong phylogenetic signals in some aspects of social structure, in particular dominance steepness and counter-aggression, and weak signals in others, such as kin-bias (Balasubramaniam *et al.*

2012a, b). The covariance between dominance trait values of adjacent taxa is strongly proportional to their shared evolutionary histories as indicated by their phylogenetic branch length distances (Kamilar, Cooper 2013).

The ability to affiliate, to reconcile with former opponents in fights, for victims to be consoled, and for aggressors to be appeased by third-parties, are usually associated with complex cognitive processing. Hence, it is not by chance that such behavior is demonstrated in humans and apes (de Waal, Roosmalen 1979; Butovskaya 2008; Butovskaya, Kozintsev 1999; Butovskaya *et al.* 2000b; Palagi *et al.* 2004; Fraser *et al.* 2008). Several functions and underlying cognitive mechanisms have been suggested for these post-conflict interactions: relieving stress, reducing the risks of redirected aggression, recruiting support, strengthening bonds with valuable partners (i. e. individuals with whom they groom the most), and substituting reconciliation (Das 2000; Koski, Sterck 2007; Romero *et al.* 2009; 2011). Initially, consolation was found to occur in apes but not in monkeys. This result has been interpreted in the light of the cognitive constraint hypothesis as indicating the limitations in cognitive capacity of monkeys (de Waal, Aureli 1996). According to this hypothesis, 'consolation' happens if a bystander recognizes that the victim is in distress and tries to alleviate the victim's distress, and monkeys were seen to lack 'cognitive empathy' (Preston, de Waal 2002). However, further studies of post-conflict behavior demonstrated that consolation was demonstrated not only in three macaque species (*M. arctoides* and *M. sylvanus*, *M. tonkeana*), but in other mammalian species, including dogs, wolves, horses and even in some birds (rooks, *Corvus frugilegus*) (Call *et al.* 2002; McFarland, Majolo 2012; Puga-Gonzalez *et al.* 2014). These findings questioned the cognitive constraint hypothesis, and stimulated researchers to concentrate on the social constraint hypothesis. This hypothesis suggested that the occurrence of 'consolation' may be related to a difference in the risks of aggression in different societies when approaching a former opponent (de Waal, Aureli 1996). The virtue is, that in species with a tolerant dominance style, the risks of further aggression after a conflict are lower than in species with an intolerant dominance style, making such affiliation more likely.

We used a combination of a computer model 'GrooFiWorld' based on self-organization (Puga-Gonzalez *et al.* 2009) and our empirical data of a tolerant species of macaques, Tonkean macaques (*M. tonkeana*), to investigate what mechanisms may underlie the occurrence of four forms of post-conflict affiliation between former opponents in a fight and bystanders. These are 'appeasement', which is when the former aggressor receives affiliation, 'consolation' when the former victim receives it, 'solicited appeasement' when the former aggressor solicits affiliation from a bystander (i. e. it initiates affiliation), and 'solicited consolation' when the former victim solicits it (Puga-Gonzalez *et al.* 2014). In both the empirical data of Tonkean macaques and the GrooFiWorld model, we found all the four categories of post-conflict affiliation between former opponents and bystanders. Our model suggests two mechanisms as causes for the emergence of these post-conflict affiliations: social facilitation and anxiety reduction. As regards affiliation received from bystanders ('consolation' and 'appeasement'), the model suggests that social facilitation is the main mechanism driving it. In the model, social facilitation increases the chances of bystanders being activated, and thus bystanders are more likely to interact with former combatants soon after the fight. As regards solicited post-conflict affiliation ('solicited consolation' and 'solicited appeasement'), the model suggests that this may emerge when former combatants intend to relieve their own anxiety by grooming bystanders. Empirical evidence seems to support both mechanisms, i. e. social facili-

tation and anxiety reduction. In the model and in Tonkean macaques, former opponents affiliated more with those bystanders with whom they had a stronger grooming relationship (*Ibid.*). This peculiarity was also found in several other primate species (McFarland, Majolo 2012; Romero, de Waal 2010; Judge, Mullen 2005; Romero *et al.* 2008; Clay, de Waal 2013).

As a rule, when valuable partners provide post-conflict affiliation to the former opponent, such behavior is interpreted as an expression of cognitive empathy (Aureli, Schaffner 2002). But, as demonstrated in our GrooFiWorld model, this pattern may simply emerge as a side effect of the spatial structure of the group because individuals have a relatively stable spatial position which causes them to interact more with some partners than with others (Puga-Gonzalez *et al.* 2014).

