



TITLE:

The evolution of group-mindedness: comparative research on top-down and bottom-up group cooperation in bonobos and chimpanzees

AUTHOR(S):

Brooks, James; Yamamoto, Shinya

CITATION:

Brooks, James ...[et al]. The evolution of group-mindedness: comparative research on top-down and bottom-up group cooperation in bonobos and chimpanzees. *Current Opinion in Behavioral Sciences* 2022, 47: 101205-101205

ISSUE DATE:

2022-10

URL:

<http://hdl.handle.net/2433/276964>

RIGHT:

© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).



ELSEVIER



The evolution of group-mindedness: comparative research on top-down and bottom-up group cooperation in bonobos and chimpanzees

James Brooks¹ and Shinya Yamamoto^{1,2}

Humans engage in a wide variety of group-based cooperation and competition, the cognitive underpinnings of which form "group-mindedness." The evolutionary basis of these tendencies has attracted significant research from theorists and human-oriented scholars, where evidence suggests a different set of strategies and solutions may be required for explicitly group-based challenges than simply an accumulation of dyadic and triadic solutions embedded in a group setting. We term these top-down and bottom-up group cooperation, respectively. Here, we review previous evolutionary accounts for human group-mindedness, empirical data on bonobos and chimpanzees (focusing on behaviour, cognition, and physiology), and propose a set of future research directions that can help to further our understanding of the evolution of group-mindedness

Addresses

¹ Wildlife Research Center, Kyoto University, Japan

² Institute for Advanced Study, Kyoto University, Japan

Corresponding Authors: James Brooks (jamesgerardbrooks@gmail.com), Shinya Yamamoto (shinyayamamoto1981@gmail.com)

Current Opinion in Behavioral Sciences 2022, 47:101205

This review comes from a themed issue on **Cognition in the Wild**

Edited by **Alexandra Rosati, Zarin Machanda** and **Katie Slocombe**

For complete overview of the section, please refer to the article collection, "[Cognition in the Wild](#)"

Available online 2nd September 2022

<https://doi.org/10.1016/j.cobeha.2022.101205>

2352-1546/© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Introduction

Large-scale cooperation and competition is one of the hallmarks of the human species. Humans across cultures engage in group-level complex coordination as well as group-based lethal aggression, sometimes simultaneously. This phenomenon of 'group-mindedness' and its evolutionary basis is vital to identify and understand. While modelers, theorists, and human-oriented researchers are devoting more attention to group-level

cooperative challenges and how they differ from dyadic (and triadic) cooperative challenges, less work has focused on overtly group-level challenges in empirical, evolutionary comparisons. Such challenges may entail different behavioral, cognitive, and physiological mechanisms with different evolutionary forces. In this paper, we aim to address this deficiency by reviewing theoretical accounts of the evolution of human group-based behavior, recent empirical research on our closest relatives bonobos and chimpanzees, and finally propose future directions for comparative empirical research on the evolutionary roots of group-mindedness.

We first lay out our theoretical perspective and definitions. Group-mindedness, as used in this paper, refers to the cognitive process of forming mental representations at the level of groups, over and above their constituent members. This includes cases involving the self, ingroup members, and outgroup members, where group identity supersedes on individual identity. Prerequisites to standard forms of group-mindedness, therefore, include taking group divisions as ontologically real, perceiving oneself as part of one's own group, and tracking the status of the group itself (including membership changes). We highlight group-mindedness for its role in achieving cooperation in explicitly group-based challenges, as opposed to classic smaller-scale dyadic (or triadic) games. Indeed, human-oriented empirical researchers have highlighted firm ingroup-outgroup distinctions [1], social identity [2], and the ability to track complex forms of group organization [3] as key cognitive processes in solving group-oriented challenges.

While dyadic games can themselves be embedded in a group structure and lead to the emergence of seemingly group-level cooperation, which we call *bottom-up group cooperation*, explicitly and necessarily group-oriented cooperative challenges are described by different game-theoretic structures, and therefore entail different solutions and forms of cognition. We call these structures *top-down group cooperative challenges*, and the resulting cooperation (when successful) *top-down group cooperation*. Canonical examples of dyadic cooperation games include the prisoner's dilemma, hawk-dove (also known as chicken or snowdrift), and stag-hunt games, while explicit group-level challenges are described in collective-action problems and public goods games. Models of multilevel selection [4] and

2 Cognition in the Wild

parochialism [5,6] have been invoked to help understand the evolutionary solutions to some group-level challenges, suggesting the need for specific group-based cognition in order to achieve success. Group-mindedness may not be necessary for achieving bottom-up group cooperation, but likely plays a vital role in enabling some forms of human top-down group cooperation.

