Tkaczynski, PJ, Behringer, V, Ackermann, CY, Fedurek, P, Fruth, B, Girard-Buttoz, C, Hobaiter, C, Lee, SM, Loehrich, T, Preis, A, Samuni, L, Zommers, Z, Zuberbuehler, K, Deschner, T, Wittig, RM, Hohmann, G and Crockford, C

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Journal of Human Evolution 147 (2020) 102869

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Patterns of urinary cortisol levels during ontogeny appear population specific rather than species specific in wild chimpanzees and bonobos

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ARTICLE INFO

Article history:
Received 9 October 2019
Accepted 3 August 2020
Available online 28 August 2020

Keywords:
Life history
Childhood
Development
Glucocorticoids
Hominin evolution

ABSTRACT

Compared with most mammals, postnatal development in great apes is protracted, presenting both an extended period of phenotypic plasticity to environmental conditions and the potential for sustained mother-offspring and/or sibling conflict over resources. Comparisons of cortisol levels during ontogeny can reveal physiological plasticity to species or population specific socioecological factors and in turn how these factors might ameliorate or exaggerate mother-offspring and sibling conflict. Here, we examine developmental patterns of cortisol levels in two wild chimpanzee populations (Budongo and Taï), with two and three communities each, and one wild bonobo population (LuiKotale), with two communities. Both species have similar juvenile life histories. Nonetheless, we predicted that key differences in socio-ecological factors, such as feeding competition, would lead to interspecific variation in mother-offspring and sibling conflict and thus variation in ontogenetic cortisol patterns. We measured urinary cortisol levels in 1394 samples collected from 37 bonobos and 100 chimpanzees aged up to 12 years. The significant differences in age-related variation in cortisol levels appeared population specific rather than species specific. Both bonobos and Taï chimpanzees had comparatively stable and gradually increasing cortisol levels throughout development; Budongo chimpanzees experienced declining cortisol levels before increases in later ontogeny. These age-related population differences in cortisol patterns were not explained by mother-offspring or sibling conflict specifically; instead, the comparatively stable cortisol patterns of bonobos and Taï chimpanzees likely reflect a consistency in experience of competition and the social environment compared with Budongo chimpanzees, where mothers may adopt more variable strategies related to infanticide risk and resource availability. The clear population-level differences within chimpanzees highlight potential intraspecific flexibility in developmental processes in apes, suggesting the flexibility and diversity in rearing strategies seen in humans may have a deep evolutionary history.

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https://doi.org/10.1016/j.jhevol.2020.102869

1. Introduction

Human life history is characterized by an extended juvenile dependence on and association with mothers and/or other caregivers relative to life span (Hill and Kaplan, 1999). In long-lived species, such as humans, most phenotypic plasticity occurs during development, with early life representing a particularly 'sensitive window' to adjust phenotypes to environmental conditions (Ellis et al., 2009). Indeed, the characteristically long development and juvenile dependence on mothers seen in humans is likely adaptively associated with prolonged brain growth and, concurrently, the acquisition of key motor skills, social competence, and knowledge required for survival into, and productivity during, adulthood (Hill and Kaplan, 1999). This long period of phenotypic plasticity during development may have been key for the radiation of humans as a species in numerous habitats and environments (Kuzawa and Bragg, 2012). However, one potential cost of this life history adaptation and extended period of high environmental sensitivity could be the accentuation of parent-offspring and sibling conflict, in which the reduction or termination of parental care is often associated with conflict between an infant's needs and the parent's level of investment in current rather than future reproductive opportunities or survival (Trivers, 1974).

On a proximate level, the hormonal stress response is one of the key ways organisms can adjust to environmental conditions and the energetic or psychological stressors associated with parent-offspring and sibling conflict over resources (Berger, 1979; Lee et al., 1991; Lee, 1996; Sapolsky et al., 2000; Tsigos and Chrousos, 2002; Trites and Donnelly, 2003; Mandalaywala et al., 2014; Wooddell et al., 2017; MacDougall-Shackleton et al., 2019). In primates, the hypothalamic-pituitary-adrenal (HPA) axis is a key component of the stress response via the release of cortisol, a glucocorticoid (GC), which stimulates gluconeogenesis for the adaptive redirection of energy and behavior to directly cope with stressors or to modulate energy balance to cope with subsequent stressors (Sapolsky et al., 2000; Tsigos and Chrousos, 2002; MacDougall-Shackleton et al., 2019). It is possible to quantify cortisol levels, and hence HPA axis activity, in blood plasma or indirectly via excreta, such as urine (Higham, 2016; Behringer and Deschner, 2017). Such monitoring of cortisol secretion throughout ontogeny can thus be a useful tool for identifying key periods of adjustment to environmental conditions, including physiological responses to parent-offspring and/or sibling conflict.

For mammalian species, an obvious source of mother-offspring conflict occurs during the process of weaning, i.e., the gradual transition of offspring from nutritional dependence on maternal milk to an adult diet, often culminating in complete nutritional independence for offspring (Humphrey, 2010). Later in ontogeny, with the onset of adolescence and assimilation into adult dominance hierarchies, individuals may again experience elevations in cortisol levels associated with increased received aggression, as well as the psychological and energetic demands of acquiring social support outside the mother-offspring dyad (Creel, 2001; Veenema, 2009). Therefore, a combination of energetic and social stressors associated with developmental transitions, such as weaning and increased social exposure, may be associated with elevated HPA axis activity.

To date, few studies have examined how cortisol levels vary throughout development in human children and other young primates. Captive monkey studies suggest blood cortisol levels peak during weaning and then decline before the onset of puberty (Castracane et al., 1981; Smail et al., 1982; Laudenslager et al., 1990). In a study focused on weaning in free-ranging rhesus macaques (*Macaca mulatta*), maternal rejection rates (e.g., denying offspring access to the nipple) during this period were positively associated with fecal GC concentrations in offspring (Mandalaywala et al., 2014). In contrast, in modern human children, salivary cortisol levels increase steadily with age and body mass (Kiess et al., 1995), with stronger elevations in cortisol levels occurring later in development during peer group formation and the onset of puberty (Shirtcliff et al., 2005; Gunnar et al., 2009).

Research on variation in cortisol levels during development in modern human children is largely limited to Western populations, wherein resource availability and medical support for child-rearing are comparatively abundant, potentially leading to reduced exposure to ecological stressors and mother-offspring conflict (Wudy et al., 2007). Ethical and practical considerations are likely to constrain future research efforts in children of other populations in which patterns of mother-offspring conflict and associated cortisol patterns may be more varied than existing data from Western children (Hens et al., 2011). Instead, direct interspecific and intraspecific comparisons of cortisol levels in appropriate nonhuman animal models enable the examination of physiological plasticity to species or population specific maternal strategies, ecological settings, and/or resource availability, particularly during periods of mother-offspring and/or sibling conflict.

