# Oxytocin reactivity during intergroup conflict in wild chimpanzees

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**Intergroup conflict is evident throughout the history of our species, ubiquitous across human societies, and considered crucial for the evolution of humans' large-scale cooperative nature. Like humans, chimpanzee societies exhibit intragroup coordination and coalitionary support during violent intergroup conflicts. In both species, cooperation among group members is essential for individuals to gain access to benefits from engaging in intergroup conflict. Studies suggest that a contributive mechanism regulating in-group cooperation during intergroup conflicts in humans involves the neuropeptide hormone oxytocin, known to influence trust, coordination, and social cognition, although evidence from natural settings is lacking. Here, applying a noninvasive method, we investigate oxytocinergic system involvement during natural intergroup conflicts in wild chimpanzees. We found that chimpanzees of both sexes had significantly higher urinary oxytocin levels immediately before and during intergroup conflict compared with controls. Also, elevated hormone levels were linked with greater cohesion during intergroup conflicts, rather than with the level of potential threat posed by rival groups, intragroup affiliative social interactions, or coordinated behavior alone. Thus, the oxytocinergic system, potentially engendering cohesion and cooperation when facing an out-group threat, may not be uniquely human but rather a mechanism with evolutionary roots shared by our last common ancestor with chimpanzees, likely expediting fitness gains during intergroup conflict.**

*Pan troglodytes* | cooperation | group cohesion | neuropeptide | parochial altruism

Recent evolutionary models suggest that parochial altruism, the link between in-group favoritism and the benefit of others at a cost to oneself, is key to understanding the evolution of humans' cooperative traits and propensity for intergroup violence (1, 2). Intergroup conflict is ubiquitous across human societies (2), repeatedly leading to devastating results of prejudice, war, and genocide (2, 3). Individuals contribute to these patterns both by supporting in-group members and acting with hostility toward the out-group. When such a combination contributes to success in intergroup conflicts, parochial altruism could have evolved (1), and biological mechanisms that sustain and promote it are likely adaptive (4).

One such proposed biological mechanism involves the neuropeptide hormone oxytocin, previously linked with various aspects of human sociality, particularly the development of mother–offspring bonds, but also tolerance, coordination, and cooperation between nonkin adults (5–7). Owing to its anxiolytic and prosocial effects, oxytocin is proposed to facilitate cooperation during risk, a mechanism potentially co-opted from maternal defense circuitry (4). Intranasal administration of oxytocin enhances in-group cooperation and trust (8, 9) and out-group defensive, but not offensive, competition in men (8). This suggests that oxytocin triggers a "tend and defend" form of parochial altruism, accentuating cooperative behavior toward the in-group as well as defensive behavior toward out-groups (4). However, these results were obtained in laboratory settings using intergroup social dilemma games and focusing on human male participants. Few, if any, studies have involved intergroup contexts and oxytocin in captive or wild nonhuman animals. Therefore, additional evidence is essential for corroborating oxytocinergic system involvement in an ecologically relevant setting.

Wild chimpanzees in almost all long-term field sites engage in competitive intergroup conflicts (10, 11), which are characterized by two sets of behavior (Movie S1), intergroup encounters and border patrols. Intergroup encounters (direct out-group contact) are characterized by coordinated attacks, with synchronous vocalizations and charges toward and combat against chimpanzees from rival groups (12, 13). In border patrols (no direct out-group contact), chimpanzees' typical foraging and traveling movements change to become more cohesive and quiet while they vigilantly scout the peripheral areas of their territory, often continuing for several kilometers (12, 13). Feeding and vocalizations are minimal. Travel is slow, often in single file, interrupted by frequent pauses in which chimpanzees may sniff forest items, such as out-group chimpanzee feces or food remnants, and are unusually alert to sounds beyond the immediate group (12, 13). Individuals appear to search for signs indicative of recent rival-group chimpanzee presence, such as vocal presence, or recent physical presence, potentially assessing the strength of their opponents.