While theorists and human-focused psychologists have continued to identify important differences between forms of cooperation, empirical comparative studies on other species have so far focused predominantly on dyadic cooperation tasks. For instance, the string-pulling paradigm (where two participants must coordinate to pull a string at the same time to bring the rewards within reach) and variations upon it, such as changing social partners and reward distributions upon success, has been widely employed to explore the cooperative abilities across species [7,8]. This style of cooperation task has provided rich insights into the varied cooperative tendencies across species, but may not reveal the whole picture, and especially may not reveal differing tendencies that have evolved in support of human-like group-mindedness. These cooperative games can help explain the emergence of bottom-up group-level cooperation, but they fail to capture top-down dynamics involved in larger-scale cooperative action, which remain largely unstudied in other species.

Evolutionary theories of human group-mindedness based on comparative studies

We here review three major hypotheses put forward by comparative researchers aimed at identifying the evolutionary roots of humans' group-mindedness. One prominent account is described in Tomasello et al. [9]. In this account, there were two key stages in the evolution of human cooperation. The first stage focuses on evolutionary pressures emerging from obligate collaborative extractive foraging, entailing the development of shared intentions and goals, or the "we mode," and more complex forms of cooperation with repeated partners in game structures such as the stag hunt. The second step focuses on the generalization of these abilities to even unknown members of the ingroup alongside the emergence of cues enabling group recognition and shared cultural social norms, permitting larger effective groups, better recognition of potential cooperative partners, and therefore effective and sustained cooperation. An important missing piece of this proposal, however, is the lack of attention toward uniquely group-level cooperation. Tomasello et al.'s [9] discussion of groups is predominantly characterized by networks of dyadic or triadic interactions, with less attention paid to groups in the context of social dilemma game structures, and the comparative empirical studies on which it is based similarly were primarily dyadic in structure. There is also limited attention paid to bonobos, taking chimpanzees to

be representative of nonhuman animals, while studies have shown considerable differences in their society, behavior, and cognition [10], discussed in detail later.

A second prominent evolutionary account of our species' group-level cooperation is that described by Wrangham [11]. He focuses on 'groupishness' as he identifies it, a term originating from Haidt [12]. He proposes that in humans' evolutionary history, there was a point where subordinates were able to unite against antisocial, dominant, and aggressive males and engage in low-risk targeted killing, setting the course for selection against aggression (and thereby toward groupishness) [11]. Wrangham's description of the consequences of targeted conspiratorial killing provides a clear picture for reduced aggression in humans, but may confound some causes and consequences of such behavior. Evidence suggests reduction in reactive aggression leads to greater tolerance and ability to solve dyadic social problems [8], but it is unclear why such selection against aggression would by itself lead to the emergence of group-mindedness and the associated skills at top-down group cooperation. The targeted conspiratorial killing on which Wrangham is focused to some degree presupposes the ability to engage in certain top-down group cooperative activities, as targeted conspiratorial killing itself is a top-down cooperative challenge among subordinates. While Wrangham's theory is focused on antisocial, dominant, and aggressive males, along with the evolutionary consequences of removing them from the gene pool, we wish to draw primary attention to the other side of the equation, the participants in a top-down cooperative act, and the prior selection that must have taken place to enable such group-based cooperation.

Another recent proposal by Yamamoto [13] describes two separate possible pathways in the evolution of cooperation in chimpanzees and bonobos, both of which he proposes are important for the evolution of the diverse forms of human cooperation. In this account, it is suggested that relatively more rich environments will promote tolerance, which in turn supports the evolution of dyadic cooperation, especially in bonobos, while harsher environments will promote stronger intergroup competition and group defense, which in turn supports the evolution of group cooperation in chimpanzees [13]. Though this is relevant to the distinction between bottom-up and top-down group cooperation, the proposal suffers from difficulty in identifying the limits and boundaries of each style, as well as a lack of direct evidence, especially for its behavioral, cognitive, and physiological mechanisms.

Recent empirical studies have slowly begun to reveal new perspectives on group-mindedness in our closest relatives, which suggest the potential for important new insights into the different evolutionary pressures responsible for top-down and bottom-up group cooperation.

