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Cortisol and oxytocin show independent activity during chimpanzee intergroup conflict

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ABSTRACT

The oxytocinergic system is involved in a range of functions, from attachment and social bonding to aggression and stress responses. Whether oxytocin is released in response to a stressor, shows contradictory results across species and potential contexts-dependent differences. To avoid unintended contextual changes due to experimental procedures, we tested this question non-invasively in wild chimpanzees in an ecologically valid context. We collected endogenous hormonal measures during exposure to a known natural stressor, intergroup conflict. Specifically, we tested for potential synchronous activation patterns between urinary oxytocin and cortisol in male and female chimpanzees during stressor exposure. Oxytocinergic system reactivity during chimpanzee intergroup conflict has already been established in this study population. Thus, we first investigated urinary cortisol levels during border patrol and intergroup encounter days, in comparison to another potential stressor, hunting, and control days. We found higher urinary cortisol levels during intergroup encounter days compared with control and hunting days. We then compared secretion patterns of oxytocin and cortisol in relation to increased levels of out-group contact and hostility ('out-group risk') during intergroup conflict. We found that increased 'out-group risk' was associated with higher cortisol levels, especially when involving direct visual or physical contact with rival groups. Although urinary oxytocin levels were high across intergroup conflict contexts, increasing levels of out-group risk showed no significant variation. Taken together, results indicate independent secretion of oxytocin and cortisol during chimpanzee intergroup conflict, emphasizing that stressor exposure in this context is not the main trigger of oxytocin secretion.

1. Introduction

The neuropeptide hormone oxytocin, known for its vital role in parturition, lactation and maternal behavior (Rilling and Young, 2014), has been implicated in an array of social behaviors in humans and non-human animals (Bartz et al., 2011; Chang et al., 2013; Neumann and Slattery, 2016; Rilling and Young, 2014). With growing investigation efforts into the effects of oxytocin on behavior, cognition and neuropsychiatry, it has become clear that the functions of oxytocin are far more multiplex than initially presumed (Bartz et al., 2011; Chang et al., 2013). For example, although oxytocin has been associated with pro-social traits, increasing trust, empathy and tolerance (Bartz et al., 2011; Insel, 2010; Kosfeld et al., 2005), social recognition, improved ability of inferring others' mental states (Domes et al., 2007; Insel, 2010; Ross and Young, 2009), and reduced anxiety (Heinrichs et al., 2003; Seltzer et al., 2010; Smith and Wang, 2014), it is also known to increase aggression, and out-group prejudice and discrimination (Bosch et al., 2005; De Dreu and Kret, 2016; Grillon et al., 2013).

Patterns across studies underline that social contexts and individual factors, such as sex, early experience, or health, influence oxytocinergic effects (Bartz et al., 2011; Rilling and Young, 2014). Furthermore, mounting evidence links the oxytocinergic system to activity of the hypothalamic-pituitary-adrenal (HPA) axis (Winter and Jurek, 2018). HPA axis is activated in response to stressors in both the physical and social environments (Goymann and Wingfield, 2004; McEwen, 2007; Romero and Wingfield, 2015), leading to the release of cortisol which generates a cascade of physiological reactions, such as the mobilization of glucose (McEwen, 2007; Sapolsky, 2002). Accordingly, the HPA axis physiological reaction is essential for flexible and immediate responses to the changing environment. However, chronic stress exposure may increase allostatic load, negatively affecting immune functions and somatic maintenance and growth processes (McEwen, 2007).

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Both physical and social stressors, typically associated with HPA axis activation such as exercise, forced swimming, pair-bond separation, or social defeat, may trigger oxytocin release centrally and/or peripherally (de Jong et al., 2015; Hinde et al., 2016; Neumann and Slattery, 2016; Pierrehumbert et al., 2010). Such findings are in support of the 'social salience' hypothesis, which states that oxytocin enhances perception to social stimulus, whether associated with positive or negative emotional values (Bartz et al., 2011; Shamay-Tsoory and Abu-Akel, 2016). Accordingly, oxytocin activation during unpredictable or threatening situations may induce anxiety and aggression (Grillon et al., 2013; Shamay-Tsoory and Abu-Akel, 2016). Conversely, the majority of studies (for review see Winter and Jurek, 2018) find that oxytocin is key in reducing anxiety during stressors, down regulating HPA axis activity, and attenuating stress responses (Heinrichs et al., 2003; Seltzer et al., 2010; Smith and Wang, 2014), potentially via the inhibition of corticotrophin-releasing factor (Jurek et al., 2015; Smith et al., 2016) a main regulator of HPA axis activity. The anxiolytic effect of oxytocin is especially pronounced in the presence of social support, known as 'social buffering' (Crockford et al., 2017; Smith and Wang, 2014). This is in line with the 'approach withdrawal' hypothesis, which suggests that the anxiolytic effect of oxytocin promotes social approach and inhibits withdrawal (Kemp and Guastella, 2011), potentially facilitating support-seeking. As discrepancies exist across studies with regard to the relation between HPA axis and oxytocinergic system activations, investigating the link between oxytocin and cortisol secretion will aid identifying causal relationships between and effects of the two systems.

One way to identify the relation between oxytocinergic system and HPA axis activation is by investigating parallels in release patterns of the two hormones during a stressor. Intergroup conflict, is defined as hostility between different social groups, and characterized by coordinated in-group behavior and out-group aggression (Samuni et al., 2017; Watts and Mitani, 2001). It is a social context associated with increased physical exertion and psychological pressure, potential stressors that can be discerned and their effect on hormone secretion tested. During intergroup conflict elevated levels of both hormones are expected to be adaptive. Cortisol facilitates rapid production of energy needed to compete (McEwen, 2007; Sapolsky, 2002) and oxytocin may promote essential in-group support required to generate a cooperative response (De Dreu et al., 2010; Samuni et al., 2017). This is supported by evidence from both human and chimpanzee studies showing oxytocinergic system involvement (De Dreu et al., 2010; Samuni et al., 2017) and HPA axis activity (Bijleveld et al., 2012; Sobolewski, 2012; Wittig et al., 2016) during intergroup conflict. As activation of both physiological pathways is expected, the secretion patterns of the two hormones in relation to varying levels of risk during intergroup conflict can be compared to facilitate identification of interdependency.