Chimpanzee group defense is energetically costly in terms of reduced foraging and increased traveling (14), and risky, as it may lead to injury or death (10). Successful attacks on rival groups, however, potentially increase the territory size of the in-group and the reproductive output of its members (14, 15), thereby increasing

## Significance

**Warfare is one of the most pervasive problems among human societies, and understanding mechanisms involved in in-group cooperation and favoritism is of paramount importance. Wild chimpanzees share key features of humans' intergroup conflict, in terms of in-group coordination, coalitionary support, and out-group hostility. The hormone oxytocin may regulate humans' intergroup conflict, although tests in natural settings are lacking. We found strong evidence that, like in humans, oxytocin is involved in chimpanzee intergroup conflict. Both intergroup conflict anticipation and participation involved high urinary oxytocin levels, irrespective of intragroup affiliations or potential threat by rivals. These results are indicative of similar physiological processes involved in intergroup violence and intragroup support in both species, likely supporting behavior that is adaptive during intergroup conflicts.**

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fitness. Access to benefits of intergroup conflict can be maintained through cooperation, providing benefits to both actor and recipient regardless of potential short-term costs to the actor (16). Chimpanzee in-group behavior during intergroup conflict is considered to be cooperative (11, 17), as it encompasses prolonged coordination and cohesion, as well as coalitionary support, which can involve individuals safe from the out-group running forward to defend an in-group member under attack from the out-group (11). In humans, cohesion and support also intensify under life-threatening situations, such as war (18). These parallels highlight key features shared by chimpanzee and human group defense and intergroup conflict (14). Also similar to humans, the oxytocinergic system in chimpanzees is involved in prosocial and cooperative behavior between both kin and nonkin group members, such as grooming (19) and food sharing (20), suggesting parallels in oxytocinergic system involvement between humans and chimpanzees.

Here we investigate whether chimpanzees' in-group behavior during border patrols and intergroup encounters (intergroup conflict) enhances group cohesion and involves the oxytocinergic system. Due to the competitive, aggressive nature of chimpanzee intergroup interactions and in accordance with the human literature, we use the term intergroup conflict (2) to describe border patrols and intergroup encounters. We assessed (*i*) whether chimpanzees' group cohesion is greater during intergroup conflicts than control periods ("defection" model). Chimpanzees live in a fission–fusion social system in which individuals from the same group split into small and dynamic subgroups of varying size, composition, and duration (12). Accordingly, we measured fissions of adult individuals as an estimate of defection. Fission may be affected by ecological, social, and spatial factors (21). Nonetheless, if intergroup conflicts require cohesion, we expected fewer fissions during intergroup conflicts than during control periods, regardless of subgroup size and composition, which may affect fission patterns, or proximity to territory border areas, where intergroup encounters often occur. We also investigated whether in-group activity during border patrols and intergroup encounters engaged the oxytocinergic system. The oxytocinergic system influences attributes likely to assist cooperation and hence successful intergroup conflict, such as in-group trust and coordination (5–7). Accordingly, we hypothesized that high oxytocin levels immediately before and during intergroup conflicts would be adaptive when influencing group cooperation. We expected both (*ii*) high oxytocin levels during intergroup conflicts ("event" model) and (*iii*) high anticipatory oxytocin levels before border patrol initiation ("anticipation" model). We expected high oxytocin levels to persist, even when controlling for the occurrence of in-group affiliative behavior, proximity to border areas, or behavior involving in-group coordination in the absence of outgroup threat, specifically hunting events where chimpanzees coordinate to capture monkeys (22).

We investigated our hypotheses using a within-subjects design, sampling naturally occurring events during intra- and intergroup interactions in wild chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Ivory Coast. We conducted focal animal sampling (23) for 20 adult male and female chimpanzees of two neighboring groups, and measured the oxytocin concentration of urine samples from all individuals using an established method to sample specific events (19, 20).