Group-mindedness and top-down group cooperation in chimpanzees and bonobos

Our two closest relatives, bonobos and chimpanzees, provide an opportunity to explore the evolutionary roots of different forms of human cooperation and competition. Chimpanzees, like humans, show group-level cooperative behaviors such as group hunting [14] and territory defense [15], while also committing lethal intergroup aggression and being characterized by largely intolerant intergroup relations [16]. Bonobos, on the other hand, have not been observed engaging in the kind of group-level cooperation and lethal competition sometimes seen in chimpanzees, but like humans, are able to manage tolerant intergroup associations (despite evidence of competition in such encounters [17] and of group distinctions [18]) [19] and cooperate more effectively than chimpanzees in most captive dyadic experiments (e.g. [8]).

Behavioral mechanisms

The behavioral mechanisms of top-down group cooperation in bonobos and chimpanzees are not well studied, but preliminary evidence supports theoretical perspectives that they have evolved skills at different styles of cooperation. In both the field and in captivity, outgroup threat has been linked with ingroup cohesion in chimpanzees [15,20], suggesting that, like in humans, chimpanzees have evolved group-level solutions to deal with the collective-action problem of group defense. In a field experiment directly comparing bonobos and chimpanzees, information-transfer efficiency in the face of a threat (a simulated snake) is higher in chimpanzees, again indicating they may have evolved specialized skills in the face of collective-action problems [21]. This is in contrast to most captive experimental work showing greater cooperation in bonobos when they have been directly compared in dyadic or triadic settings (including [8,22,23]), or work showing chimpanzees often fail to cooperate or settle on strategies in dyadic game structures [24]. In captive home-group settings, chimpanzees showed more prosociality in a group-service paradigm than bonobos [25,26] and more tolerance in a group setting [27], yet chimpanzees often fail to engage in spontaneous reciprocity in dyadic prosocial choice tasks [28–30] in captive experiments. In the wild, chimpanzees engage in group hunting [14] (though this may be observed only in some specific sites and the level of active coordination is still debated), cooperative border defense [15] and dominant males act as crossing guards to their group at dangerous road crossings [13,31], which are not regularly observed in bonobos. While bottom-up processes building on more tolerant relationships seem to be able to explain the emergence of some types of group cooperation in bonobos, given chimpanzees' frequent failure to regularly cooperate or demonstrate any prosociality (even in mother–infant dyads [30]) in the same settings, bottom-up cooperation is unlikely to be

able to fully explain their skill at and the continued maintenance of complex forms of chimpanzee group cooperation. We emphasize not that chimpanzees are incapable of dyadic cooperation (this may be a matter of motivation more than cognitive restriction [32]), but that the two species differ in their baseline propensities (whether by skill or motivation) for engaging in top-down versus bottom-up group cooperation.

Cognitive mechanisms

The ingroup–outgroup distinction, social identity, and social organization during cooperation have been highlighted in human studies as cognitive prerequisites for group-mindedness and top–down group cooperation. In terms of the ingroup–outgroup distinction, in the wild, it has been shown that chimpanzees react differently to the calls [33] and scents [34] of outgroup compared with ingroup members, and captive experimental eye-tracking work has shown differences in attention toward ingroup and outgroup faces [35]. This ingroup–outgroup distinction seems to be more conspicuous in chimpanzees than in bonobos, where chimpanzees do not contagiously yawn toward unfamiliar chimpanzees, but do with ingroup members [36], while bonobos show less obvious patterns [37–39].

Social identity has received even less attention, but potentially of note, wild chimpanzees can distinguish vocalizations of known outgroup members compared with completely unfamiliar vocalizations [33], and following group fissions, former ingroup members may become outgroup (and are therefore subject to lethal coalitionary intergroup aggression) [40], together suggesting that they do not rely entirely on a familiar/unfamiliar distinction in categorizing other individuals as has been suggested [9]. Lemoine et al. [6] develop and review extensive evidence for a model of chimpanzee parochial cooperation, entailing simultaneous and mutually reinforced ingroup favoritism and outgroup hostility.