To investigate the relation in activation patterns between the oxytocinergic system and HPA axis we analyzed urine samples collected from male and female chimpanzees of the Taï Forest, Côte d'Ivoire, well-habituated to human observers. Oxytocin reactivity during intergroup behavior has been previously shown in males and females of this study population (Samuni et al., 2017). Therefore, our aims were to a) investigate HPA axis activity during intergroup conflicts, a known stressor in other chimpanzee populations, and b) assess whether stressor exposure and out-group hostility activates not only cortisol but as well oxytocin secretion.

To address our first aim we assessed urinary cortisol levels during the same border patrols (i.e., individuals scout the border areas of their territory without out-group contact) and intergroup encounters (i.e., hostile vocal and/or visual interactions with out-group) studied in Samuni et al. (2017). Chimpanzee intergroup behavior involves substantial physical exertion (Amsler, 2010). Thus, we compared urinary cortisol levels collected during either border patrol or intergroup encounter days, with days in which chimpanzees participated in another group behavior involving extensive physical effort but without out-group threat, namely hunting for monkeys, and with days in which chimpanzees did not participate in neither hunting nor any type of intergroup conflict. In accordance with other studies (Sobolewski, 2012; Wittig et al., 2016) we expected physical effort and psychological stressors to activate the HPA axis, thus we predicted an increase in urinary cortisol levels in relation to both types of intergroup conflict and hunting behavior. However, since intergroup encounters are expected to be a stronger stressor due to the risk of injury or death, we predict an additional increase in urinary cortisol levels during intergroup encounter days in comparison to border patrol and hunting days.

To address our second aim, we examined the effect of the potential stressors during intergroup encounters, namely out-group risk and hostility, on urinary oxytocin and cortisol levels, using an experimental-like approach of targeted event sampling. Following the 'social salience' hypothesis (Bartz et al., 2011; Shamay-Tsoory and Abu-Akel, 2016) which proposes that oxytocinergic system activation during unpredictable and threatening situations (for instance stressor exposure) may induce aggression, we would expect higher levels of both cortisol and oxytocin during exposure to rising out-group risk and hostility. However, if oxytocin secretion is independent of stressor exposure, we would expect increasing risk imposed by out-group threat, or out-group aggression, to show correspondingly higher urinary cortisol but not urinary oxytocin levels. Furthermore, we would expect other potential stressors during the intergroup activity (i.e., proximity to border, subgroup size) to influence cortisol but not oxytocin secretion.

2. Methods

2.1. Data collection

Data collection was conducted between October 2013 - May 2014 and September 2014 - May 2015, at the Taï National Park, Côte d'Ivoire (5°45′N, 7°7′W). The study focused on 20 adult individuals of two well-habituated neighbouring chimpanzee (*Pan troglodytes verus*) groups (i.e., East and South). We conducted all day focal animal sampling (Altmann, 1974) of all adult males and a subset of parous females (5 males and 5 females in each group; see SI), using the CyberTracker software (v3.389), resulting in a total of 2278 observation hours in East group and 2255 in South group. During focal follows, we documented every occurrence of territorial border patrol (n = 31), intergroup encounter (n = 56), and hunting observed (n = 143).

2.2. Border patrols, intergroup encounters, and hunting behaviour

Border patrols are characterized by a distinctive set of behaviors, in which chimpanzees' movement patterns become more cohesive, slow and quiet, and their foraging behavior decreases (Samuni et al., 2017; Watts and Mitani, 2001). Chimpanzees on patrols vigilantly scout the border areas of their territory, and are highly alert to signs of rivals and sounds beyond the immediate group (Samuni et al., 2017; Watts and Mitani, 2001). We defined the start of a border patrol whenever individuals began to exhibit these patterns of behavior. In the case when chimpanzees encounter indirect out-group signs (i.e., feces, nests) or when vocalizations by rivals are heard, individuals may whimper, grin and engage in tactile reassurance (e.g., embrace, genital holding, grooming). Not every vocal detection leads to a vocal response by the group, and individuals will either retreat back to their core area, or more often, approach silently. In some cases individuals will engage in aggressive vocal interactions with rivals, including drumming, pant-hooting and barking, or in contact encounters that are characterized by vocalizations, displays and attacks (Samuni et al., 2017; Watts and Mitani, 2001). We marked the occurrence of intergroup encounters when chimpanzee encountered direct vocal or visual signs of rivals. Furthermore, we recorded location data to assess the proximity of the focal subject to the border areas of the territory during patrols and encounters (see SI). In addition to border patrol and intergroup

encounters, we documented another group activity of chimpanzees that involves physical effort, however without out-group threat, that is hunting for monkeys (Samuni et al., 2018a; Sobolewski, 2012; Watts and Mitani, 2002). Hunting was defined whenever one or more individuals chased monkeys in the forest canopy and until all hunters returned to the ground or captured a monkey (Boesch and Boesch-Achermann, 2000; Samuni et al., 2018a; Watts and Mitani, 2002). Although, border patrols, intergroup encounters and hunting are predominantly male behaviours, in Taï both sexes regularly participate in hunting and intergroup conflict (Boesch and Boesch-Achermann, 2000; Samuni et al., 2018a, 2017), with females participating in over 90% of intergroup interactions, and actively hunting together with males or more rarely in all-female sub-groups.