In humans' closest living relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), the immature phase (incorporating infancy, i.e., dependency on maternal milk, and juvenility, namely, the period after weaning and before puberty; Bogin, 1999) occupies between 20% and 25% of the total life span, which is only a little less than in humans (approximately 27%), and is longer than the 17% of the life span estimated for large monkey species such as macaques or baboons (Harvey and Clutton-Brock, 1985; Robson and Wood, 2008; Walker et al., 2018). Observational and isotope studies of dental and fecal samples in wild *Pan* populations suggest that the dietary weaning process (the transition to nonmaternal milk nutrition) can begin in offspring as early as 2 years, but the behavioral weaning process (i.e., gradual cessation of suckling) can continue beyond nutritional dependence in both species, lasting in some cases until offspring are 5–6 years (Fahy et al., 2014; Bădescu et al., 2017; Lee et al., 2020; Samuni et al., 2020).

Postweaning, maternal provisioning of hard-to-access food, such as meat or honey, occurs intermittently in both chimpanzees and bonobos (Boesch and Boesch-Achermann, 2000; Hohmann, 2009; Wittig et al., 2014; Yamamoto, 2015; Samuni et al., 2018). Although the degree of alloparental care and support observed in human populations is typically absent in most *Pan* populations (Bădescu et al., 2016), postweaning food provisioning occurs and maternal associations lasting the entirety of ontogeny appear key for growth and development (Bründl et al., 2020; Samuni et al., 2020). Therefore, these long-term associations with and dependencies on mothers may make developmental transitions less extreme than that observed via cortisol levels in nonhominoid primates. Despite broad similarities in the societal structure (a high degree of fission-fusion dynamics, male philopatry), there are key differences between the two *Pan* species in terms of their socioecological environments. These may lead to differences in the nature of maternal rearing strategies and mother-offspring conflict, which may be reflected in cortisol secretion patterns. In our study, we use data from two different chimpanzee populations (Taï and Budongo), allowing us to compare the effect of these factors on cortisol levels during development not only between species but also between populations.

The 'terrestrial herbaceous vegetation (THV) hypothesis' proposes that the consistent and abundant availability of THV within the bonobo ecological range reduces feeding competition for this species, facilitating greater social cohesion than that observed in most chimpanzee populations, for which THV availability may be more seasonal or scarce in general (Wrangham, 1986; Furuichi,

2009). Disregarding the fact that the nutritional quality of THV is unlikely to support all the energetic needs of weaning or weaned individuals, it is possible that reduced feeding competition in general may make the transition to nutritional and social independence less difficult for young bonobos than for chimpanzees and thus reduce mother-offspring conflict during ontogeny. Furthermore, adult bonobos exhibit codominance between the sexes, with most females ranking higher than most males (Surbeck and Hohmann, 2013). In contrast, all male chimpanzees are dominant to adult females (Smuts, 1987; Wittig and Boesch, 2003). This species specific difference in dominance may lead to variation in the resource holding potential of certain chimpanzee and bonobo mothers, which in turn may lead to species-level differences in resources available directly or indirectly (good feeding spots in fruit trees, for example) to offspring (Nurmi et al., 2018). In both of our study chimpanzee populations, party sizes reduce during periods of low fruit availability (Newton-Fisher et al., 2000; Wittiger and Boesch, 2013), leading to greater variation in feeding competition and the social environment between seasons and over years. During periods of high feeding competition, the energetic stressors anticipated during dietary transitions such as weaning could become accentuated in chimpanzees as compared with bonobos.

Bonobo infant survival rates are higher than those observed in chimpanzees (Furuichi et al., 1998; Hill et al., 2001). Furthermore, infanticide by both males and females occurs in many chimpanzee populations (Wilson et al., 2014), but has not yet been observed in bonobos (Hohmann et al., 2019). Bonobos show tolerant intergroup relations, whereas chimpanzees are highly territorial (Samuni et al., 2017; Fruth and Hohmann, 2018; Lucchesi et al., 2020). There are also population-level differences in violence within chimpanzees (Wilson et al., 2014). Intragroup killing has not been reported in Taï chimpanzees (Wittig and Boesch, 2019), whereas intergroup infanticide is extremely rare (Boesch et al., 2008; Wilson et al., 2014). However, intracommunity killing and infanticide have been repeatedly reported in Budongo chimpanzees (Fawcett and Muhumuza, 2000; Wrangham et al., 2006; Lowe et al., 2019a), and Budongo females with young offspring adopt strategies of male avoidance (Lowe et al., 2019b). Taï females generally maintain high levels of gregariousness regardless of reproductive status (Wittiger and Boesch, 2013). Where mothers adopt asocial and avoidant strategies, this will reduce social exposure and competition for their offspring. However, mother-offspring conflict predicts that there are limits to the duration of maternal investment, during which mothers avoid males (Emery Thompson et al., 2016). Therefore, at some point, they must look for new reproductive opportunities and actively seek out males with which to socialize (Emery Thompson et al., 2016). This may lead to a sudden social exposure for their current offspring and increased stress levels. For bonobos, and potentially in Taï chimpanzees, wherein levels of gregariousness are relatively consistent, offspring will experience consistent levels of social exposure, which may reduce variation in stress across ontogeny.

In Gombe chimpanzees, mothers with sons tend to be more gregarious (Murray et al., 2014), and immature males are faster to socialize outside of the mother-infant dyad than females (Lonsdorf et al., 2014). Generally, among chimpanzee populations, males are more likely to receive aggression than females (Wilson et al., 2014). Therefore, we anticipated that socialization pressures for male chimpanzees would lead to higher weaning- and postweaning-associated cortisol levels as compared with female chimpanzees. In bonobos, males demonstrate lifelong preferences to associate with kin, especially mothers (Hohmann et al., 1999), and intragroup killings are yet to be reported in this species. Accordingly, we anticipated that reduced socialization challenges and the lower threat of violence would contribute to lower weaning-associated stress and limit sexual dimorphism in cortisol levels in young bonobos. Furthermore, given the described population differences in violence in chimpanzees, particularly toward immatures, we predicted higher social stress during weaning and later ontogeny in Budongo chimpanzees than in Taï chimpanzees.

2. Methods

2.1. Study site and subjects

Data on wild chimpanzees were collected at two separate field sites from two subspecies: Taï National Park, Côte d'Ivoire (5°52′N, 7°20′E; three communities: North, South, and East; *Pan troglodytes verus*; Wittig, 2018), and Budongo Conservation Field Station, Budongo, Uganda (2°03′N, 31°46′E; two communities: Sonso and Waibira; *Pan troglodytes schweinfurthii*; Hobaiter et al., 2017). Data on wild bonobos were collected at the LuiKotale field site, Democratic Republic of the Congo (02°46′S, 20°23′E; two communities: Bompusa East and Bompusa West; Hohmann and Fruth, 2003; Fruth and Hohmann, 2018).