With regard to social organization, in humans, hierarchical structure with fixed leadership has been proposed as important to regulating top–down styles of group cooperation [41,42]. The social organization of chimpanzees has been characterized as more rigid and hierarchical, with dominance relations in males strictly defined [43], than bonobos. The cognition involved in tracking these relations and forming group-ordered social organization may thus be more developed in chimpanzees, and there is evidence that more dominant chimpanzees volunteer in captive collective-action problems [44], which has so far not been tested in bonobos. Social organization during intergroup encounters in chimpanzees deserves further research attention, but recent work shows that it is predicted by both participation of close bond partners, as well as number of

4 Cognition in the Wild

participants, but importantly that these two factors worked independently of one another [15].

The cognition involved in wild group hunting has been regularly debated, and whether it can emerge purely from bottom-up processes or necessarily involves top-down processes as well will necessitate future studies. Evidence from some (but not all) communities has suggested distinguished roles [14], coordination between hunters [45], and a complex calculus in distributing the rewards of successful hunts across a wide variety of social partners simultaneously [46], skills not required in the cooperative tasks typically characteristic of captive experiments. While bonobos have been observed hunting in groups as well [47], few direct observations preclude direct comparisons. The game-theoretic structure of group hunting remains similar across sites, where the probability of hunting success (but also the chance for free-riding) rises with number of hunters [45]. The exact factors explaining the level of coordination (and whether any constitute truly group-minded strategies) observed in chimpanzee hunting in some but not other field sites are not yet entirely clear. This possible intraspecies variability in strategies employed in situations of group-scale cooperation may be a valuable source of empirical, naturalistic data to test hypotheses on the ecological contexts that can promote group-mindedness.

Physiological mechanisms

Physiologically, recent studies have highlighted the potential importance of the hormone neuropeptide oxytocin. Of note, in several recent human studies, oxytocin has been linked to group-based ally selection [48], coordinated outgroup attack [49], ingroup defense [50], ethnocentrism [51], and liking of national symbols [52], among other group-minded behaviors. In comparison, oxytocin has been linked to classic affiliative behaviors such as food sharing [53], social grooming [54,55], GG-rubbing [56], and reconciliation [57] in bonobos and chimpanzees, but recent studies in Taï Forest have reported that it is also linked to both group hunting [46] and border patrols [58]. Oxytocin may have additional importance in expanding chimpanzee cooperation to the group level and managing top-down cooperative processes, as it does in humans. In captive studies administering exogenous oxytocin, null results have been found in two chimpanzee studies [24,59], while another found different effects of oxytocin on eye contact between bonobos and chimpanzees [60]. Further, oxytocin promotes outgroup attention in both species [61], eliminating the effects described in Lewis et al. [35]. The oxytocin system and related genes and neuroendophenotypes have been highlighted in humans as supporting the divergence and regulation of social systems [62], and oxytocin-receptor differences between chimpanzees and bonobos have been described and highlighted for future work in a number of recent studies [63–65]. Oxytocin's

evolutionary pathways and effects may represent a physiological mechanism involved in regulating and maintaining top-down styles of group cooperation and group-minded behaviors.

Future perspectives

The theoretical perspectives and empirical studies described give strong reason to conduct further comparative research on group-mindedness and the evolution of top-down group cooperation. In this section, we focus on important novel directions and existing gaps in comparative studies into the origins of group-mindedness. We briefly highlight a selection of future studies necessary to identify more clearly and precisely the evolutionary processes involved in group-mindedness and top-down group cooperation in nonhuman animals.

Mechanistic level

The exact hormonal, genetic, and psychological mechanisms at play in promoting group-level behavior can be compared across species. We echo some previous studies in highlighting the potential importance of the oxytocin system, especially with regard to oxytocin's role in intergroup encounters across species, exogenous oxytocin's direct effect during different kinds of cooperation tasks with varied reward structures, and the genetic and neural variation that is associated with differences within and between species. On the cognitive side, while we describe top-down group cooperation purely with respect to the game structures and solutions, whether individuals' mental representation of the group structure itself is better described as top-down or bottom-up (within the context of group-mindedness) may also warrant direct study. Compared with classic dyadic or triadic tasks, in top-down group cooperation, the mental representation of the cooperative partner may be replaced by a more abstract representation of the 'group' or acting unit, which should be investigated experimentally.

Ontogenetic level

More attention should be paid to the developmental link between various group-minded behaviors and forms of cooperation. Evidence in humans links the emergence of ingroup love and outgroup hate and suggests they emerge around 5 years of age [66]. Long-term field data linking the trajectory of participation in the behaviors highlighted throughout this paper, alongside longitudinal captive studies across ages in group-based tasks, will be essential to trace the ontogeny of group-mindedness.