2.3. Urine sample collection and analysis

We collected every urine sample possible of the focal subjects, from leaf litter using a plastic pipette, and immediately stored the cryo vials containing the urine in a thermos can with frozen cool packs. For every urine sample we prioritized the analysis of cortisol (10–100 µl urine) and creatinine (20 µl urine). In case a minimum volume of 350 µl of urine was obtained, we additionally analyzed oxytocin. For oxytocin analysis, while in the field and shortly after urine collection, we transferred a pre-defined volume of urine (200–1000 µl using a 1 ml Eppendorf pipette) into a second cryo vial containing 100 µl of 0.5 N H_3PO_4 (Samuni et al., 2017) to prevent hormone degradation. Thus, fewer samples were available for the analysis of oxytocin in comparison to cortisol. Upon arrival in camp, and within 12 h of collection, samples were transferred into liquid nitrogen. All urine samples collected were shipped frozen on dry ice to the Laboratory of Endocrinology at the Max Plank Institute for Evolutionary Anthropology in Leipzig, Germany, where we stored them at −80 °C until analysis.

We measured urinary cortisol levels using liquid chromatography–tandem mass spectrometry (LC–MS/MS) and examined via MassLynx (version 4.1; QuanLynx-Software). Steroid extraction followed Hauser et al., (Hauser et al., 2008), and cortisol levels were quantified using the internal standard of prednisolone (see SI). We extracted and analyzed oxytocin samples following the protocol described in Samuni et al. (Samuni et al., 2017), using the commercially available enzyme immunoassay kit (Assay Designs, Catalog No. 901-153A-0001).

The secretion patterns of cortisol and oxytocin into urine differ. The estimated clearance rate of oxytocin into urine after an event is approximately 15–60 min (Amico et al., 1987), whereas for cortisol it is approximately 2–4.8 hrs (Bahr et al., 2000). As the clearance rate for cortisol is a suggested minimum rate obtained from a single individual in a captive setting, here, we used a more conservative time window of 1–5 hrs. Due to the shorter time window of oxytocin in comparison to cortisol, again, fewer oxytocin samples were collected within the time window of hormone secretion after a specific event. Thus, we were able to analyze 241 oxytocin (14.17 ± 12.41 samples/ subject) samples and 470 cortisol samples (31.33 ± 24.58 samples/ subject) in relation to intergroup conflicts. For cortisol, we as well analyzed urine samples collected during hunting and control days, resulting in an overall 1701 cortisol samples from 18 subjects (mean ± sd: 94.5 ± 79.03 samples/ subject).

2.4. Statistical analysis

We fitted Linear Mixed Models (LMM (Baayen, 2008)) with Gaussian error structure and identity link function to investigate: a) the effect of group hunting, territorial border patrols and intergroup encounters on urinary cortisol levels (cortisol event-day model); and b) the effect of out-group risk during intergroup interactions on urinary cortisol (cortisol outgroup-risk model) and oxytocin (oxytocin outgroup-risk model) levels. Urinary cortisol and oxytocin levels were expressed as pg/mg creatinine (see SI) and log-transformed.

2.4.1. Cortisol event-day model (a)

In the 'cortisol event-day model', we investigated urinary cortisol samples collected during days (hereafter referred to as 'event days') in which individuals participated in: i) hunting (308 samples during 47 days); ii) territorial border patrol without direct contact with rivals (148 samples during 19 days); and iii) intergroup encounters (322 samples during 46 days). As we expected intergroup encounters to be a stronger stressor than border patrols, if on a given day the two co-occurred we categorized the day as intergroup encounter. We compared the three types of 'event days' to control days in which no hunting, border patrols or intergroup encounters occurred (923 samples during 140 days). To be able to reliably estimate the effect of the test predictor on urinary hormone levels, we controlled for other factors previously shown to influence cortisol (e.g., time of day, seasonality; see SI). Furthermore, we included the random effects of subject and event identity to account for non-independent or unbalanced sampling of certain subjects or events disproportionally affecting hormone levels, thus avoiding pseudo-replication (Baayen, 2008). In addition, we added random slopes (see SI).

In the first analysis we used values from all samples collected on 'event days', irrespective of sample collection timing relative to the event. This is because it has previously been shown that chimpanzee participation in hunting and intergroup conflict is associated with anticipatory high urinary cortisol levels (Sobolewski, 2012). Nevertheless, we fitted additional models accounting for sample collection timing relative to the event, and for the estimated clearance rate of cortisol into urine. Thus, similar to Sobolewski (2012), we tested HPA axis activity before (anticipation) and during a particular event.

2.4.2. Post-hoc cortisol event-day model

As post-hoc analysis we fitted an additional model, that account for sample collection timing in relation to the event (pre- or during- event). Otherwise, this model is identical to the 'cortisol event-day model' with regard to the fixed and random effect structure. To do so, we assigned samples collected either before or up until 1 h after the start of the event as pre samples, and samples that were collected after the first hour of the event and up until 5 h after the end of the event as event samples. We did not include post samples (n = 45), defined as samples collected more than 5 h after the end of the event. This approach resulted in a test predictor with six degrees of freedom: control (n = 923), pre-hunt (n = 187), hunt (n = 98), pre-border patrol (n = 84), border patrol (n = 57), pre-intergroup encounter (n = 135), intergroup encounter (n = 172). The same definitions of pre, event, or post cortisol samples were applied in the subsequent analyses.

2.4.3. Cortisol and oxytocin out-group risk models (b)

Finally, to investigate secretion patterns of urinary cortisol and oxytocin, we tested the effect of 'out-group risk' on hormone levels. We evaluated out-group risk by distinguishing increasing levels of out-group contact during intergroup interactions (Table 1). Since the two hormones differ in their clearance rate, we were unable to directly correspond values of one hormone to the other. As such, we could not test the causal effect of one hormone on the other in a single analysis. To overcome this, we fitted two comparable analyses in which we investigated the effect of 'out-group risk' on hormone levels during the same competitive intergroup interactions, and compared the secretion patterns of the two hormones. We assigned oxytocin samples according to the different levels of out-group contact experienced by subjects, that occurred within the excretion time window for oxytocin (15–60 min). We defined oxytocin urine samples collected before the start of the intergroup conflict event as pre, and more than 1 h after the end as post. Furthermore, we expected the proximity to border areas to be a psychological stressor to chimpanzees (Samuni et al., 2017; Sobolewski, 2012), thus to influence cortisol. Furthermore, we expected increased

Table 1
Sample sizes per definition of varying degrees of out-group risk during intergroup conflict, used in the cortisol and oxytocin out-group risk LMMs.