The degree of hierarchical steepness varies both between species as well as between populations within species, due to personality factors, group size and kin structure (Butovskaya 2004; Godelier 2004). The variations between groups of the same species may differ by a number of important social parameters, affiliative frequencies in the first rate, not only due to adaptation to environmental pressures, but due to personality factors and differences in group size as well (Butovskaya *et al.* 1994; 1995). As demonstrated recently, “group size had a stronger influence on grooming modularity and clustering coefficient than either dominance traits or social styles” (Balasubramaniam *et al.* 2018: 12).

Balasubramaniam and co-authors (Balasubramaniam *et al.* 2018) examined the impact of phylogenetic relatedness and sociodemographic factors, including group size and living condition, on interspecific variation in higher-order aspects of dominance and grooming social structure across macaques. The social network approach provided the evidence that “while dominance social network traits showed strong phylogenetic signals, grooming network traits showed weak signals and were not strongly covariant with social style or with dominance traits. Rather, two aspects of grooming network structure, modularity and clustering coefficient, were strongly influenced by group size independently of current living condition” (*Ibid.*: 11).

To conclude, macaques are unique among the primate genera in the extent to which interspecific variation in social traits is consistent with phylogeny, and covariant with social style (Balasubramaniam *et al.* 2012a; Thierry *et al.* 2008). The new findings confirm the statement, mentioned above, that differences within *Macaca* genus may cast some light on the possible variation in social traits exhibited in ancestral *Hominini* genera. At the same time, even though some macaque species, such as *M. nigra*, *M. nigrescens* or *M. tonkeana*, seem to have shallow hierarchies, with high level of tolerance between high and low ranking group-members, as well as friendly relations between females from high and low ranking matriline, none of these species may be considered egalitarian in the meaning of this terminology accepted in anthropological literature, *e. g.*: “Egalitarian societies are those in which little or no formal structure exists that places authority and power into the hands of certain individuals or groups on the basis of hereditary right or positions of authority. Indeed, in egalitarian societies there are no positions of authority” (anthropology.iresearchnet.com/egalitarian-societies). The term ‘egalitarianism’ in anthropology is used “to describe the social organization of peoples who have been empirically observed to practice a cultural ethos which encourages sharing, peaceful cooperation, and equality, while discouraging property accumulation, status seeking, conflict, and authoritarianism” (Townsend 2018: 1). Note that, along with the absence of hierarchical relations and authoritative leadership, Townsend stresses the “demand sharing of food

and material goods; the absence of particularistic social ties and dyadic relations of indebtedness; mobility; flexibility in living arrangements; and avoidance as the preferred means of conflict resolution” (*Ibid.*). No demand sharing exists in Macaque societies, while social ties are arranged according to matrilineal lineages, and conflict resolution strategies are widely practiced and involved a broad range of participants (former opponents, their relatives, their friends, as well as higher ranking males and females).

Chimpanzee and bonobo social structures: in search of egalitarianism in apes

Bonobos and chimpanzees live in relatively large, multi-male, multi-female groups, with male philopatry and female dispersal, and a high degree of fission-fusion dynamics. Many primatologists have noted the principle differences between the two *Pan* species, *P. paniscus* and *P. trogladites*. In particular, bonobo females are more gregarious, more central in the social network, and travel in mixed sex subgroups more often, than chimpanzee females. Female bonobos are co-dominant with males and actively practice socio-sexual behaviors to buffer conflicts and facilitate social integration and coalition formation, compared to chimpanzees. The two *Pan* species differ in several important aspects of their sociality. Understanding the drivers of these differences may inform us about the evolutionary pressures leading to characteristic traits of human sociality.

Chimpanzees, as our close relatives, logically attract attention in discussions on the basic principles of the evolution of social organization and group functioning in humans. Numerous data suggest that chimpanzees, particularly males, practice high levels of affiliation within their social network, directing grooming and cooperation towards relatives (Langergraber *et al.* 2007) and friends (Massen, Koski 2014; Engelmann, Herrmann 2016). The influence of kinship on cooperative behavior was described in male chimpanzees from the large community at Ngogo in Kibale National Park, Uganda. Using long-term field observations and molecular genetic techniques to identify kin relations between individuals, Langergraber with co-authors demonstrated that males clearly prefer to affiliate and cooperate with their maternal brothers, but paternal brothers do not selectively affiliate and cooperate, probably because they cannot be reliably recognized. Direct rather than indirect fitness benefits may be the driving force behind chimpanzee cooperation (Mitani *et al.* 2002).