Functional level

Group-level cooperation tasks and greater attention to cooperation in home groups, such as those deployed in [25,67–69], can reveal the kinds of solutions employed across species. Group collective-action problems, such as

through expanding string-pulling tasks to the group setting, should be used to directly test whether chimpanzees are more skilled than bonobos and how the rewards of those solutions are distributed to group members. The impact of different values and distributions of rewards, presence of external competitors, and necessity of differentiated roles, alongside analysis of group structure and the possible role of leaders (sometimes suggested to be a human-unique) can help provide empirical support for particular solutions to various collective-action problems from a comparative perspective. Continued attention to intergroup encounters and group hunting in the wild will further be necessary to understand the causes and consequences of top-down group cooperation, and when it cannot be reduced to the sum of its dyadic parts.

Phylogenetic level

Finally, more varied species comparisons can elucidate the exact factors that support top-down cooperation, and which factors reliably covary, suggesting what evolves together. Comparisons across groups, their relations to one another, and how social organization predicts engagement in group-cooperation problems will be key to investigate (both from the perspective of individual members and from the group itself). Comparisons across human societies highlight variation in leadership patterns, as well as the importance of leadership strategies beyond simple dominance (such as through prestige [70]). Wider species comparisons following the analysis methods of cross-cultural studies, alongside direct investigation of the possibility of leadership and social organizational structures beyond linear dominance hierarchies in nonhuman animals, may generate empirical tests of hypotheses so far tested only in our own species.

Conflict of interest statement

The authors declare no conflicts of interest.

Data availability

No data were used for the research described in the article.

Acknowledgements

This study was funded by Japan Society for the Promotion of Science KAKENHI #21J21123 to JB, KAKENHI #19H00629, #22H05653, #22H04451 to SY.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest.

1. Brewer MB: **Ingroup identification and intergroup conflict: When does ingroup love become outgroup hate?** In *Social identity*,

intergroup conflict, and conflict reduction. Edited by Ashmore RD, Jussim L, Wilder D. Oxford University Press; 2001:17-41.

2. Tyler T, Blader S: **Cooperation in Groups: Procedural Justice, Social Identity, and Behavioral Engagement**. Routledge; 2000.
3. Hodgkinson GP, Healey MP: **Cognition in organizations**. *Annu Rev Psychol* 2008, **59**:387-417.
4. Wilson DS, Sober E: **Reintroducing group selection to the human behavioral sciences**. *Behav Brain Sci* 1994, **17**:585-608.
5. Choi J-K, Bowles S: **The coevolution of parochial altruism and war**. *Science* 2007, **318**:636-640.
6. Lemoine SRT, Samuni L, Crockford C, Wittig RM: **Parochial cooperation in wild chimpanzees: a model to explain the evolution of parochial altruism**. *Philos Trans R Soc B: Biol Sci* 2022, **377**:20210149.
7. Hirata S, Fuwa K: **Chimpanzees (*Pan troglodytes*) learn to act with other individuals in a cooperative task**. *Primates* 2007, **48**:13-21.
8. Hare B, Melis AP, Woods V, Hastings S, Wrangham R: **Tolerance allows bonobos to outperform chimpanzees on a cooperative task**. *Curr Biol* 2007, **17**:619-623.
9. Tomasello M, Melis AP, Tennie C, Wyman E, Herrmann E: **Two key steps in the evolution of human cooperation**. *Curr Anthropol* 2012, **53**:673-692.
10. Hare B, Yamamoto S: **Minding the bonobo mind**. In *Bonobos: Unique in Mind, Brain and Behavior*. Edited by Hare B, Yamamoto S. Oxford University Press; 2017:1-13.
11. Wrangham RW: **Targeted conspiratorial killing, human self-domestication and the evolution of groupishness**. *Evolut Hum Sci* 2021, **3**:e26.

Review of studies aiming to explain human-unique group cooperative behaviour with direct reference to chimpanzees.

12. Haidt J: **The Righteous Mind: Why Good People Are Divided by Politics and Religion**. Knopf Doubleday Publishing Group; 2012.
13. Yamamoto S: **The evolution of cooperation in dyads and in groups: two-by-two research comparing chimpanzees and bonobos in the wild and in the laboratory**. In *Chimpanzees in Context*. Edited by Hopper L, Ross SR. The University of Chicago Press; 2021.