Out-group risk	Cortisol		Oxytocin	
	sample	subject	sample	subject
Patrol - neither direct nor indirect contact with rivals	57	10	56	8
Rivals detected - direct (e.g., vocalizations) or indirect signs of rivals	125	12	55	11
Vocal encounter - in-group members and rivals participating in vocal exchange	19	9	38	12
Contact encounter - visual and/or physical contact with rival chimpanzees	31	10	24	11
Pre - before or up until 1 hr after the start of the event	208	14	35	12
Post - more than 5 hrs after the end of the event	30	7	28	12

sub-group size (chimpanzees live in a dynamic fission-fusion social system) to potentially buffer cortisol secretion during intergroup conflicts. Consequently, we included border proximity and sub-group size as test predictors in the cortisol outgroup-risk model. In the oxytocin outgroup-risk model we included sub-group size and border proximity as control predictors, as we do not expect a direct influence of the two on urinary oxytocin levels (Samuni et al., 2017).

In contrast to our previous study (Samuni et al., 2017), where we demonstrated that intergroup conflict participation is associated with high oxytocinergic system activity. Here, we examine variation in oxytocin secretion in relation to different degrees of out-group risk during chimpanzee intergroup conflict. As per the 'cortisol event-day model', we also included control predictors, random effects and random slopes in both the cortisol and oxytocin out-group risk models (see SI).

2.4.4. Models design and validations

We used R (version 3.4.4 (R Core Team, 2016)) to fit all models with the *lmer* function of the R package 'lme4' (Bates et al., 2015). We compared the fit of all full models with those of a respective null model lacking only the test predictors, but otherwise being identical to the respective full model in all other terms, using a likelihood ratio test. Prior to fitting the models, we checked for deviations from model assumptions, collinearity, and assessed model stability (see SI). All data used to fit the models are available upon request.

3. Results

Urinary cortisol levels expressed as pg/mg creatinine were at daily means (mean ± sd) of 46.98 ± 41.59 for control days, 43.13 ± 31.74 for hunting days, 57.69 ± 40.76 for border patrol days and 64.57 ± 49.33 for intergroup encounter days. When investigating the effect of the type of event day on urinary cortisol levels we found a significant effect (full-null model comparison likelihood ratio test: $\chi2 = 21.899$, df = 3, $P < 0.001$; Table 2; Fig. 1). Specifically, intergroup encounter days but not border patrol days had a significant positive effect on urinary cortisol levels in comparison to control (encounter vs. control: z-value = 4.578, $P < 0.001$; patrol vs. control: z-value = 1.047; P = 0.295; Table S1). Conversely, we found significant higher cortisol levels during both intergroup encounter and border patrol days in comparison to hunting days (encounter vs. hunt: z-value = 5.202, $P < 0.001$; patrol vs. hunt: z-value = 2.218; P = 0.026; Table S1). Cortisol levels during intergroup encounter days were only marginally higher than border patrol days (z-value = 1.814; P = 0.069). Hunting days had a significant negative effect on urinary cortisol levels in comparison to control days (z-value = -2.054; P = 0.040). Furthermore, the non-significant interaction between type of event day and sex (P = 0.714; see SI) indicated that these effects were similar for both males and females across all types of event days. Urinary cortisol levels showed a typical circadian diurnal decline ($P < 0.001$), and seasonal variation (likelihood ratio test comparing the full model with one lacking the two terms accounting for season: $\chi2 = 52.375$, df = 2, $P < 0.001$). Moreover, we found a decrease in cortisol levels with an increase in sub-group size (P = 0.045) and higher cortisol levels in South group in comparison to East group (P = 0.011). We also found a strong trend towards higher urinary cortisol levels in older individuals, and in the presence of parous fully-tumescent females. Sex and dominance rank had no significant effect on urinary cortisol levels.

As a post-hoc analysis we investigated the effect of pre- or event samples on cortisol levels during the same events as the 'cortisol event-day model' (full-null model comparison likelihood ratio test: $\chi2 = 46.517$, df = 6, $P < 0.001$). Specifically, we found a significant positive effect of intergroup encounter compared with pre-intergroup encounter (encounter vs. pre-encounter: z-value = 3.273; P = 0.001; Table S2; Fig. S1) and control (encounter vs. control: z-value = 5.675; $P < 0.001$). There was no significant effect between hunting to pre-hunting (z-value = 0.896; P = 0.370) or control (z-value = -1.594; P = 0.110), or between border patrol to pre- border patrol (z-value = 0.819; P = 0.412) or control (z-value = 1.634; P = 0.102). In terms of anticipatory increase, we found a significant positive effect of pre- intergroup encounter, but not pre- border patrol, compared with control (z-value = 2.730; P = 0.006). We as well found a significant negative effect of pre- hunting compared with control (z-value = -2.533; P = 0.011).