## Results and Discussion

As with humans, chimpanzee group defense requires coordination and coalitionary support to be effective (11, 17), and when such cooperative behavior is maintained, access to benefits is more likely. For instance, in chimpanzees, intergroup lethal violence occurs predominantly at times of power imbalance in favor of attackers (10), and thus group cohesion may reduce the likelihood of suffering costs. To investigate the influence of intergroup conflict on group cohesion (defection model), we counted fissions per individual as an estimate of defection (Table 1). We determined for each adult individual the number of times it left the subgroup from the onset to the end of the intergroup conflict ($n = 23$), or during a matched control period ($n = 23$). Controls were defined as periods with similar duration, subgroup size, and composition on days that did not include intergroup conflicts or hunting behavior. We found similar numbers of leaves per individual during intergroup conflict periods that included direct interactions with rival groups (intergroup encounters $n = 11$) and those that did not (border patrols $n = 12$) (Table 1). Accordingly, we fitted a Poisson generalized linear mixed model (GLMM) (24) to analyze how the response varied between both types of intergroup conflict and controls. We controlled for group identity, proximity to border areas where encounters with rivals are more likely, and subgroup duration.

We found that during intergroup conflicts, individuals were significantly less likely to leave the subgroup than during control periods (GLMM, likelihood ratio test: $\chi^2 = 13.484$, df = 1, $P < 0.001$; estimate ± SE −1.732 ± 0.446; Table S1). This effect was not driven by proximity to border areas, where encounters with rivals are more likely. We also found an effect of group identity (Table S1), with South group individuals being significantly less likely to leave the subgroup than East group individuals; however, this parameter was associated with some instability. Contextual variation in defection numbers showed that, in comparison with control contexts, intergroup conflict promoted group cohesion. Similarly, human soldiers increase their cohesion and affiliation when going into battle (18). Although cohesion is fundamental in promoting group cooperation, it remains unclear whether intergroup hostilities have contributed to the proliferation of chimpanzee cooperative capacities, as is theorized for humans.

At an endocrinological level, we investigated whether chimpanzee in-group activity during border patrols and intergroup encounters engaged the oxytocinergic system. In case a direct

**Table 1. Behavioral fission data: Comparison of fission numbers between intergroup conflict and control periods**

| | Fission events* | | | Individual fissions† | | | Subgroup size‡ | | Proportion of adult leaves§ | |
|---|---|---|---|---|---|---|---|---|---|---|
| Events | *n* | Mean | SD | *n* | Mean | SD | Mean | SD | Mean | SD |
| Control, $n = 23$ | 65 | 2.826 | 2.145 | 312 | 1.079 | 0.974 | 10.043 | 3.268 | 0.697 | 0.329 |
| Intergroup conflict, $n = 23$ | 25 | 1.089 | 1.276 | 91 | 0.365 | 0.694 | 10.304 | 3.096 | 0.257 | 0.279 |
| Border patrol, $n = 12$ | 16 | 1.454 | 0.934 | 44 | 0.382 | 0.539 | 9.333 | 2.269 | 0.341 | 0.234 |
| Intergroup encounter, $n = 11$ | 9 | 0.750 | 1.484 | 47 | 0.350 | 0.806 | 11.363 | 3.613 | 0.173 | 0.298 |

*Adult individuals leaving the subgroup within at most 1 min were counted as having left during the same fission event.
†Number of times each adult individual left the subgroup.
‡Subgroup size at the start of each event.
§The proportion of adult individuals that left the subgroup at least once to the total adult individuals present in the subgroup.

contact with rival groups occurred within the time window for oxytocin secretion, urine samples were assigned as intergroup encounters, and those that did not include any contact as border patrols. Both types of intergroup conflict had a significant positive effect on log-transformed urinary oxytocin levels (pg/mg creatinine), in contrast to control situations with no positive social interactions ["type" model; linear mixed model (LMM), likelihood ratio test: $\chi^2 = 44.600$, df = 2, $P < 0.001$; Fig. S1 and Table S2]. However, log-transformed urinary oxytocin levels did not differ between the two types of intergroup conflict (Table S3; see *SI Methods* for tests separating these two contexts). Thus, although border patrols represent only a covert out-group threat, they are subject to similar urinary oxytocin and cohesion levels as time periods including intergroup encounters. Hence, we combine them as one context in the following event model (see *SI Methods*, Fig. S2, and Table S4 for tests only including intergroup encounters).