On the other hand, chimpanzees are capable of extreme violence. The facts of lethal intergroup violence in the wild have been reported in different wild populations, and thus may be considered to be a part of the natural behavioral repertoire of this species, as an adaptation strategy of males that provides the winners with an opportunity to enlarge their territory, increase their food supply and, potentially, attract more mates (Mitani *et al.* 2010; Wilson *et al.* 2014). “The essential functional reasons for intergroup competition are consistent across group-living primates and humans: strength in numbers predicts long-term access to resources” (Crofoot, Wrangham 2010: 171). Lethal violence between adult males may occur within groups as well, although rarely. Such aggression may be rare due to the importance of coalitions between males during inter-group encounters. As a rule, the victims of within-group lethal violence were low-ranking males, but lethal aggression may also flare up during periods of male hierarchy instability (Mitani *et al.* 2010).

In contrast to chimpanzees, agonistic coalitions among bonobos are more prevalent among females than males (Nurmi *et al.* 2018). Increased cooperativeness may result from higher social tolerance in bonobo, compared to chimpanzee, females. In addition, bonobo females join forces in conflicts with males, which practically never happens amongst chimpanzees (Parish 1996; Surbeck, Hohmann 2013; Tokuyama, Furuichi 2016). In bonobos, male infanticide has never been observed, but male aggression against immature individuals is likely to trigger agonistic aid among females (Surbeck, Hohmann 2013). Other evidence for female bonobos counteracting aggressive male mating strategies includes extended periods and reduced precision of sexual signaling compared to chimpanzees (Douglas *et al.* 2016), and earlier maturation of females (Behringer *et al.* 2014), coupled with early bonding with young immigrant females amongst bonobos versus delayed dispersal due to resistance from residents amongst chimpanzees (Pusey 1990; Kahlenberg *et al.* 2008). Female bonobos are obviously more cohesive than their chimpanzee counterparts, and feeding competition remains a prominent factor of such cooperativeness among the resident females, independent of their age, parity, and kinship. The Cooperative Defense Hypothesis is the most valuable for the explanation of the origin of bonobo sociality (Nurmi *et al.* 2018).

Are bonobo really more egalitarian and peaceful than chimpanzees?

Traditionally, the discussion has been whether chimpanzees or bonobo may serve as a better model for the human-chimpanzee last common ancestor. As a rule, bonobos are preferred by supporters of peaceful nature of our ancestors, while chimpanzees by those who suggested that they were quite aggressive. Humans and their two closest relatives, chimpanzees and bonobos, form multi-male/multi-female groups, which suggests that this trait is homologous in the three species and shared with their last common ancestor (Wrangham 1987; Foley 1989). It seems reasonable to suggest that early hominins formed multi-male/multi-female fission-fusion groups and had a promiscuous mating system. Stable breeding bonds and biparental families evolved at some point after the Pan Homo split, producing the multifamily composition (Chapais 2010: 27–28). The last common ancestor of chimpanzees, bonobos, and humans, along with multi-male/multi-female composition, probably shared the following traits: territoriality, male philopatry and female transfer, male kin groups and kin recognition. Given the developed cognitive abilities in chimpanzees and bonobos, the kin recognition potential of chimpanzees is enormous (Chapais 2010). Along with primary maternal kin (mothers, daughters, sons, and maternal siblings), it encompasses secondary maternal kin (grandsons and their maternal grandmothers, maternal uncles and their sororal nephews) as well, which is not surprising given the cognitive sophistication of chimpanzees (Goodall 1990).

Territoriality characterizes both chimpanzees and bonobos (Fruth, Hohmann 2002; Wilson, Wrangham 2003). Male chimpanzees are territorial, and hostility between males belonging to distinct groups is a distinct feature. The local group represents the highest level of social organization here, as no between-group alliances have ever been observed. In contrast, bonobo are known to share food with out-group individuals, and are even able to form coalitions with non-group partners (Fruth, Hohmann 2018; Tokuyama *et al.* 2019). Importantly, coalitions both within

and between group members are formed among females against males (Nurmi *et al.* 2018). The main goal of such coalitions is in access to feeding patches (Tokuyama, Furuichi 2016). While in other species such female coalitions are formed with close kin, bonobos, because of their dispersal, are no more genetically related within a group than females across groups (Ishizuka *et al.* 2018). Hence, bonobo females may select coalition partners irrespective of their groups when the coalition yields direct benefits (Nurmi *et al.* 2018).