Subsequently, when testing the effect of out-group risk, full-null model investigations revealed significance for the cortisol, but not for the oxytocin model (likelihood ratio test: cortisol-risk model - $\chi2 = 67.921$, df = 7, $P < 0.001$; oxytocin-risk model - $\chi2 = 6.091$, df = 5, P = 0.297; Tables 3 and 4). Specifically, we found that the degree of out-group risk had a significant effect on urinary cortisol levels but not on urinary oxytocin levels (Fig. 2). Moreover, cortisol levels significantly decreased with an increase in sub-group size (Estimate ± SE: -0.103 ± 0.029; P = 0.001) and increased the closer chimpanzees were to border areas (Estimate ± SE: 0.102 ± 0.041; P = 0.028). We also found a circadian diurnal decline ($P < 0.001$) and seasonal variation ($\chi2 = 14.053$, df = 2, $P < 0.001$) in urinary cortisol levels. Model results revealed a trend towards higher urinary cortisol levels in older individuals (P = 0.089) and South group (P = 0.089). The linear and non-linear terms of latency, sex, dominance rank and presence of fully tumescent parous females had no effect on cortisol levels. Furthermore, the highest degree of out-group risk of contact intergroup encounters, had significant positive effects on urinary cortisol levels in comparison to all other types of out-group risk ($P < 0.001$; Table S3). In addition, we also found higher urinary cortisol levels after detecting rival groups in comparison to pre territorial activity (P = 0.017), and patrol without rivals' detection (P = 0.028). The effect of out-group risk on urinary cortisol levels was comparable across males and females, indicated by the non-significant interaction terms between out-group risk and sex (P = 0.822; see SI).

4. Discussion

Key goals of this study were to investigate the effects of a) intergroup conflict participation on HPA axis activity, and of b) out-group risk during chimpanzee intergroup competition on HPA and oxytocinergic system activities, and by this to determine if oxytocinergic

Table 2
LMM (cortisol event-day model) testing the effect of hunting, border patrols and intergroup encounters on urinary cortisol levels (log transformed). N = 1701 samples, 18 subjects.

Term	Coded level	Estimate	SE	CI_{lower}	CI_{upper}	Chisq	P
Intercept		3.394	0.128	3.142	3.655	–	–
Test predictor levels							
Event day (control)	**Hunting**	**−0.154**	**0.075**	**−0.307**	**−0.006**		
	Border patrol	**0.110**	**0.105**	**−0.091**	**0.302**	**21.899**	**< 0.001**
	Intergroup encounter	**0.316**	**0.069**	**0.189**	**0.452**		
Control predictors							
Time of day [a]		**−0.369**	**0.023**	**−0.416**	**−0.322**	**46.056**	**< 0.001**
Sub-group size[b]		**−0.035**	**0.015**	**-0.066**	**-0.005**	**4.011**	**0.045**
Reproductive status (non-cycling)	Fully-tumescent	0.103	0.053	0.003	0.206	3.594	0.058
Group (East)	**South**	**0.296**	**0.104**	**0.087**	**0.522**	**6.440**	**0.011**
Age[c]		0.105	0.052	0.004	0.211	3.781	0.052
Sex (female)	Male	0.224	0.128	−0.034	0.481	2.877	0.090
Dominance rank[d]		0.043	0.031	−0.020	0.106	1.742	0.187
Sine (Julian date)		**−0.341**	**0.045**	**−0.426**	**−0.249**	**52.433**	**< 0.001**
Cosine (Julian date)		**−0.151**	**0.057**	**−0.255**	**−0.029**		

The reference categories are indicated in parenthesis. Statistically significant results ($P \leq 0.05$) appear in bold.
[a−d]z-transformed, mean ± SD of the original variables: [a]727.41 ± 181.43 (range 370–1104 min), [b]8.9 ± 4.16, [c]19.03 ± 8.48, [d]0.64 ± 0.24 (range 0–1 with 1 being the highest social rank in each sex category).

system activity during intergroup conflict is triggered by exposure to a stressor.

4.1. HPA axis activity during chimpanzee intergroup conflict

We found increased HPA axis activity in both males and females on days in which individuals participated in territorial activity in comparison to control days, but only if direct or indirect contact with rivals occurred (intergroup encounters). In support of previous study (Sobolewski, 2012), we found increased HPA axis activity both prior (anticipatory) and during intergroup encounters. In contrast with one of our predictions, chimpanzee participation in border patrols, a territorial activity without any rival contact, thought to be energetically demanding as it involves extended travel periods and reduced feeding time (Amsler, 2010), had no clear effect on HPA-axis activity in comparison to control days. Furthermore, both the linear and non-linear terms of latency from sample collection to the start of the intergroup conflict, accounting for potential physical effort, had no significant effect on cortisol release. These findings suggest that in the context of intergroup conflict, psychological stressors may have a stronger effect on HPA axis activity than physical ones. We also found lower urinary cortisol levels during hunting days in comparison to border patrols, intergroup encounters and control days, despite assumed increased physical activity during hunting behavior.

4.2. Cortisol release likely due to psychological more than energetic stress exposure

The proximity to the border area, as a measure of potential risk, had a positive influence on cortisol levels, indicating that a psychological stressor (potential distance to rivals) increases HPA axis activity in chimpanzees. Furthermore, while controlling for seasonality and presence of fully-tumescent parous females, we found lower urinary cortisol levels with larger sub-group sizes in both cortisol analyses, supporting a previous study in chimpanzees (Sobolewski, 2012). Although competition and conflict are suggested to escalate with an increase in the size of sub-groups (Muller, 2002), our findings emphasize the beneficial aspect of wider association patterns on physiology. In another chimpanzee study, individuals that engaged in an intergroup encounter with non-bond partners compared to those with a social bond partner present showed higher urinary cortisol levels, suggesting that the presence of a predictable coalition partner buffers the stress response (Wittig et al., 2016), likely as a result of coalitionary support. It thus may be that social support is more predictable in larger association groups, resulting in social buffering and reduced HPA axis activity. For instance, large association groups and increased support may reduce the risk of predation during every day activities (Boesch, 1991), and reduce the risk of injury during intergroup encounters as suggested by the 'imbalance of power' hypothesis (Wrangham, 1999). It may also be that lower cortisol levels associated with an increase in sub-group size is confounded with variation in food availability, as increased food availability may lead to larger sub-groups and lower cortisol levels (Muller and Wrangham, 2004). Nonetheless, by controlling for seasonality we expect to account for some of the known seasonal variation in food availability in Taï, which follows a sinusoidal curve (Wessling et al., 2018). Thus, here, the effect of sub-group size on cortisol levels is likely independent from food availability. Strength in numbers, a mechanism that may regulate and facilitate access to benefits of intergroup