Here we tested the impact of different events and confounding factors on urinary oxytocin levels (event model). Because affiliation frequently occurs during in-group out-group contexts and might impact urinary oxytocin levels (19), we divided intergroup conflict samples into two categories: group members participating in intergroup conflict (*i*) without in-group affiliation (11 subjects, $n = 103$ samples of 37 events), or (*ii*) with in-group affiliation (grooming or play with multiple partners; 15 subjects, $n = 64$ samples of 24 events). We contrasted intergroup conflict with three control events excluding intergroup conflict or food sharing, as the latter shows association with high oxytocin levels in chimpanzees (20): (*i*) 90-min time periods in which no positive social interactions, except vocalizations, occurred ("control without affiliation"; 20 subjects, $n = 178$ samples of 150 events); (*ii*) multipartner grooming of at least 10-min duration ("control with affiliation"; 19 subjects, $n = 100$ samples of 87 events); and (*iii*) participation in group hunting of monkeys, a coordinated behavior (22) that does not involve in-group out-group contexts ("control with coordination"; 9 subjects, $n = 23$ samples of 17 events). The two latter contexts allowed us to control for the in-group affiliative and coordinated behavior often observed during intergroup conflicts, respectively. All samples relating to a target context were collected within the time window of oxytocin excretion into urine at least 15 min after the start and up to 60 min after the end of interactions (19, 20). We fitted an LMM (event model) (24) to test for the influence of intergroup conflict, coordination, and affiliation on log-transformed urinary oxytocin levels (pg/mg creatinine). To control for other factors that might influence hormone levels, we included individuals' sex and rank, subgroup size, group identity, and proximity to border areas to evaluate potential risk. Our dataset for the event model included 468 samples from 20 different individuals from 296 different events.

Overall, the full-null model comparison was significant (LMM, likelihood ratio test: $\chi^2 = 51.253$, df = 4, $P < 0.001$; Fig. 1*A* and Table 2). More specifically, intergroup conflicts with and without affiliation were associated with higher urinary oxytocin levels than the three controls (Table 2 and Tables S5, S6, and S7). We also found a positive effect of group coordinated hunting behavior on urinary oxytocin levels compared with both the control with and without affiliation, although less pronounced than the effect of intergroup conflict (Table S7). These effects were neither driven by individual rank or sex, subgroup size, nor proximity to border areas. However, we found a group effect, with East group having higher urinary oxytocin levels than South group (Table 2), despite having similar group sizes and little ecological variance or genetic differentiation (25). Moreover, in post hoc analyses comparing intergroup conflict with and without affiliation, we found no significant effect of affiliation on urinary oxytocin levels within this context (LMM: $\chi^2 = 0.136$, df = 1, $P = 0.334$; Table S5).

When facing rival groups, chimpanzee in-group behavior was positively linked with urinary oxytocin levels. This was true even when accounting for affiliative interactions and potential threat from rival groups, suggesting that, similar to humans, the oxytocinergic system is an influential mechanism involved in chimpanzee in-group out-group contexts. The stimulus that triggers oxytocin release in intergroup contexts, however, remains unknown for either humans or chimpanzees. Affiliative contact has been proposed as an oxytocin trigger (26), but our results concur with other studies, of both humans and chimpanzees, suggesting that physical contact is not necessarily required (20, 27) nor sufficient (19) for oxytocin secretion. Here, neither the presence of affiliation during intergroup conflict nor multipartner affiliation without intergroup conflict (Table 2) led to urinary oxytocin levels that differed from nonaffiliative intergroup conflict or control samples, respectively. This is in agreement with recent evidence that the mere act of grooming is not linked with an oxytocin