Despite the usual image of bonobos as a peaceful creatures, physical aggression is practiced, although more frequently on the inter-group than within-group level. Bonobos increase cooperation with within-group members to attack out-group individuals, while they decrease aggression among within-group members during inter-group association. Female aggression across groups was sometimes intense and involved injuries. According to field observations, female bonobos support their sons against other males within-groups (Furuichi 2011). The fact that female bonobos are fighting in coalitions against males, as well as supporting their sons with-in groups, does not mean that male-male aggression in this species is absent. On the contrary, they fight more against out-group individuals, and the higher-ranking males direct aggression toward out-group individuals more frequently than lower-ranking males (Ishizuka *et al.* 2018; Surbeck, Langergraber *et al.* 2017). However, when compared to chimpanzees, physical aggression, as well as occurrence of injuries in bonobo, is less frequent.

To conclude, chimpanzees and bonobo share more features of social structure and social behavior than was previously expected. Both species practice aggression at the within and inter-group levels, although lethal injuries have so far only been reported amongst chimpanzees. The tendency for males of different groups to compete may be best considered as protecting mating opportunities, and is present in both chimpanzees and bonobo. However, these two species are different, as regards to female social strategies and, particularly, within-group female superiority over males, and affiliative and cooperative relationships within and across groups. There is no reason to suggest that one or other species is a better model for early hominini societies. None of these species may be viewed as egalitarian. Dominant males in both species seem to be more successful in reproduction as compared to low ranking males. Females are organized in hierarchies, and high ranking females gain benefits to their status, both in terms of food and infant survival.

Life history plasticity, cognitive development and fairness as a prerequisite of human egalitarianism

As discussed above, multi-male/multi-female primate species (*Macaca* genus had been used as an example), demonstrate a variety of dominance steepness, differences in symmetry of agonistic and affiliative behavior, reconciliation, and third party post-conflict appeasement. Without denying the importance of cognitive abilities in the development of empathy and altruism, we have presented convincing evidence, that consolation may be present in Old World Monkeys. *M. tonkeana*, known for its social tolerance, being the example (Puga-Gonzalez *et al.* 2014). The computer model 'GrooFiWorld', used in parallel with these empirical data, suggests that consolation behavior may potentially be developed without any increase in cognition, but as a simple outcome of the spatial distribution of group-members. Numerous data from chimpanzee and bonobo communities suggests that the social life of these apes is far

more advanced, when compared to the macaques. Their phylogenetically more advanced cognitive skills equip them with strategic planning in social interactions, better memory, more sophisticated kin recognition, empathy and cooperation. Contra earlier representations, chimpanzee and bonobo in reality appear to be more similar to each other: both demonstrate physical aggression and injure conspecifics, form coalitions to contest other group members or members of other groups, cooperate, and use tools for food extraction and social interactions. Although, bonobos are less aggressive, and female bonobos are known to form alliances against males, there is no reason to suggest they are more cognitively advanced, as well as being more egalitarian than chimpanzees.

Human evolution was marked by a set of unique morphological transformations (associated with bipedalism, hidden estrus, reduction of gut and colon, improved aerobic capacities, encephalization, birth of undeveloped newborns and extended parental care), as well as unprecedented cognitive development. Humans are cooperative breeders, their child-caring strategies are more like some New World Primates from genera *Saguinus*, *Callimico*, *Leontopithecus*, or *Callicebus*, rather than *Pan troglodytes* or *Pan paniscus*. The unique human transformations were realized through gene-cultural coevolution. The control of fire, cooking practice invention, improved running capacities, along with more sophisticated cognitive abilities and cooperative child breeding, had probably evolved by the time of *H. erectus* (Burkart, van Schaik 2010). All these innovations were important preconditions for the emergence of a human moral order (Gintis *et al.* 2019). Most probably, *H. sapiens* evolved in the context of immediate-return systems, similar to those of current nomadic hunter-gatherers (Woodburn 1982). The origin of egalitarianism in humans may be dated back to Pleistocene times, when the survival of human groups was enabled by the combination of interdependence (labor distribution between men the hunters as meat providers, and women as gatherers, cooks and cooperative child breeders) and the ability to punish transgressors (Gintis *et al.* 2019).

To conclude, egalitarianism was imposed by the community, insisting that their leaders behave with modesty, generosity, and fairness (Boehm *et al.* 1993), and was rooted in anti-hierarchical feelings (Boehm 2009). From the evolutionary perspective, egalitarianism in humans is an outcome of a complex of unique consequent evolutionary innovations, resulted in the emergence of a normative order and social organization based on ethical behavior and reversed hierarchical order (Gintis *et al.* 2019). The culturally-evolved egalitarian norms amongst humans provided an evolutionarily novel mechanism for social behavior, and unprecedented development of cooperation in human groups (Apicella, Silk 2019).

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