Regular daily observations of subjects from Taï began with the North community in 1982 (North community: 1982–present; South community: 1993–present; East community: 2000–present; Boesch and Boesch-Achermann, 2000; Wittig, 2018). Regular daily observations of subjects from Budongo began in 1994 with the Sonso community (Reynolds, 2005) and in 2011 with the Waibira community (Samuni et al., 2014; Hobaiter et al., 2017). Members of the Bompusa West and East communities in LuiKotale have been habituated and followed since 2007 and 2015, respectively (Fruth and Hohmann, 2018). For all populations, we included individuals aged between 0 and 12 years in our study: although we specifically predicted elevations in cortisol levels associated with weaning and increased social exposure in each population, identifying these peaks requires a complete mapping of cortisol levels during ontogeny. For the Taï East, Taï South, Taï North, and Sonso communities, we had reliable information of the year and month of birth for the majority of individuals, and in case the day of birth was unknown, we assigned the 15th of the respective birth month as the day of birth. For certain older individuals from the more recently habituated individuals and communities (e.g., Waibira and Bompusa East), birth dates were estimated with an approximate accuracy of ±1 year based on established growth curves for both species (120 individuals with known ages; 17 individuals with estimated ages). Table 1 shows the distribution of samples across the different communities and demographics within each community.

2.2. Urine sample collection and cortisol analyses

During observations, we collected urine samples from individuals we could identify. We collected urine into 2 ml cryovials using plastic pipettes and then stored the samples in liquid nitrogen in camps at the earliest opportunity and always on the same day of the urination (i.e., within 14 h of collection). Urine sampling began in Taï in 2000, in Budongo in 2005, and in LuiKotale in 2008. The study data set includes samples collected up to and including August 2018. The samples were shipped to the Laboratory of Endocrinology at the Max Planck Institute for Evolutionary Anthropology, Germany, and remained frozen at a minimum of −20 °C until analysis.

We determined urinary cortisol levels via liquid chromatography-tandem mass spectrometry using Hauser et al.'s. (2008) method. We corrected cortisol levels using cortisol d4 as the internal standard. For each sample, we measured specific gravity (SG) using a refractometer (TEC, Ober-Ramstadt, Germany).

Table 1
Distribution of individuals and samples across the different study communities and species in the data set (1394 urine samples from 137 subjects).

Community	No. of male subjects	No. of female subjects	No. of male samples	No. of female samples	Mean (SD) samples per subject
Taï					
North	9	10	71	112	9.63 (7.57)
South	10	16	101	163	10.15 (8.50)
East	9	10	140	68	10.94 (12.31)
Budongo					
Sonso	11	14	129	267	15.84 (16.14)
Waibira	7	4	31	23	4.91 (3.91)
LuiKotale (bonobos)					
Bompusa East	7	7	40	32	5.14 (2.85)
Bompusa West	7	16	45	172	9.43 (4.88)

SG values were used to correct cortisol measurements for variation in water content in the urine using the formula outlined by Miller et al. (2004):

$$\text{SG corrected cortisol} = \text{raw hormone concentration} \times \frac{\left(SG_{\text{population mean}} - 1.0\right)}{\left(SG_{\text{sample}} - 1.0\right)}$$

The population means were derived from the samples included in this analysis (i.e., rather than a mean of the total population including adult individuals). The SG population mean was 1.021 for Taï, 1.019 for Budongo, and 1.014 for LuiKotale.

We excluded samples collected during a period when study subjects displayed symptoms of sickness or injury because cortisol levels may increase during such periods (Barton, 1987; McIntosh, 1987; Muehlenbein and Watts, 2010). If a subject's mother died during the study period, all samples collected after this death were also excluded from the data set as maternal separation during early life affects cortisol levels in primates (Sánchez et al., 2005; Feng et al., 2011). Furthermore, our main study aim was to examine cortisol levels in relation to weaning, which is clearly affected by maternal loss. In total, 1394 samples were included in the study: 289 samples from 37 bonobo individuals and 1105 from 100 chimpanzee individuals (450 samples from Budongo chimpanzees and 655 samples from Taï chimpanzees; Table 1). Figure 1 illustrates the density of sampling at different ages in each population.

The data set analyzed during the present study is available to be downloaded from Figshare (https://doi.org/10.6084/m9.figshare.11980095.v1).

2.3. Ethical approval

All methods were noninvasive and were approved by the Institut Congolaise pour la Conservation de la Nature, Ministries of Research and Environment of Côte d'Ivoire, Office Ivoirien des Parcs et Réserves, and the Ugandan Wildlife Authority. 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 (https://www.eva.mpg.de/primat/ethical-guidelines.html), for the ethical treatment of nonhuman primates.

2.4. Statistical analysis

Data processing and statistical analyses were performed using R v. 3.4.4 (R Core Team, 2016). To investigate species and sex differences during ontogeny of HPA axis activity in young chimpanzees and bonobos, we fitted a linear mixed model (Baayen, 2008) with Gaussian error structure ('age variation model'). The dependent variable was the SG-corrected cortisol concentration (ng/ml SG) of urine samples. We included as test predictors population (coded with three levels to differentiate between LuiKotale bonobos, Taï, and Budongo chimpanzees), sex, age, and their two- and three-way interactions. As we anticipated a weaning-related peak in cortisol levels for both species, we included the cubic function of age (and thus also the linear and quadratic functions) to effectively model cortisol levels across ontogeny.

Urinary cortisol concentrations vary diurnally, typically decreasing throughout the waking day (Muller and Lipson, 2003); therefore, time of collection was included as a control variable. We controlled for circannual variation in cortisol levels attributable to seasonal variation in rainfall, temperature, and humidity (Wessling et al., 2018) by converting Julian dates into a circular variable and including its sine and cosine into the model (Stolwijk et al., 1999; Wessling et al., 2018). We z-transformed the age and collection time variables (Schielzeth, 2010). To account for repeated measures from individuals, different offspring of the same mother, and individuals within certain communities, we included individual identity, mother identity, and community as random effects (Baayen, 2008). We included a maximum random slope structure when sufficient variation within a fixed effect was present (Schielzeth and Forstmeier, 2009; Barr et al., 2013): this resulted in random slopes for the age variables, seasonality variables, and collection time being included within individual identity, community, and mother identity.

In a second model ('weaning category model'), we specifically tested whether the latter stages of weaning, a key period of mother-offspring conflict, were associated with elevations in urinary cortisol levels. In the absence of direct behavioral or nutritional data related to the weaning stage, we subset our initial data set to individuals that had younger siblings. Using demographic birth data, we then assigned samples for each of these individuals to one of the four categories depending on when the sample was collected: 'early ontogeny,' 'year before the birth of a younger sibling,' 'year after the birth of a younger sibling,' and 'late ontogeny.' While it is still possible for an individual chimpanzee or bonobo to be carried or nursed by its mother after the birth of a sibling (personal observations; Lee et al., 2020), this point represents a clear change in maternal resource availability to an older sibling, i.e. our study individuals in this model. After subsetting our data to include only individuals with younger siblings born within our sampling period, our data set included 1025 samples: 252 from 28 bonobos, 511 from 48 Taï chimpanzees, and 262 from 9 Budongo chimpanzees.