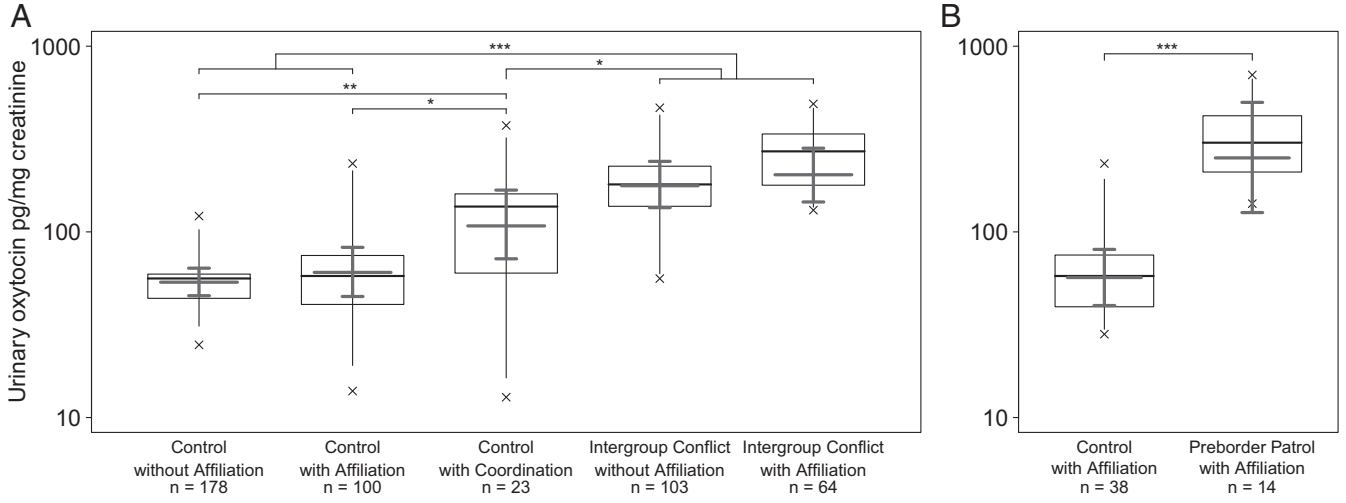


**Fig. 1.** (*A*) Effects of intergroup conflict with and without in-group affiliation on urinary oxytocin levels in wild chimpanzees in East and South groups ($n = 468$ samples, 20 subjects, 296 events). (*B*) Effects of imminent intergroup conflict in East group chimpanzees on urinary oxytocin levels ($n = 52$ samples, 9 subjects, 43 events). Shown are medians (thin horizontal lines), quartiles (boxes), percentiles (2.5 and 97.5%; vertical lines), minimum and maximum (laying crosses), as well as the fitted model and its 95% confidence intervals (thick lines). ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

**Table 2. Event model: Effect of intergroup conflict and in-group affiliation on urinary oxytocin levels, log-transformed**

| Term | Estimate | SE | $CI_{lower}$ | $CI_{upper}$ | $\chi^{2}$* | *P* |
|---|---|---|---|---|---|---|
| Intercept | 4.353 | 0.212 | 3.943 | 4.783 | – | – |
| Test predictor levels | | | | | | |
| Control with affiliation[†] | 0.122 | 0.160 | −0.199 | 0.411 | 0.549 | 0.459 |
| **Control with coordination[†]** | **0.698** | **0.222** | **0.254** | **1.137** | **6.556** | **0.010** |
| **Intergroup conflict without affiliation[†]** | **1.197** | **0.171** | **0.840** | **1.576** | **36.044** | **<0.001** |
| **Intergroup conflict with affiliation[†]** | **1.333** | **0.193** | **0.928** | **1.718** | **27.298** | **<0.001** |
| Control predictors | | | | | | |
| **Group[‡]** | **−0.319** | **0.127** | **−0.579** | **−0.048** | **5.916** | **0.015** |
| Sex[§] | −0.307 | 0.200 | −0.717 | 0.054 | 2.292 | 0.130 |
| Proximity[¶] | −0.035 | 0.057 | −0.153 | 0.070 | 0.378 | 0.538 |
| Subgroup size[#] | 0.082 | 0.049 | −0.010 | 0.186 | 2.714 | 0.099 |
| Rank[‖] | 0.077 | 0.100 | −0.105 | 0.269 | 0.574 | 0.449 |

Statistically significant results ($P \leq 0.05$) appear in bold. CI, confidence interval.