Identifies the difference in bonobo and chimpanzee-typical styles of cooperation and their possible evolutionary background.

14. Boesch C: **Cooperative hunting roles among tai chimpanzees**. *Hum Nat* 2002, **13**:27-46.
15. Samuni L, Crockford C, Wittig RM: **Group-level cooperation in chimpanzees is shaped by strong social ties**. *Nat Commun* 2021, **12**:539.

First study to reveal the social factors that promote participation in chimpanzee intergroup conflict using long-term field data.

16. Wilson ML, Wrangham RW: **Intergroup relations in chimpanzees**. *Annu Rev Anthropol* 2003, **32**:363-392.
17. Cheng L, Lucchesi S, Mundry R, Samuni L, Deschner T, Surbeck M: **Variation in aggression rates and urinary cortisol levels indicates intergroup competition in wild bonobos**. *Horm Behav* 2021, **128**:104914.
18. Samuni L, Langergraber KE, Surbeck MH: **Characterization of Pan social systems reveals in-group/out-group distinction and out-group tolerance in bonobos**. *Proc Natl Acad Sci USA* 2022, **119**:e2201122119.

19. Furuichi T: **Female contributions to the peaceful nature of bonobo society**. *Evolut Anthr: Issues News Rev* 2011, **20**:131-142.

20. Brooks J, Onishi E, Clark IR, Bohn M, Yamamoto S: **Uniting against a common enemy: perceived outgroup threat elicits ingroup cohesion in chimpanzees**. *PLoS One* 2021, **16**:e0246869.

Experimental evidence that ingroup cohesion and outgroup competition are linked in chimpanzees.