We fit a linear mixed-effect model with the dependent variable of SG-corrected cortisol concentration of urine samples and a main predictor of the weaning category with four levels (early ontogeny, year before sibling birth, year after sibling birth, and late ontogeny) in interaction with species and sex. As age is correlated with the weaning stage, we did not include age as a predictor in this model. However, the rest of the model was the same in

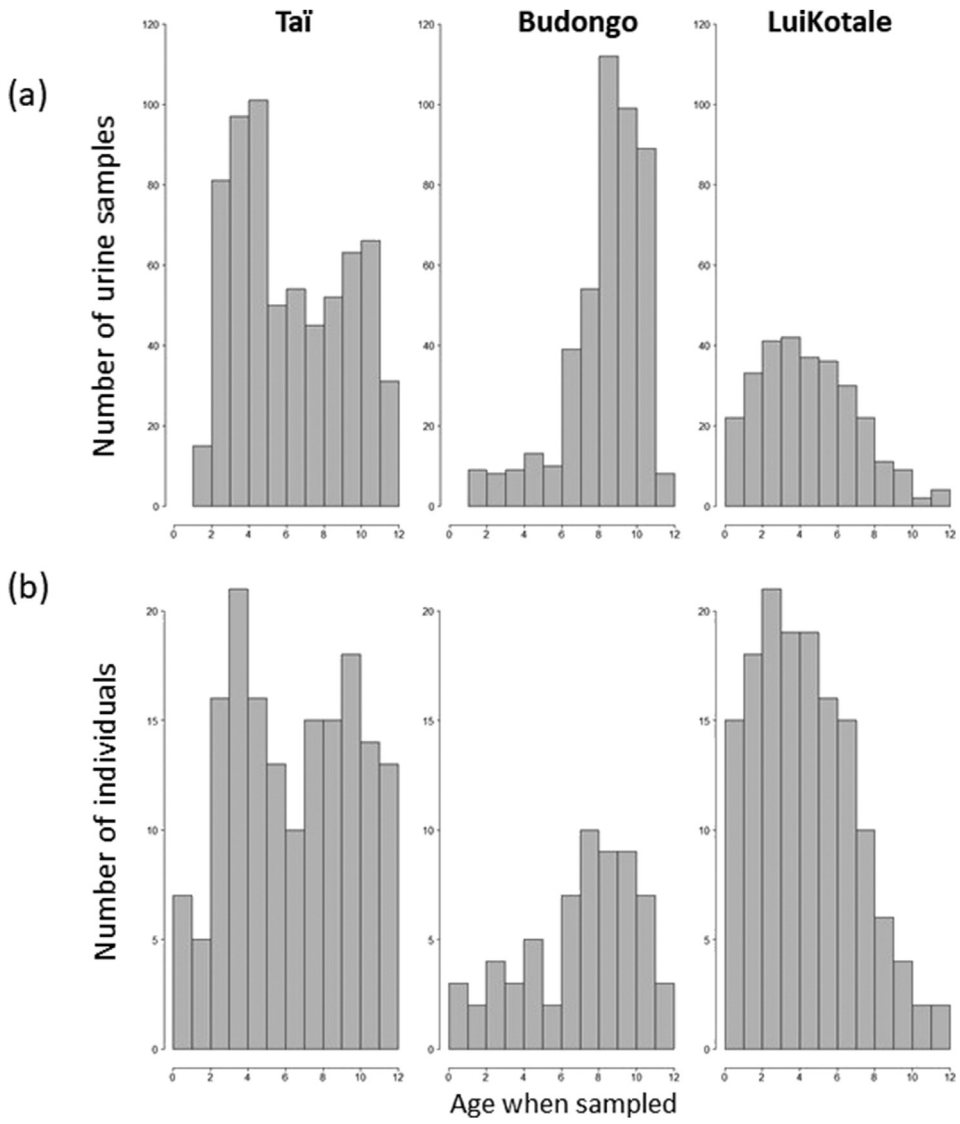

Figure 1. Frequencies of samples collected (a) and individuals sampled across age (b) in Taï (western chimpanzees), Budongo (eastern chimpanzees), and LuiKotale (bonobos) during our study period.

structure as our first model, therefore including collection time and seasonal variation control variables. Again, we included random effects of individual identity, community and mother identity, and a maximal random slope structure. This resulted in random slopes of collection time and seasonality variables included within individual identity, within community, and within mother identity; random slopes of the weaning category within individual and mother identity; and random slopes of sex within mother identity.

We tested for collinearity issue between our predictor variables using the function VIF from the R package 'car' (Fox et al., 2011). Collinearity was not an issue between these variables (all VIF < 1.22).

Before fitting the models, we checked the distribution of the response and of all predictors. As a result, we log transformed SG-corrected cortisol levels to achieve a more symmetrical distribution. We used the function lmer of the R package 'lme4' (Bates et al., 2015) to fit the full models, as well as a null model lacking the test predictors. We compared the fit of the full models relative to the null models using a likelihood-ratio test (Forstmeier and Schielzeth, 2011). Interspecies comparisons in absolute urinary cortisol levels provide a limited explanatory value as there are potential species differences in physiological factors such as receptor densities and the metabolism of cortisol into urine (MacLarnon et al., 2015). Therefore, we do not consider the differences in absolute cortisol levels, only the patterns in cortisol levels in each population across age or the weaning stage in our respective models. Thus, to test our 'age variation model,' the null model was identical to the full model but lacked the three-way interaction between age (linear, quadratic, and cubic terms), sex, and species. Owing to an insufficient sample size within each weaning category in each population, fitting a three-way interaction between the weaning stage, sex, and population in our 'weaning category model' was not possible. Instead, we tested the effects of the weaning category in each population in separate models (one model per population); in each model, the null model was identical to the full model but lacked the weaning category. For the reduced Budongo data set, all samples were in the 'late ontogeny' category, meaning it was impossible to test the effects of the weaning stage in this population.

We verified the assumptions of normally distributed and homogeneous residuals by visual inspection of qq-plots and residuals

plotted against fitted values. We dropped nonsignificant interactions (i.e., $p < 0.05$) and obtained individual p-values using the drop1 function in R, by systematically dropping each fixed effect from the model one at a time (Barr et al., 2013) and comparing the respective reduced model lacking the individual fixed effects with the full model using a likelihood-ratio test. Model stability was determined by excluding the levels of the random effects (individual and mother identity and community) sequentially one at a time and comparing estimates derived from these subsets with those derived from the full data set. This evaluation revealed no problems with overly influential levels of the random effects within either model. Confidence intervals were calculated from parametric bootstraps using the bootMer function of the 'lme4' package. Effect sizes (R^2; explained by the fixed effects [marginal-R^2m] and by the fixed and random effects [conditional-R^2c]; Nakagawa and Schielzeth, 2013) were calculated using the r.squaredGLMM function from the 'MuMIn' package (Bartoń, 2018). For the 'weaning category' models, we performed post hoc Tukey's test to compare cortisol levels between the different weaning categories using the 'multcomp' package (Hothorn et al., 2008).