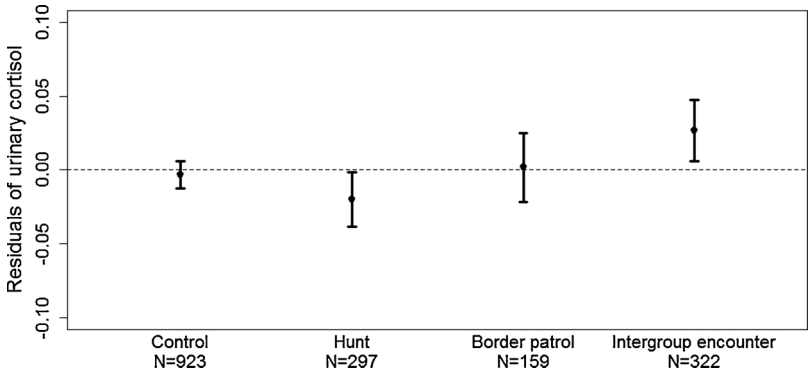

Fig. 1. The effect of days in which chimpanzees engaged in hunting, border patrols or intergroup encounters on urinary cortisol levels. The y axis represents the residuals of log-transformed cortisol levels obtained from a model identical to the 'cortisol' LMM but lacking the term 'event day'. Shown is the mean cortisol and SE across type of day.

Table 3
LMM (cortisol out-group risk model) testing the effect of out-group risk (i.e., degree of contact with rivals), sub-group size and border proximity on urinary cortisol levels (log-transformed). N = 470 samples of 15 subjects.

Term	Coded level	Estimate	SE	CI_{lower}	CI_{upper}	Chisq	P
Test predictor levels							
Intercept		3.531	0.185	3.154	3.916	–	–
	Patrol	**−0.011**	**0.083**	**−0.184**	**0.138**		
Out-group	**Rivals detected**	**0.176**	**0.074**	**0.024**	**0.316**		
Risk (Pre)	**Vocal encounter**	**0.151**	**0.129**	**−0.118**	**0.405**	**45.132**	**< 0.001**
	Contact encounter	**0.706**	**0.112**	**0.477**	**0.904**		
	Post	**−0.030**	**0.152**	**−0.360**	**0.270**		
Sub-group size [a]		**−0.103**	**0.029**	**−0.158**	**−0.047**	**10.602**	**0.001**
Proximity to the border [b]		**0.102**	**0.041**	**0.023**	**0.180**	**4.811**	**0.028**
Control predictors							
Time of day [c]		**−0.429**	**0.069**	**−0.566**	**−0.282**	**27.157**	**< 0.001**
Latency [d]		0.009	0.089	−0.164	0.190	0.010	0.921
Latency^2		−0.009	0.027	−0.062	0.042	0.111	0.739
Group (East)	South	0.289	0.165	−0.059	0.636	2.889	0.089
Sex (female)	Male	0.297	0.191	−0.101	0.727	2.315	0.128
Dominance rank [e]		−0.014	0.041	−0.109	0.079	0.102	0.749
Age [f]		0.172	0.077	0.012	0.339	2.895	0.089
Reproductive status (non-cycling)	Full-tumescence	−0.043	0.090	−0.222	0.134	0.224	0.636
Sine (Julian date)		**−0.298**	**0.075**	**−0.442**	**−0.157**	**14.053**	**< 0.001**
Cosine (Julian date)		**−0.109**	**0.116**	**−0.344**	**0.117**		

The reference categories are indicated in parenthesis. Statistically significant results (P ≤ 0.05) appear in bold.
[a−f]z-transformed, mean ± SD of the original variables: [a]10.15 ± 4.03, [b]69.21 ± 26.28 (range 5–99), [d]140.14 ± 197.30 (range -422-635 min), [e]0.62 ± 0.25 (range 0–1 with 1 being the highest social rank in each sex category), [f]19.03 ± 8.40.

conflict (Wrangham, 1999), is as well a potential regulator of HPA axis activity during chimpanzee intergroup conflict.

A study on a different chimpanzee population showed increased HPA axis activity in male chimpanzees on intergroup conflict days both before and during the intergroup activity (Sobolewski, 2012), however without distinguishing if an encounter with rivals occurred. Intergroup encounters are expected to be a greater psychological stressor than border patrols as they involve contact with an out-group and are thus riskier. Distinguishing HPA axis activity separately for border patrols and intergroup encounters, is an important step for disentangling the effects of psychological versus physical stressor exposure during intergroup conflicts on cortisol secretion, an approach which was previously unexplored. Therefore, it remains to be tested whether border patrols and encounters are independently associated with cortisol secretion at other sites. The same study demonstrated an increase in cortisol levels before and during hunting activity, and concluded that the activation of the HPA axis and production of cortisol may facilitate physically demanding activities in chimpanzees (Sobolewski, 2012). Whether discrepancies between our and Sobolewski's results are explained by forest structure or degree of coordination (Samuni et al., 2018a; Watts and Mitani, 2002) which may alter energy expenditure during hunting, or by patterns of meat sharing which in Taï are suggested to involve long-term social factors rather than harassment (Samuni et al., 2018b), remains to be tested.

4.3. Oxytocin secretion is not influenced by stressor exposure

Previous studies in Taï chimpanzees demonstrated increased oxytocinergic system activity both as an anticipatory response to and during territorial border patrols and intergroup encounters, and hunting in comparison to controls (Samuni et al., 2017, 2018a). Here, we did not find an increase in cortisol levels after border patrols or hunting, hinting that oxytocin secretion during these group activities occurs independently from cortisol release. Furthermore, although border proximity influenced urinary cortisol levels, we did not find an effect of proximity to the border on urinary oxytocin levels.