*Degrees of freedom are 1.

[†,‡,§]$\chi^{2}$ and *P* values refer to comparison with the reference categories: [†]control without affiliation, [‡]East group, and [§]female.

[¶,#,‖]*z*-transformed, mean ± SD of the original variables: [¶]61.59 ± 29.21 (range 5 to 99), [#]11.77 ± 5.87, and [‖]0.62 ± 0.24 (range 0 to 1, with 1 being the highest social rank).

response but rather the social context in which the grooming occurs (19). Also, proximity to border areas, where encounters with rival groups are more likely, did not affect urinary oxytocin levels. The latter suggests that a potential threat by out-groups alone is not sufficient for triggering oxytocin excretion. The finding that both coordinated activities (i.e., hunting and intergroup conflict) showed higher urinary oxytocin levels than control with and without affiliation suggests that coordinated behavior is linked to the oxytocinergic system. Given that intergroup conflicts had significantly higher oxytocin levels than hunting indicates that this effect is likely reinforced in the context of out-group threat. It is therefore possible that in-group coordinated activity and the perception of an in-group out-group context act in synergy during intergroup conflicts. However, because we are lacking a behavioral measure of the degree of coordination, we cannot rule out that the oxytocinergic system reactivity observed in intergroup conflicts is a mere function of a greater level of coordination when facing hostile rival groups. Nonetheless, whether in-group out-group perception drives group coordination, oxytocin secretion, or both, our results suggest that chimpanzee in-group cohesive behavior in the face of out-group threat is likely supported by the same physiological mechanism suggested for human parochial altruism, the oxytocinergic system.

Moreover, it is unclear whether oxytocin release results from or precipitates participation in intergroup conflicts. Owing to the beneficial value of cooperative group action during intergroup conflict, we expect that an anticipatory oxytocin increase would be adaptive when influencing group cohesion. Because in the Taï Forest, chimpanzee border patrols are often preceded by grooming with multiple group members, the majority of preborder patrol samples collected involved grooming interactions. Accordingly, to investigate anticipatory oxytocin increase (anticipation model), we contrasted urine samples collected after multipartner grooming sessions: (*i*) shortly before the initiation of border patrols ("preborder patrol with affiliation"; 6 subjects, $n = 14$ samples of 10 intergroup conflict events) or, as a control, (*ii*) on days without intergroup conflict (control with affiliation; 9 individuals, $n = 38$ samples of 34 events). This model included samples from a single chimpanzee group, East group, because no preborder patrol with affiliation samples were attained for South group. We fitted an LMM controlling for duration of grooming, subgroup size, individuals' sex and rank, and proximity to border areas. We found a significant positive impact of imminent border patrols on urinary oxytocin levels (LMM, likelihood ratio test: $\chi^{2} = 11.132$, df = 1, $P < 0.001$; Fig. 1*B* and Table S8), an effect that was not driven by the duration of multipartner grooming or other control predictors.

Our results demonstrate an anticipatory increase in urinary oxytocin in a similar manner to the anticipatory testosterone increase found in intergroup conflicts (28) and intragroup competition (29) in chimpanzees. The observed high urinary oxytocin levels before border patrol initiation suggest that individuals may anticipate imminent intergroup conflict. Moreover, when comparing preborder patrol with affiliation with intergroup conflict with affiliation, we found no significant effect on urinary oxytocin levels (LMM: $\chi^{2} = 0.181$, df = 1, $P = 0.669$; Fig. S3 and Table S9). This suggests that the observed anticipatory increase remains high throughout the intergroup conflict. The anxiolytic effect of oxytocin is proposed to facilitate social cohesion during highly risky situations that might otherwise precipitate defection away from threat (4). Accordingly, when group defense provides individuals with fitness advantages, mechanisms involving anticipatory high oxytocin potentially maintain cooperation and safeguard against defection.