3. Results

3.1. Age variation model

For the 'age variation model,' the full vs. null model comparison was significant (likelihood-ratio test: $\chi^2 = 26.733$, df = 9, $p = 0.001$), suggesting an effect of age, species, and/or sex on urinary cortisol levels. Removing nonsignificant interactions, we found a significant effect of the two-way interaction between the cubic term of age and species/population on urinary cortisol levels (linear mixed model, $p = 0.020$; Fig. 2; Table 2). Taï chimpanzees and LuiKotale bonobos demonstrated comparatively stable cortisol levels during ontogeny, whereas Budongo chimpanzee cortisol levels declined during early development and rose gradually from 6 to 9 years, before a small decline in the latter two years of development (Fig. 2; Table 2).

3.2. Weaning category model

LuiKotale bonobo interbirth intervals (IBIs) ranged between 2.20 and 8.56 years, with a mean (±SD) IBI of 5.18 (±1.21) years; Taï chimpanzee IBIs ranged between 3.41 and 7.73 years, with a mean (±SD) IBI of 5.00 (±1.06) years; and Budongo chimpanzee IBIs ranged between 3.97 and 6.99 years, with a mean (±SD) IBI of 5.82 (±0.96) years.

As our age variation model did not identify significant sex differences in cortisol levels in each species, we did not include an interaction between the weaning category and sex in either the Taï or LuiKotale full models. The full vs. null model comparison was not significant for Taï (likelihood-ratio test: $\chi^2 = 6.092$, df = 3, $p = 0.107$) but was significant for LuiKotale (likelihood-ratio test: $\chi^2 = 11.947$, df = 3, $p = 0.008$), indicating significant variation in cortisol levels between the different weaning categories in our bonobo population, but not in Taï chimpanzees (Table 3). The post hoc analysis revealed that cortisol levels in LuiKotale bonobos were higher in the 'year after the birth of a younger sibling' ($\beta = 0.238$, $p = 0.001$) and 'late ontogeny' ($\beta = 0.138$, $p = 0.045$) category than in the 'early ontogeny' category (Table 4; Fig. 3).

4. Discussion

Despite their close phylogenetic relatedness to each other (Prüfer et al., 2012), chimpanzees and bonobos exhibit striking and well-explored morphological, physiological, behavioral, and sociological differences (Doran, 1993; Stanford, 1998; Behringer et al., 2014a, b, 2016; Hare and Wrangham, 2017; Surbeck et al., 2017a, b; Furuichi, 2019). Although our results revealed differences in ontogenetic cortisol levels between Budongo chimpanzees and LuiKotale bonobos, the contrasts between Taï chimpanzees and LuiKotale bonobos were less clear. Budongo chimpanzees showed a marked decline in cortisol levels early in ontogeny, followed by a gradual increase between the ages of 6 and 9 years, and a decline in later ontogeny. Meanwhile, LuiKotale bonobos and Taï chimpanzees had comparatively stable cortisol levels, with gradual increases in the latter stages of ontogeny clearest among bonobos. Contrary to our predictions, we observed no sex differences in either species/population. Although significant variation in cortisol levels between weaning stages was observed in the LuiKotale bonobos, this was not distinguishable from the age effect of gradually increasing cortisol levels in this population.

The general pattern of declining cortisol levels during early ontogeny in the Budongo chimpanzees of our study is broadly akin to that observed in a recent study on Kanyawara chimpanzees (another eastern chimpanzee population; Sabbi et al., 2019). Here, the authors tentatively related this decline in cortisol levels to concurrent increases in the secretion of the adrenal androgen dehydroepiandrosterone sulfate (DHEAS), a hormone which is implicated in physical, neurological, and cognitive development, but is also thought to inhibit GC secretion (Sabbi et al., 2019). As the authors describe, the functional coordination of cortisol and DHEAS levels remains to be confirmed, and this association would not necessarily explain the species/population differences we observe in our study as bonobos also demonstrate increases in DHEAS during development in a pattern broadly similar to that of chimpanzees (Behringer et al., 2012; Sabbi et al., 2019). Given that our observed patterns are not specific to a particular species, it suggests that socioecological factors have greater impact than phylogenetic influences. Specifically, we propose that population-level variation in ontogenetic cortisol patterns reflects physiological plasticity to variation in maternal association patterns driven by population-level variation in socioecological factors.

4.1. Resource availability and feeding competition

Our results are in keeping with our predictions based on the level and consistency of feeding competition between the species and populations. The THV hypothesis (Wrangham, 1986; Hohmann et al., 2006; Furuichi, 2009) suggests bonobos can be more consistently gregarious owing to the availability of reliable, if not nutrient-rich, resources. This is not to say that feeding competition is absent in bonobos; indeed, recent studies in adult LuiKotale bonobos demonstrate that feeding competition influences behavior (Nurmi et al., 2018) and can affect access to key nutrients such as protein (Oelze et al., 2016), while in captive bonobos, direct competition over monopolizable foods can lead to short-term elevations in cortisol levels (Hohmann et al., 2009). Nevertheless, occupying a habitat with comparably reliable nutritional resources may result in a consistent experience of feeding competition throughout ontogeny and thus relatively stable cortisol levels in LuiKotale bonobos.

Feeding competition and resource availability affect association patterns in both Budongo and Taï chimpanzees (Newton-Fisher et al., 2000; Wittiger and Boesch, 2013). Taï chimpanzees have been characterized as more consistently gregarious than most of the other chimpanzee populations, which may be a result of greater resource abundance and/or greater predation risk (Boesch, 1991; Riedel et al., 2011; Wittiger and Boesch, 2013). The group sizes in Taï are also comparatively small compared with many other