21. Girard-Buttoz C, Surbeck M, Samuni L, Tkaczynski P, Boesch C, Fruth B, Wittig RM, Hohmann G, Crockford C, Wittig RM:

6 Cognition in the Wild

- Information transfer efficiency differs in wild chimpanzees and bonobos, but not social cognition.** *Proc R Soc B: Biol Sci* (1929) 2020, **287**:20200523.
Field experiment demonstrating that in some contexts chimpanzees do surpass bonobos in cooperative performance.
22. Nolte S, Call J: **Targeted helping and cooperation in zoo-living chimpanzees and bonobos.** *R Soc Open Sci* 2021, **8**:201688.
 23. Tan J, Kwetuenda S, Hare B: **Preference or paradigm? Bonobos show no evidence of other-regard in the standard prosocial choice task.** *Behaviour* 2015, **152**:521-544.
 24. Hall K, Smith M, Russell JL, Lambeth SP, Schapiro SJ, Brosnan SF: **Chimpanzees rarely settle on consistent patterns of play in the Hawk Dove, Assurance, and Prisoner's Dilemma games, in a token exchange task.** *Anim Behav Cogn* 2019, **6**:48-70.
 25. Verspeek J, van Leeuwen EJC, Laméris DW, Staes N, Stevens JMG: **Adult bonobos show no prosociality in both prosocial choice task and group service paradigm.** *PeerJ* 2022, **10**:e12849.
 26. Burkart JM, Allon O, Amici F, Fichtel C, Finkenwirth C, Heschl A, Huber J, Isler K, Kosonen ZK, Martins E, et al.: **The evolutionary origin of human hyper-cooperation.** *Nat Commun* 2014, **5**:4747.
Large-scale comparative study across species exploring cooperative tendencies in home group settings.
 27. Cronin KA, De Groot E, Stevens JMG: **Bonobos show limited social tolerance in a group setting: a comparison with chimpanzees and a test of the relational model.** *Folia Primatol* 2015, **86**:164-177.
 28. Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaró J, Schapiro SJ: **Chimpanzees are indifferent to the welfare of unrelated group members.** *Nature* 2005, **437**:1357-1359.
 29. Brosnan SF, Silk JB, Henrich J, Mareno MC, Lambeth SP, Schapiro SJ: **Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task.** *Anim Cogn* 2009, **12**:587-597.
 30. Yamamoto S, Tanaka M: **Do chimpanzees (*Pan troglodytes*) spontaneously take turns in a reciprocal cooperation task? *J Comp Psychol* 2009, **123**:242-249.**
 31. Hockings KJ, Anderson JR, Matsuzawa T: **Road crossing in chimpanzees: a risky business.** *Curr Biol* 2006, **16**:R668-R670.
 32. Yamamoto S: **"Unwilling" versus "Unable": understanding chimpanzees' restrictions in cognition and motivation.** *Psychologia* 2021, **63**:174-190.
 33. Herbinger I, Papworth S, Boesch C, Zuberbühler K: **Vocal, gestural and locomotor responses of wild chimpanzees to familiar and unfamiliar intruders: a playback study.** *Anim Behav* 2009, **78**:1389-1396.
 34. Henkel S, Setchell JM: **Group and kin recognition via olfactory cues in chimpanzees (*Pan troglodytes*).** *Proc R Soc B* 2018, **285**:20181527.
 35. Lewis LS, Kano F, Stevens JMG, DuBois JG, Call J, Krupenye C: **Bonobos and chimpanzees preferentially attend to familiar members of the dominant sex.** *Anim Behav* 2021, **177**:193-206.
 36. Campbell MW, de Waal FBM: **Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy.** *PLoS One* 2011, **6**:e18283.
 37. Tan J, Ariely D, Hare B: **Bonobos respond prosocially toward members of other groups.** *Sci Rep* 2017, **7**:14733.
 38. Demuru E, Palagi E: **In bonobos yawn contagion is higher among kin and friends.** *PLoS One* 2012, **7**:e49613.
 39. Norscia I, Caselli M, De Meo G, Cordoni G, Guéry J, Demuru E: **Yawn contagion in bonobos: another group, another story.** *Am J Primatol* 2022, **84**:e23366, <https://doi.org/10.1002/ajp.23366>
 40. Sandel AA, Watts DP: **Lethal coalitionary aggression associated with a community fission in chimpanzees (*Pan troglodytes*) at Ngogo, Kibale National Park, Uganda.** *Int J Primatol* 2021, **42**:26-48, <https://doi.org/10.1007/s10764-020-00185-0>
 41. Chen FX, Zhang X, Laustsen L, Cheng JT: **Harsh but expedient: dominant leaders increase group cooperation via threat of punishment.** *Psychol Sci* 2021, **32**:2005-2022, <https://doi.org/10.1177/09567976211031208>
 42. Gavrillets S, Fortunato L: **A solution to the collective action problem in between-group conflict with within-group inequality.** *Nat Commun* 2014, **5**:3526.
 43. Parish AR, De Waal FBM, Haig D: **The other "closest living relative": how bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and intersexual interactions, and hominid evolution.** *Ann N Y Acad Sci* 2000, **907**:97-113.
 44. Schneider A-C, Melis AP, Tomasello M: **How chimpanzees solve collective action problems.** *Proc R Soc B: Biol Sci* 2012, **279**:4946-4954.
 45. Watts DP, Mitani JC: **Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda.** *Int J Primatol* 2002, **23**:1-28.
 46. Samuni L, Preis A, Deschner T, Crockford C, Wittig RM: **Reward of labor coordination and hunting success in wild chimpanzees.** *Commun Biol* 2018, **1**:138.
 47. Surbeck M, Hohmann G: **Primate hunting by bonobos at LuiKotale, Salonga National Park.** *Curr Biol* 2008, **18**:R906-R907.
 48. De Dreu CKW, Greer LL, Handgraaf MJJ, Shalvi S, Van Kleef GA: **Oxytocin modulates selection of allies in intergroup conflict.** *Proc R Soc B: Biol Sci* 2012, **279**:1150-1154.
 49. Zhang H, Gross J, De Dreu C, Ma Y: **Oxytocin promotes synchronized out-group attack during intergroup conflict in humans.** *eLife* 2019, **8**:e40698, <https://doi.org/10.7554/eLife.40698>
 50. De Dreu CKW, Kret ME: **Oxytocin conditions intergroup relations through upregulated in-group empathy, cooperation, conformity, and defense.** *Biol Psychiatry* 2016, **79**:165-173.
 51. De Dreu CKW, Greer LL, Van Kleef GA, Shalvi S, Handgraaf MJJ: **Oxytocin promotes human ethnocentrism.** *Proc Natl Acad Sci USA* 2011, **108**:1262-1266.
 52. Ma X, Luo L, Geng Y, Zhao W, Zhang Q, Kendrick KM: **Oxytocin increases liking for a country's people and national flag but not for other cultural symbols or consumer products.** *Front Behav Neurosci* 2014, **8**:266.
 53. Wittig RM, Crockford C, Deschner T, Langergraber KE, Ziegler TE, Zuberbühler K: **Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees.** *Proc R Soc B: Biol Sci* 2014, **281**:20133096.
 54. Crockford C, Wittig RM, Langergraber K, Ziegler TE, Zuberbühler K, Deschner T: **Urinary oxytocin and social bonding in related and unrelated wild chimpanzees.** *Proc R Soc B: Biol Sci* 2013, **280**:20122765.
 55. Brooks J, Kano F, Yeow H, Morimura N, Yamamoto S: **esting the effect of oxytocin on social grooming in bonobos.** *bioRxiv* 2021, <https://doi.org/10.1101/2021.11.30.468796>
 56. Moscovice LR, Surbeck M, Fruth B, Hohmann G, Jaeggi AV, Deschner T: **The cooperative sex: sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions.** *Horm Behav* 2019, **116**:104581.
 57. Preis A, Samuni L, Mielke A, Deschner T, Crockford C, Wittig RM: **Urinary oxytocin levels in relation to post-conflict affiliations in wild male chimpanzees (*Pan troglodytes verus*).** *Horm Behav* 2018, **105**:28-40.
 58. Samuni L, Preis A, Mundry R, Deschner T, Crockford C, Wittig RM: **Oxytocin reactivity during intergroup conflict in wild chimpanzees.** *Proc Natl Acad Sci USA* 2017, **114**:268-273.
 59. Proctor D, Calcutt SE, Burke K, de Waal FBM: **Intranasal oxytocin failed to affect chimpanzee (*Pan troglodytes*) social behavior.** *Anim Behav Cogn* 2016, **3**:150-158.
 60. Brooks J, Kano F, Sato Y, Yeow H, Morimura N, Nagasawa M, Kikusui T, Yamamoto S: **Divergent effects of oxytocin on eye**