Table 4
LMM (oxytocin out-group risk model) testing the effect of out-group risk (i.e., degree of contact with rivals) on urinary oxytocin levels (log-transformed). N = 241 samples, 17 subjects.

Term	Coded level	Estimate	SE	CI_{lower}	CI_{upper}	Chisq	P
Test predictor levels							
Intercept		2.823	0.424	2.008	3.643	–	–
	Patrol	**0.275**	**0.178**	**−0.082**	**0.643**		
Out-group	**Rivals detected**	**0.183**	**0.177**	**−0.197**	**0.573**		
Risk (Pre)	**Vocal encounter**	**0.407**	**0.205**	**0.027**	**0.810**	**6.091**	**0.297**
	Contact encounter	**0.250**	**0.231**	**−0.193**	**0.753**		
	Post	**−0.034**	**0.203**	**−0.438**	**0.384**		
Control predictors							
Sub-group size [a]		−0.003	0.069	−0.142	0.135	0.002	0.968
Proximity to the border [b]		0.125	0.079	−0.039	0.275	2.422	0.120
Affiliation occurrence (no)	yes	0.125	0.101	−0.068	0.330	1.439	0.230
Group (East)	**South**	**−0.385**	**0.180**	**−0.747**	**−0.020**	**4.129**	**0.042**
Sex (female)	Male	−0.259	0.149	−0.565	0.027	2.952	0.086
Dominance rank [c]		−0.082	0.056	−0.183	0.028	1.934	0.164
Data collection period (first)	**Second**	**1.253**	**0.201**	0.855	1.647	**30.130**	**< 0.001**

The reference categories are indicated in parenthesis. Statistically significant results (P ≤ 0.05) appear in bold.
[a−c]z-transformed, mean ± SD of the original variables: [a]9.70 ± 3.82, [b]78.89 ± 23.46 (range 5–99), [c]0.63 ± 0.26 (range 0–1 with 1 being the highest social rank in each sex category).

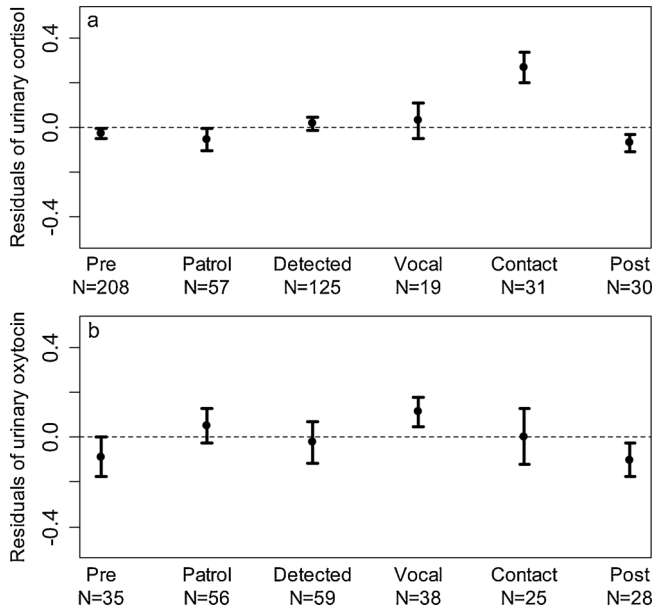

Fig. 2. The effect of varying degrees of out-group risk on urinary **a)** cortisol and **b)** oxytocin levels. The y axis represents residuals of log-transformed **a)** cortisol or **b)** oxytocin levels obtained from models identical to the 'cortisol outgroup-risk' or 'oxytocin outgroup-risk' LMM, but lacking the test predictor 'out-group risk'. Shown is the mean hormone values and SE across out-group risks. Note, although not shown here, oxytocin levels of "patrol", "detected", "vocal" and "contact" are significantly higher than non-social oxytocin control samples (Samuni et al., 2017).

To test the relation between activation patterns of cortisol and oxytocin levels we investigated the effect of varying degrees of 'out-group risk' on urinary hormone levels measured after the same behavioral events. In accordance with our predictions for independent endocrine activity we found an effect of 'out-group risk' on cortisol but not on oxytocin levels. Specifically, the highest degree of assumed out-group risk during visual and/or physical encounters with rival groups had the strongest effect on cortisol levels in comparison to other types of out-group risks but showed no higher influence on oxytocin secretion. Thus our results give no indication that exposure to a stressor, in this case intergroup conflict, is the main trigger of oxytocin release in large, measurable amounts, in chimpanzees. Oxytocin release during intergroup conflict (Samuni et al., 2017) is thus likely triggered by the social context associated with the stressor rather than exposure to the stressor itself.

To pursue the in-group out-group aspect further. Contact intergroup encounters with rivals do not only carry the highest risk of injury – or death, but also involve heightened aggressive behavior towards the out-group. Therefore, if oxytocin secretion is associated with aggressive behavior towards the out-group, we expected higher urinary oxytocin levels in association with rising degrees of out-group hostility. In contrast, we found comparable oxytocin secretion across varying degrees of out-group aggression. This result is in accordance with recent findings demonstrating dissociation between chimpanzee within group aggression and oxytocinergic activity (Preis et al., 2018), and is similar to human studies showing oxytocinergic system involvement in in-group cooperation and defensive (but not offensive) aggression against out-group (De Dreu and Kret, 2016). Our results highlight the potential stronger link between in-group cooperative and cohesive behavior, rather than out-group hostility, and oxytocinergic activity in male and female chimpanzees.

In this study we employed a non-invasive, non-experimental sampling methodology which limits our ability to infer causality between the oxytocinergic and HPA axis endocrine systems. However, whereas human studies of intergroup conflict are mainly focused on a single sex and restricted to laboratory settings, one of the strengths of this study is in observing naturally occurring intergroup interactions in wild living animals of both sexes, without unintentionally influencing the social contexts.