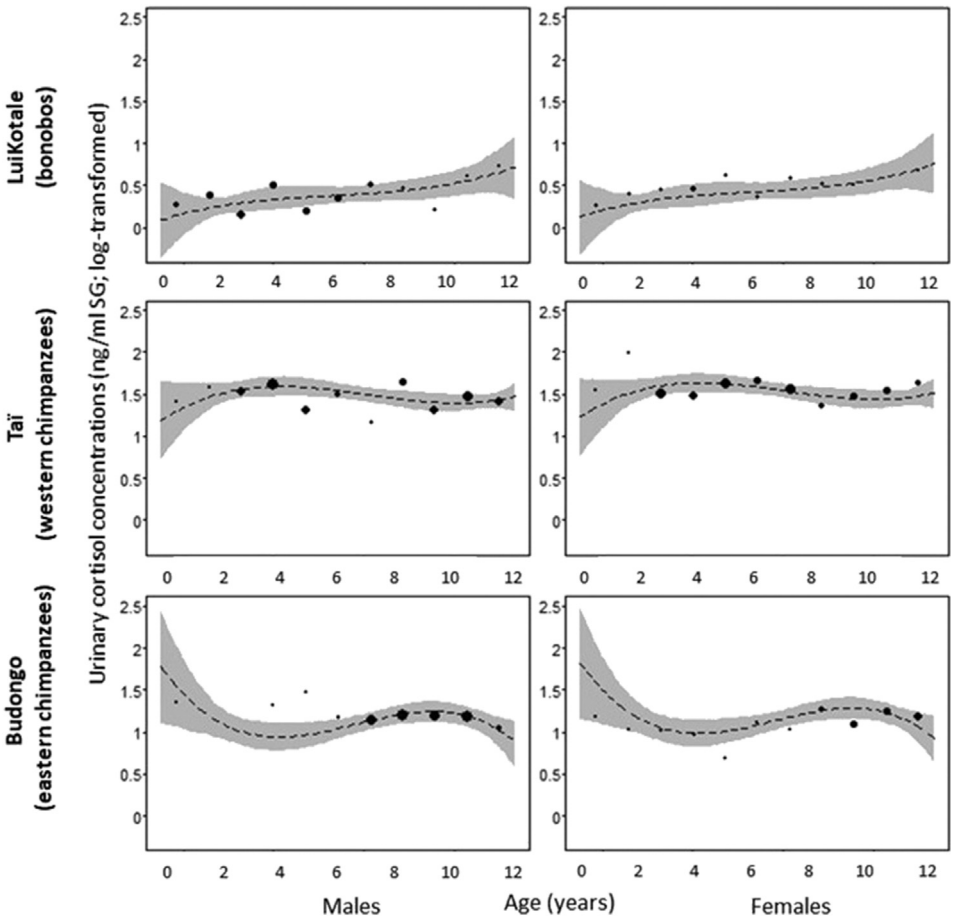

Figure 2. Age-related changes in specific gravity-corrected urinary cortisol concentrations (ng/mL specific gravity [SG]; log-transformed) in Budongo and Taï chimpanzees and LuiKotale bonobos. The plot is divided into populations and sex categories. Each point is scaled as per the sample number for that age category (see Table 1 and Fig. 1 for sample sizes). The shaded gray areas represent the 95% confidence interval ranges around the regression lines (dotted line) for each population-sex plot.

Table 2
Linear mixed-effect model results investigating the effects of sex, species, and age on urinary cortisol concentrations (n = 1394 samples); $R^2M = 0.616$, $R^2C = 0.726$.

Term	Reference category	Estimate (SE)	95% CI	χ^2 (df)	p
Intercept		0.404 (0.046)	0.313, 0.502	—	—
Sex	Female	0.043 (0.027)	−0.009, 0.097	1.995 (1)	0.158
Species/population	LuiKotale bonobo			—	—
Budongo chimpanzees		0.714 (0.062)	0.585, 0.842	—	—
Taï chimpanzees		1.099 (0.054)	0.979, 1.220	—	—
Age	—	0.070 (0.087)	−0.124, 0.255	—	—
Age^2	—	0.028 (0.040)	−0.059, 0.109	—	—
Age^3	—	0.026 (0.040)	−0.060, 0.113	—	—
Age: species/population	LuiKotale bonobo			—	—
Age: Budongo chimpanzees		0.196 (0.108)	−0.063, 0.467	—	—
Age: Taï chimpanzees		−0.221 (0.095)	−0.443, 0.002	—	—
Age^2: Species/population	LuiKotale bonobo			—	—
Age^2: Budongo chimpanzees		−0.060 (0.050)	−0.174, −0.056	—	—
Age^2: Taï chimpanzees		−0.038 (0.046)	−0.141, 0.057	—	—
Age^3: Species/population	LuiKotale bonobo			7.786	0.020
Age^3: Budongo chimpanzees		−0.151 (0.051)	−0.278, −0.031	—	—
Age^3: Taï chimpanzees		0.027 (0.044)	−0.080, 0.128	—	—
Collection time	—	−0.168 (0.016)	−0.198, −0.134	19.024	<0.001
Sine (Julian date)	—	−0.016 (0.034)	−0.082, 0.051	62.731 (41)	0.016
Cosine (Julian date)	—	0.013 (0.034)	−0.060, 0.079		

chimpanzee populations, including Budongo, potentially limiting intragroup feeding competition (Wittig and Boesch, 2019). Again, as with LuiKotale bonobos, this does not imply that feeding competition or seasonal effects are absent in Taï. Indeed, in adult Taï chimpanzees, cortisol levels vary seasonally (Wessling et al., 2018), and females directly compete for food resources in food patches, whereas in other populations, females may be less gregarious and occupy different areas within a territory to avoid direct competition for resources (Wittig and Boesch, 2003). Therefore, young Taï chimpanzees, like young LuiKotale bonobos, may undergo a more

Table 3
Linear mixed-effect model results investigating the effects of the weaning category on urinary cortisol concentrations in Taï chimpanzees ($n = 511$ samples; $R^2M = 0.220$, $R^2C = 0.445$) and LuiKotale bonobos ($n = 252$ samples; $R^2M = 0.359$, $R^2C = 0.387$).[a]

Term	Reference category	Estimate (SE)	95% CI	χ^2 (df)	*p*
Taï chimpanzees					
Intercept	—	1.542 (0.077)	1.364, 1.700	—	—
Weaning category	Early ontogeny			6.093 (3)	0.107
Year before sibling birth		0.147 (0.080)	−0.042, 0.333	—	—
Year after sibling birth		0.019 (0.089)	−0.163, 0.207	—	—
Late ontogeny		−0.026 (0.072)	−0.175, 0.134	—	—
Sex	Female			0.559	0.455
Male		−0.007 (0.040)	−0.098, 0.093	—	—
Collection time	—	−0.177 (0.023)	−0.224, −0.132	10.948 (1)	0.001
Sine (Julian date)	—	−0.034 (0.042)	−0.119, 0.050	38.559 (41)	0.580
Cosine (Julian date)	—	0.029 (0.036)	−0.042, 0.106		
LuiKotale bonobos					
Intercept	—	0.222 (0.042)	0.139, 0.313	—	—
Weaning category	Early ontogeny			11.947 (3)	0.008
Year before sibling birth		0.087 (0.071)	−0.053, 0.219	—	—
Year after sibling birth		0.238 (0.074)	0.091, 0.371	—	—
Late ontogeny		0.138 (0.053)	0.034, 0.241	—	—
Sex	Female			3.072 (1)	0.080
Male		0.096 (0.051)	−0.013, 0.195	—	—
Collection time	—	−0.190 (0.023)	−0.234, −0.144	7.286 (1)	0.007
Sine (Julian date)	—	−0.107 (0.040)	−0.188, −0.023	12.564 (23)	0.961
Cosine (Julian date)	—	0.056 (0.032)	−0.012, 0.124		

[a] The full vs null model comparison was nonsignificant for the Taï chimpanzees.