Possibly resulting from a male propensity to participate in intergroup hostility (30), experimental approaches investigating cooperation during intergroup conflict have been mainly limited to male behavior (31). However, in a recent study, intranasal administration of oxytocin enhanced in-group cooperation during an in-group out-group setting in both men and women (32). This suggests oxytocin as an influential physiological mechanism in both sexes in in-group out-group contexts. Accordingly, we investigated sex differences during natural intergroup conflicts in chimpanzees. In the Taï Forest, both sexes participate in intergroup conflict (12), and females participated in 91% of intergroup conflicts in this study (proportion of all adult females and parous females 0.44 ± 0.21 and 0.35 ± 0.2, respectively). An interaction between event and sex was not significant, showing that female and male chimpanzees have similar oxytocin reactivity across events. Male chimpanzees are more likely to be the victims of lethal intergroup aggression (10). Nonetheless, the risk of intergroup infanticide and female hostage taking by rival groups are substantial threats for females (10, 11) and may increase the likelihood of female avoidance of intergroup conflicts (13). However, in the Taï Forest, rates of intergroup lethal violence are low in comparison with other chimpanzee field sites (10). Whether this is a cause or an effect of the likelihood of both sexes to cooperate in threatening situations remains unknown. Nonetheless, our findings emphasize that selective pressures may have led to similar oxytocinergic system involvement in intergroup conflict in both sexes. Future investigations of the hormonal mechanisms involving in-group out-group contexts in women in natural settings will aid understanding of the reported sex differences (30) in human intergroup violence.

This study used a within-subjects design, requiring repeated sampling of the same wild chimpanzees when engaged in different natural events. We achieved this by using peripheral oxytocin measures that could be noninvasively collected. The biological validity of peripheral oxytocin measurements with respect to central oxytocin patterns nonetheless is debated (33–35). However, an increasing body of evidence shows that oxytocin pathways can involve coordinated central and peripheral oxytocin release, indicating that high peripheral measures reflect the release of central oxytocin. Furthermore, an increasing number of studies demonstrate the same effects of behavior, social context, and social relationships on both central and peripheral oxytocin measures (35–37).

Using an ecologically relevant paradigm, we found that the oxytocinergic system, a highly conserved physiological mechanism (5), is involved in cohesion during intergroup conflict in chimpanzees, as suggested for humans (8). Given that in-group favoritism in humans and chimpanzees may be underpinned by the same physiological mechanism, the most parsimonious explanation for such similarities is that this mechanism was present in our common ancestor, regulating in-group bias. Accordingly, it may be that some aspects thought to play a role in human parochial altruism rest on more ancient evolutionary origins than has been presumed.

The fundamental need for within-group support in times of rising between-group conflict is not uniquely human but apparently also present in one of our closest living relatives, the chimpanzee (11, 17). The link between human intergroup violence, group division, categorization, and attribution clearly is a current and pressing topic (3, 38). Understanding the evolutionary mechanisms underlying in-group out-group interactions, the pressures that switch intergroup collaboration to conflict and vice versa, and the interplay between behavior and hormones in these contexts may eventually assist the building of cooperation rather than destruction in fragile human between-group relations.

## Methods

Fieldwork was conducted with the Taï Chimpanzee Project located at the Taï National Park, Ivory Coast (5°52′N, 7°20′E), between October 2013 and April 2014 as well as between September 2014 and May 2015, observing the well-habituated East and South neighboring chimpanzee (*P. t. verus*) groups. We conducted all-day focal animal sampling (23) on 20 individuals (5 males and 5 parous females in each group) for a total of 2,278 observation hours in East group and 2,164 in South group, along with noninvasively collected urine samples (analysis included $n = 482$ samples, 23.4 ± 14.55 samples per individual). During focal follows, we documented changes in the behavior, social interactions, and vocalizations emitted by and directed toward the focal individual, using CyberTracker software (version 3.389; www.cybertracker.org/). We continuously updated the subgroup composition and size. Every occurrence of a border patrol or an intergroup encounter was recorded ad libitum. During the study period, 67 instances of intergroup conflict were observed in East group, a rate of 1 every 5 d, out of which 28 involved both a border patrol (with no direct out-group contact) and an intergroup encounter (with direct out-group contact; 42%; 1 every 11 d); 25 instances of intergroup conflict were observed in South group, a rate of 1 every 12 d, out of which 17 involved both a border patrol and an intergroup encounter and a single instance involving only an intergroup encounter (72%; 1 every 16 d). None of the intergroup encounters observed resulted in lethal aggression.