4.4. Oxytocin reactivity patterns, supporting theories, and future directions

Taken together, we did not find strong support for parallel activation of the oxytocinergic system and HPA activity. Whilst both urinary oxytocin and cortisol were higher than controls during intergroup encounters, peaks of urinary oxytocin levels did not coincide with peaks in urinary cortisol levels. Specifically, whilst urinary cortisol levels increased with out-group risk, urinary oxytocin levels did not. The 'social salience' hypothesis posits that oxytocin effects on behavior occur independent of valence, for instance by promoting aggression in response to unpredictable and threatening environments (Bartz et al., 2011; Shamay-Tsoory and Abu-Akel, 2016). A context such as intergroup encounter is highly unpredictable, involves substantial threat and out-group hostility, and acts as a stressor to male and female participants. Thus, in line with the 'social salience' hypothesis one would expect an association between oxytocin and increased out-group threat and aggression. Conversely, our results oppose predictions of the 'social salience' hypothesis as oxytocin secretion was not specifically influenced by exposure to increasing levels of risks nor to threatening circumstances, and did specifically increased in the context of out-group aggression.

Although not directly tested here, following the 'approach withdrawal' hypothesis, increased oxytocin secretion during intergroup competition may attenuate withdrawal related behaviours associated with physiological stress, for instance defection, in order to facilitate approach. Approach behavior is required for group cohesion and in-group support, vital components for winning encounters against rival groups (Wrangham, 1999). A mechanism that facilitates cooperation and cohesive participation such as the oxytocinergic system is thus likely to be adaptive. Endocrine systems commonly operate in synergy, and human studies found that in addition to oxytocin, the steroid hormone testosterone likely promotes in-group cooperation and bias, but as well out-group hostility and aggression (Reimers and Diekhof, 2015). It may be that testosterone and oxytocin jointly modulate these underlying components of group psychology not only in humans but also in chimpanzees. Future studies into the relation between testosterone and oxytocin activity in in-group out-group contexts seem promising in advancing our understanding of the mechanisms promoting in-group cooperation on one hand and out-group competition on the other.

4.5. Potential relation between the oxytocinergic system and HPA axis

Oxytocinergic system activation is associated with the cooperative behaviors of territorial border patrols, intergroup encounters, and hunting in Taï (Samuni et al., 2017, 2018a), but in other chimpanzee populations this association has not been tested. It may be that comparable cortisol levels between controls and hunting and border patrols in Taï chimpanzees reflect an attenuate effect of the oxytocinergic system on the stress response (Heinrichs et al., 2003). During encounters with rivals, fast mobilization of glucose is essential in order to regulate the fight-or-flight response (McEwen, 2007; Sapolsky, 2002), thus maintaining high cortisol levels whilst exposed to stressor is expected to be adaptive. Conversely, when encounters with rivals are unlikely, or when hunting activity ends, a mechanism that rapidly downregulates HPA axis activity, and hence conserves energy, such as is thought to occur with the oxytocinergic system in certain contexts, is likely to be under positive selective pressure. As opposed to hunting and border patrols, intergroup encounters often involve multiple interactions with rivals over extended periods of time, each having the potential of activating the stress response. Thus, it may be that the

oxytocinergic system is effective in downregulating HPA axis activity when social support is given (Smith and Wang, 2014; Wittig et al., 2016) only after the stressor has terminated. The majority of studies investigate the social buffering effect of oxytocin after a single stressor exposure (for example: Heinrichs et al., 2003; Seltzer et al., 2010; Smith and Wang, 2014). We suggest that a future avenue for studies should be to examine the effectiveness of the oxytocinergic system, both in magnitude and time scale, in downregulating HPA axis activity during multiple stressors.

5. Conclusion

The relation between oxytocin and cortisol secretion patterns was a previously unexplored topic in wild non-human animals. Overall, we showed that intergroup encounters, but not border patrols or hunting, are associated with elevated cortisol levels in male and female chimpanzees. Finding a similar effect in both sexes underlines the fact that despite intergroup conflict participation is considered a male-led behavior, some of the proximate mechanisms involved in intergroup conflict operate similarly in both sexes. Furthermore, we showed no consistent relation between the degree of stress exposure during intergroup encounters and urinary oxytocin levels. Increasing degrees of out-group hostility influenced cortisol secretion, but were not associated with variance in oxytocin secretion which were similarly high across varying degrees of out-group risk and aggression. Thus, although oxytocinergic system activity is associated with chimpanzee in-group out-group interactions (Samuni et al., 2017), it is not specifically influenced by stressor exposure or the threatening environment, and is not associated with out-group aggression. These results oppose some of the predictions of the 'social salience' hypothesis, which states that oxytocinergic system activation is associated with increased stress and aggression. Taken together, our results support previous studies showing that oxytocinergic and HPA systems effects depend on the social context. Here, we investigated hormone secretion patterns in relation to specific events. The other side of the coin would be to explore how variation in hormone secretion may influence cooperative participation versus defection during costly social interactions, a promising future avenue.

Ethics

All methods used in this study were non-invasive and were approved by the Ministries of Research and Environment of Côte d'Ivoire, and Office Ivoirien des Parcs et Réserves. All aspects of the study comply with the ethics policy of both the Max Planck Society and the Department of Primatology of the Max Planck Institute for Evolutionary Anthropology, Germany, and the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

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Competing interests

The authors declare no competing interests.

CRediT authorship contribution statement

L. Samuni: Conceptualization, Methodology, Formal analysis, Software, Funding acquisition, Investigation, Visualization, Writing - original draft, Writing - review & editing. **A. Preis:** Formal analysis, Investigation, Funding acquisition, Writing - review & editing. **T. Deschner:** Conceptualization, Resources, Supervision, Validation, Writing - review & editing. **R.M. Wittig:** Conceptualization, Funding acquisition, Resources, Project administration, Supervision, Writing - review & editing. **C. Crockford:** Conceptualization, Funding acquisition, Resources, Project administration, Supervision, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.psyneuen.2019.02.007.

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