Table 4
Post hoc Tukey's test results examining variation in cortisol levels between different weaning categories in Luikotale bonobos ($n = 272$ samples).

Levels compared	Estimate (SE)	z value	*p*
Early ontogeny − year before sibling birth	0.088 (0.071)	1.230	0.601
Early ontogeny − year after sibling birth	0.238 (0.074)	3.219	0.001
Early ontogeny − late ontogeny	0.138 (0.053)	2.596	0.045
Year before sibling birth − year after sibling birth	0.151 (0.088)	1.716	0.308
Year before sibling birth − late ontogeny	0.051 (0.072)	0.707	0.892
Year after sibling birth − late ontogeny	−0.100 (0.075)	−1.342	0.529

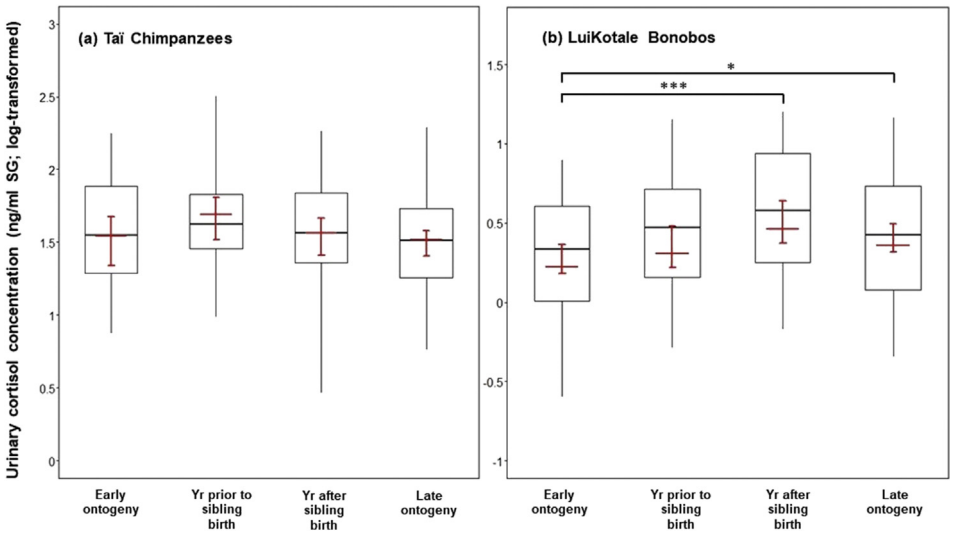

Figure 3. Variation in specific gravity-corrected urinary cortisol concentrations (ng/mL specific gravity; log-transformed) between weaning categories in Taï chimpanzees (a) and LuiKotale bonobos (b). The boxes illustrate the 25% and 75% quartiles, the horizontal thick lines within the boxes represent the median, and the whiskers from the boxes represent the 10% and 90% deciles. The model predictions are represented by the red error bars, illustrating the predicted mean and 95% confidence intervals.

consistent experience of feeding competition during development and, therefore, more stable ontogenetic cortisol levels.

For Budongo chimpanzees, the fruits of fig (*Ficus*) trees are a key food resource (Newton-Fisher, 1999), which becomes markedly less abundant during the dry seasons (Tweheyo and Lye, 2003). In Budongo, a strong reliance on fig fruits for nutrition may result in a more competitive environment, particularly during seasonal shortages. This may exaggerate the stress associated with dietary

transitions such as weaning or later in ontogeny during integration into dominance hierarchies when competition-related aggression given and received may increase. Although we found no clear evidence that the weaning phase itself was a period of elevated stress in Taï chimpanzees or LuiKotale bonobos, more data are required to test this in young Budongo chimpanzees. Cortisol levels in Budongo chimpanzees do begin to gradually rise from the ages of 5–6 years (the mean IBI for subjects in this population), which may reflect increasing experience of feeding competition concurrent within increasing nutritional independence from maternal provisioning.

To accurately examine an effect of nutritional or energetic stress on variation in cortisol levels in young *Pan* individuals, one could directly relate behavioral data reflecting feeding competition to physiology. Specifically, one could compare if rates of feeding, feeding-related displacement and aggressions, and general activity rates differ between *Pan* populations at different ages and then examine how variation in these behavioral variables relates to elevations in cortisol levels. Using urinary C-peptide concentrations, it would also be possible to examine how these behavioral data relate to energy balance (Deschner et al., 2008; Emery Thompson et al., 2009; Girard-Buttoz et al., 2011; Surbeck et al., 2015).

4.2. Population density and violence

In *Pan*, population density (the number of individuals per km^2) influences intergroup competition and encounter frequency, making it a major predictor for rates of violence and killings, especially intergroup infanticide in different populations (Wilson et al., 2014). In Budongo, a *Pan* population with a comparatively high population density (9.2 individuals per km^2; Wilson et al., 2014), infanticide is a prominent cause of infant mortality, whereas for LuiKotale bonobos (1.3 individuals per km^2; Wilson et al., 2014), this risk is apparently absent (Wilson et al., 2014; Hohmann et al., 2019), and for Taï chimpanzees (1.7 individuals per km^2; Wilson et al., 2014), infanticide is extremely rare (Boesch et al., 2008). However, adult male bonobos sometimes harass immature individuals using considerable physical force, and the probability of being exposed to male harassment increases when mothers give birth to another infant (Hohmann et al., 2019). This increase in male aggression would offer a plausible explanation for the increase in urinary cortisol levels in the years after the birth of a sibling, but more specific sampling in the context of such interactions is required to test this assumption.

Intragroup infanticide across chimpanzee populations occurs early in offspring ontogeny, and typically in Budongo, not after the first 3 months of life (Lowe et al., 2019a). Therefore, mothers living in populations with a high population density and associated risk of infanticide can adopt short-term male and large party avoidance strategies to minimize this risk. These maternal strategies have most clearly been demonstrated in Budongo and Kanyawara chimpanzees (Otali and Gilchrist, 2006; Lowe et al., 2019b), both of which exhibit similar ontogenetic patterns in cortisol levels. These maternal strategies may lead to an initial isolation from social stressors for their offspring. However, the threat of violence from nongroup members, particularly in Budongo and Kanyawara communities, is not limited to infant chimpanzees (Wilson et al., 2014). Maintaining social isolation in the core of the territory may be difficult; therefore, avoiding males may require sacrificing the safety of the group and occupying isolated parts of the territory, which is not strategic in the long term as it could increase exposure to predators or intergroup violence (Wrangham et al., 2007). For Kanyawara mothers, it takes around two years after birth for association rates with males to reach approximate equivalence with nonmothers (Otali and Gilchrist, 2006). This delayed and gradual social exposure may create novel physiological and psychological challenges for offspring in populations such as Budongo, and therefore, clearer increases in cortisol levels later in ontogeny as compared with Taï chimpanzees and LuiKotale bonobos.