To determine dynamic changes in dominance relationships over time within each group, we used the Elo-rating (39), based on unidirectional submissive pant grunt vocalizations (40). We continuously recorded the location of the focal subject using a Garmin Rino 610 global positioning system set on the automatic tracklog recording function. This was done to control for changes in the chimpanzee's endocrinological response in relation to proximity to peripheral territorial areas and, thus, the potential to encounter rival chimpanzee groups. We then assessed the proximity of the focal individual to the border areas of the territory. We used a kernel density estimate (41) in R (version 3.2.3) (42) to construct polygons representing the percentage of home-range use kernels ranging from 5 to 99, with 5 representing the very core of the home range and 99 being the border area (Fig. S4).

As an estimate of defection, we measured for each adult individual the number of times it left the subgroup of the focal individual during instances of prolonged intergroup conflicts (East group $n = 21$; South group $n = 2$; duration, mean ± SD 102.4 ± 41.48 min; Table 1). All intergroup conflict periods used in this model included border patrol behavior. Whereas some periods included direct contact with rival groups and were labeled as intergroup encounters ($n = 11$), others did not include out-group contact and were labeled as border patrols ($n = 12$). We defined separate fission events as any adult who left the subgroup per min, such that leaves that occurred >1 min apart were counted as separate fission events (Table 1). Accordingly, $n = 25$ fission events occurred during intergroup conflicts at a rate of 1 every 96 min (fissions per period, mean ± SD 1.089 ± 1.276, with 3.64 ± 2.36 individuals leaving during each fission event). We compared this with matched control periods of the same duration and within 1 to 3 d before or after the intergroup conflict (East group $n = 21$; South group $n = 2$), on days that did not include intergroup conflicts or hunting behavior, and with similar subgroup size and composition. A total of $n = 65$ fission events occurred during matched control periods at a rate of 1 every 37 min (fissions per period, mean ± SD 2.826 ± 2.145, with 4.8 ± 3.23 individuals leaving during each fission event).

**Urine Sample Collection and Analysis.** We took the clearance of oxytocin into urine in chimpanzees to be 15 to 60 min after secretion (19, 20), adapted from a human clearance study (43). Urinary oxytocin measures show biobehaviorally relevant levels following target behaviors or social interactions that occur within this time window (19, 20). Sample collection, extraction, and analysis followed the event sampling protocol used by Crockford et al. (19), incorporating minor changes (*SI Methods*). Analysis was done using a commercially available enzyme immunoassay kit (Assay Designs; 901-153A-0001; *SI Methods*). We measured creatinine levels in all urine samples and expressed urinary oxytocin values as pg/mg creatinine, to control for variation in urine volume and concentration (44). Because very low creatinine values may lead to overestimation of urinary oxytocin levels, we excluded all urine samples with creatinine levels ≤0.04 mg/mL ($n = 5$, <1.2% of the samples included).

All methods were noninvasive and approved by the Ministries of Research and Environment of Ivory Coast and Office Ivorien des Parcs et Reserves. Our study complies with the ethics of both the Max Planck Society and the Max Planck Institute for Evolutionary Anthropology primatology department ethics policy (www.eva.mpg.de/primat/ethical-guidelines.html).

**Statistical Analysis.** We conducted a series of linear mixed models (24) with Gaussian error structure and identity link function, and a Poisson generalized linear mixed model (24) with log link function in R [version 3.3.0 (42)], using the functions lmer and glmer of the R package lme4 (45). In each model, we included factors that might influence hormone levels (as described above; Datasets S1–S3). Furthermore, to keep type I error rate at the nominal 5%, we included random slopes (46, 47) (*SI Methods*). We compared the fit of the full models with those of a respective null model lacking only the test predictors of event or period type but otherwise identical to the respective full model in all other terms (48), using a likelihood ratio test (*SI Methods*).

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