contact in bonobos and chimpanzees.

Psychoneuroendocrinology 2021, **125**:105119.

First study to demonstrate an effect of exogenous oxytocin on behaviour in non-human great apes.

61. Brooks J, Kano F, Kawaguchi Y, Yamamoto S: **Oxytocin promotes species-relevant outgroup attention in bonobos and chimpanzees.** *Horm Behav* 2022, **143**:105182.
62. Lee M, Lindo J, Rilling JK: **Exploring gene-culture coevolution in humans by inferring neuroendophenotypes: a case study of the oxytocin receptor gene and cultural tightness.** *Genes Brain Behav* 2022, **21**:e12783, <https://doi.org/10.1111/gbb.12783>
63. Staes N, Stevens JMG, Helsen P, Hillyer M, Korody M, Eens M: **Oxytocin and vasopressin receptor gene variation as a proximate base for inter- and intraspecific behavioral differences in bonobos and chimpanzees.** *PLoS One* 2014, **9**:e113364.
64. Staes N, Guevara EE, Helsen P, Eens M, Stevens JMG: **The Pan social brain: an evolutionary history of neurochemical receptor genes and their potential impact on sociocognitive differences.** *J Hum Evol* 2021, **152**:102949.

Detailed genomic study showing divergence between bonobos and chimpanzees at important receptor genes, including oxytocin.

65. Kovalaskas S, Rilling JK, Lindo J: **Comparative analyses of the Pan lineage reveal selection on gene pathways associated with diet and sociality in bonobos.** *Genes Brain Behav* 2020, **20**:e12715, <https://doi.org/10.1111/gbb.12715>
66. Aboud FE: **The formation of in-group favoritism and out-group prejudice in young children: are they distinct attitudes?** *Dev Psychol* 2003, **39**:48-60.
67. Suchak M, Eppley TM, Campbell MW, Feldman RA, Quarles LF, de Waal FBM: **How chimpanzees cooperate in a competitive world.** *Proc Natl Acad Sci USA* 2016, **113**:10215-10220.
68. Suchak M, Eppley TM, Campbell MW, de Waal FBM: **Ape duos and trios: spontaneous cooperation with free partner choice in chimpanzees.** *PeerJ* 2014, **2**:e417.
69. Campbell MW, Watzek J, Suchak M, Berman SM, Waal FBM: **Chimpanzees (*Pan troglodytes*) tolerate some degree of inequity while cooperating but refuse to donate effort for nothing.** *Am J Primatol* 2020, **82**:e23084.
70. Henrich J, Gil-White FJ: **The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission.** *Evol Hum Behav* 2001, **22**:165-196.