For bonobos and Taï mothers, the low risk of infanticide for their offspring may reduce pressure to avoid large parties and males during early ontogeny and lead to generally fewer protective behaviors being required throughout development. Indeed, a recent study found that young bonobos in LuiKotale spend more time at greater distances from their mothers than young Gombe (eastern) chimpanzees, suggesting a generally more relaxed, less protective maternal style in bonobos (Lee et al., 2020). LuiKotale mothers are also more likely than Gombe mothers to carry their offspring at later stages of development (Lee et al., 2020). These bonobo mothers may be able to invest energetically for longer in offspring (carrying for longer) because of consistent resource availability and lower costs to ensure infant survival than the costs incurred by chimpanzee mothers in certain populations. These chimpanzee mothers instead are required to develop potentially energetically costly, protective rearing strategies. We propose that in LuiKotale bonobos and Taï chimpanzees, consistency in social exposure derived from consistent levels of gregariousness, likely due to reduced food competition, contributes to consistency in cortisol levels across ontogeny. Reduced food competition is expected owing to reduced seasonality in food availability combined with lower population densities compared with Budongo and Kanywara populations. Further behavioral data on association rates and specific maternal behaviors in both Taï and Budongo chimpanzees are required to confirm this.

In Taï and LuiKotale, feeding competition, intragroup infanticide, and intergroup violence may be less severe threats than in Budongo. However, these two populations, and the mothers within them, face predation pressures that have become largely absent in most other *Pan* populations (Boesch, 1991; D'Amour et al., 2006; Wood et al., 2017), including in Budongo. Therefore, the comparatively stable levels of gregariousness demonstrated by Taï and LuiKotale mothers may manifest not only from benign low levels of competition and violence but also as larger groups offer better protection against predation. In Budongo and other populations where *Pan* predators are absent, mothers may have more flexibility in rearing strategies and association patterns, which is additionally advantageous if population densities and resource availability heighten competition.

5. Conclusions

Our results suggest that within *Pan*, population-level differences in ontogenetic patterns of cortisol levels are clearer than species-level differences, although further intraspecific, between-population comparisons are required to confirm this, particularly comparisons with other western chimpanzee and bonobo populations. Nevertheless, the population-level differences in ontogenetic processes in our study add to growing evidence of influential intraspecific diversity in behavior and physiology among populations in apes (Potts, 2013; Kühl et al., 2019). Developmental plasticity is likely to have influenced human niche expansion (Kuzawa and Bragg, 2012), while great apes have limited habitat variation. Our results suggest that, on a physiological level, chimpanzees, and potentially bonobos, can adjust to variable socio-ecological and developmental settings. Therefore, identifying other elements of plasticity that differentiate humans from apes would facilitate our understanding of the selection pressures on plasticity during human evolution.

We propose that population differences in feeding competition, population density, and related lethal risk posed by conspecifics and/or predators variably affect maternal association patterns and

thus the social environment and experience of immature *Pan* individuals, resulting in variation of cortisol levels across development. The hormonal stress response is adaptively dynamic, allowing organisms to adjust to heterogeneous environments and circumstances (Sapolsky et al., 2000; Tsigos and Chrousos, 2002; MacDougall-Shackleton et al., 2019). Testing our hypotheses using our proposed combinations of observations and physiological markers could illustrate how endocrinological flexibility to socioecological factors facilitates development in hominins. Much of our current knowledge about cortisol levels during ontogeny in humans is limited to Western populations (Wudy et al., 2007), yet numerous studies have revealed great diversity in rearing strategies in extinct and extant human populations (Konner and Worthman, 1980; Blurton Jones, 1993; Wright and Schwarcz, 1998; Mays, 2003; Kennedy, 2005; Clayton et al., 2006; Eerkens and Bartelink, 2013; Joannes-Boyau et al., 2019). Determining whether different socioecological settings have driven different rearing styles and associated cortisol levels across extant nonhuman ape and human populations will help our understanding of the variable nature of development and childhood during hominin evolution and the socioecological pressures that have shaped them.

Author contributions

V.B. and P.J.T. conceived the study; P.J.T., P.F., T.D., Z.Z., L.S., S.M.L., A.P., C.G.-B., C.Y.A., and T.L. collected data; G.H., T.D., L.S., C.H., K.Z., C.C., B.F., and R.M.W. provided long-term data; V.B., P.J.T., G.H., T.D., L.S., C.C., and R.M.W. helped design the study; P.J.T. performed the statistical analyses; T.D. oversaw the laboratory analyses; P.J.T. wrote the first draft of the manuscript; all authors contributed to subsequent editing, with notable contribution and discussion from C.C., T.D., G.H., and V.B.

Competing interests

None of the authors have competing interests to report.

Acknowledgments

In the Democratic Republic of Congo, we thank the Institut Congolais pour la Conservation de la Nature (ICCN) for issuing permits to collect and export urine samples and the staff of the LuiKotale Bonobo Project for contributing the collection of samples and long-term records. We thank the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, the Ministère de Eaux et Fôrests in Côte d'Ivoire, the Office Ivoirien des Parcs et Réserves, the Institut Congolais pour la Conservation de la Nature (ICCN), the Uganda Wildlife Authority, and the Uganda National Council for Science and Technology for permitting the study. In Côte d'Ivoire, we are grateful to the Centre Suisse de Recherches Scientifiques en Côte d'Ivoire and the staff members of the Taï Chimpanzee Project for their support. In Uganda, we thank the management and staff of the Budongo Conservation Field Station. We are indebted to the efforts of many field and research assistants who contributed data to this project. We are extremely grateful for the work conducted in the laboratory of Tobias Deschner in Max Planck Institute of Evolutionary Anthropology, Leipzig, Germany, specifically the efforts of Róisín Murtagh, Vera Schmeling, Janette Gleiche, and Jared Cobain. We also thank Roger Mundry for advice on the statistics. Finally, we thank David Alba and three anonymous reviewers for helpful comments and feedback throughout the review process. P.J.T., C.C., and R.M.W. were supported by the European Research Council (ERC; grant agreement no. 679787). L.S. was supported by the Minerva Foundation, C.Y.A. received funding from the LSB Leakey Foundation, Subvention Egalité (University of Neuchâtel, Switzerland), and Fonds des Donations (University of Neuchâtel, Switzerland). S.M.L. received funding from the Leakey Foundation, George Washington University, and the Wenner-Gren Foundation. Core funding for the Taï Chimpanzee Project was provided by the Max Planck Society since 1997 and currently via the Evolution of Brain Connectivity Project. Long-term funding for the LuiKotale Bonobo Project comes from the Centre for Research and Conservation of the Royal Zoological Society of Antwerp, the Leakey Foundation, Liverpool John Moores University, and the Max Planck Society.

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