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Wild bonobo and chimpanzee females exhibit broadly similar patterns of behavioral maturation but some evidence for divergence

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Abstract

Objectives: Primates exhibit variation in rates of growth and development. Variation in female growth and development across ape species appears to be explained by the Ecological Risk Aversion Hypothesis (ERAH). Indeed, existing data on variation in somatic growth and reproductive maturation between humans' closest living ape relatives, bonobos and chimpanzees, appear to be consistent with this hypothesis. However, existing data on behavioral maturation between the two species appear to contradict this hypothesis. We present novel behavioral data on infant and juvenile females from wild populations of both species in order to further evaluate predictions of the ERAH as it relates to the speed of behavioral maturation.

Materials and methods: We analyzed 3 years of behavioral data on 17 female bonobos (<8 years of age) from LuiKotale, Democratic Republic of the Congo and 40 years of behavioral data on 30 age-matched female chimpanzees from Gombe, Tanzania. We compared the timing of (a) the attainment of independence from mothers and (b) the development of social skills using the following proxies: proximity between females and their mothers and the time that females spent engaged in eating, suckling, social play, social grooming, and riding on their mothers.

Results: We did not find species differences in the proportion of time that females spent in contact with their mothers or engaged in eating, suckling, social play, or social grooming. Female bonobos spent more time riding on their mothers than did female chimpanzees. Female bonobos spent more time at distances greater than 5 m from their mothers during the ages of 3–8 years, but females did not differ during the ages of 0–3 years.

Discussion: Behavioral maturation is largely similar between females of the two species based on the ages and proxies considered herein. We propose alternative explanations for the differences that we found in proximity and riding that do not invoke differences in underlying rates of maturation.

KEYWORDS

development, ecological risk aversion, infanticide, *Pan*, self-domestication

1 | INTRODUCTION

Primates in general, and great apes in particular, exhibit protracted periods of immaturity when compared to most other mammals (Harvey & Clutton-Brock, 1985; Robson & Wood, 2008; Stearns, 2000; van Schaik & Isler, 2012). However, a growing body of data demonstrates considerable variation in the timing of maturation across primate species (Altmann & Alberts, 2003; Galbany et al., 2017; Garber & Leigh, 1997; Kappeler, 1996; Leigh & Bernstein, 2006; Leigh & Shea, 1996; Robbins & Robbins, 2018; Stoinski, Perdue, Breuer, & Hoff, 2013; van Noordwijk et al., 2018). Among the great apes, this variation appears to be explained within the context of the Ecological Risk Aversion Hypothesis (ERAH) (Breuer, Hockemba, Olejniczak, Parnell, & Stokes, 2009; Galbany et al., 2017; McFarlin et al., 2013; Stoinski et al., 2013), which posits a relationship between ecological risk and growth rates (Janson & van Schaik, 1993). When starvation risk is high, usually in frugivorous species that face intense intraspecific feeding competition, offspring should grow slowly to reduce energetic needs per unit time. When the risk of starvation is lower, usually in folivorous species that experience relaxed intraspecific feeding competition, offspring should grow faster to minimize the risk of predation. The ERAH may be especially relevant for understanding variation in female life history strategies given the high metabolic costs of pregnancy and lactation, such that delays in response to ecological risk extend beyond physical growth to other components of maturation (Janson & van Schaik, 1993).

Early studies of body weight growth among captive apes support predictions of the ERAH, showing that more folivorous gorillas (*Gorilla gorilla gorilla*) attain adult body weight at earlier ages than more frugivorous bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*) (Leigh & Shea, 1996). These differences are indeed most pronounced between females. More recent studies provide additional support for the ERAH by characterizing variation in growth rates across gorilla species: wild populations of eastern mountain gorillas (*Gorilla beringei beringei*) that rely heavily on folivorous resources—even more so than other gorilla species (Robbins & Robbins, 2018)—attain adult body length at earlier ages than more frugivorous western lowland gorillas (*G. gorilla gorilla*) (Breuer et al., 2009; Galbany et al., 2017). Inter-ape variation in additional components of maturation also conform to expectations of the ERAH: orangutans (*Pongo* spp.) experience what appears to be the highest ecological risk among apes due to their reliance on mast fruiting (Knott, 2001), and thus wean and begin reproducing at the latest ages (van Noordwijk et al., 2018). At the other extreme, eastern mountain gorillas at Karisoke appear to experience the least ecological risk among apes due to their highly folivorous diet, and thus wean and begin reproducing at the earliest ages (Robbins & Robbins, 2018). Furthermore, in line with intra-gorilla variation in somatic growth, western lowland gorilla infants develop independence from their mothers more slowly when compared to eastern mountain gorilla infants as measured by the development of spatial proximity and locomotion (Nowell & Fletcher, 2007). This suggests that predictions of the ERAH extend beyond somatic growth to

aspects of behavioral development. Based on these results, one might expect more frugivorous apes to also exhibit delays in the onset of social interactions with peers given delays in the development of spatial and locomotor independence. But to our knowledge, this has not been tested.

Bonobos and chimpanzees have received considerable attention because the two species are humans' closest living relatives and exhibit key differences in feeding ecology and the timing of female life history that are consistent with the ERAH. The habitat of bonobos, when compared to that of chimpanzees, appears to be characterized by less severe seasonality, larger, denser food patches, and an abundance of terrestrial herbaceous vegetation, which provide an important fallback food when preferred ripe fruit is scarce (Hohmann, Fowler, Sommer, & Ortmann, 2006; Malenky & Wrangham, 1994; White & Wrangham, 1988). Several lines of evidence suggest that, among chimpanzees, feeding ecology is characterized by more intense competition than among bonobos: female east African chimpanzees (*P. t. schweinfurthii*) typically range alone in their core areas with only their dependent offspring, female dominance rank covaries with the food resource quality of their core areas (Murray, Eberly, & Pusey, 2006), the food resource quality of core areas covaries with lactating females' energetic condition as measured by urinary C-peptide levels (Emery Thompson, Muller, & Wrangham, 2012), and females aggressively defend their core areas against other females (Miller et al., 2014). Among west African chimpanzees (*P. t. verus*), females form linear dominance hierarchies and higher-ranking females are more likely to win contests over food (Wittig & Boesch, 2003). In contrast, female bonobos cooperate in various contexts, including defending and sharing food resources (Hohmann & Fruth, 1996; White & Wood, 2007; Yamamoto, 2015) and engaging in coalitionary aggression against males (Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016). Cooperative behavior among females is facilitated by what appears to be a universal pattern of high female gregariousness across populations, as females at multiple long-term study sites are rarely observed in the absence of other mature females (Wamba: Furuichi, 2009; Lomako: Hohmann & Fruth, 2002; Waller, 2011; LuiKotale: Moscovice et al., 2017). Importantly, dominance rank in one study was not related to C-peptide levels across female bonobos, indicating that habitual intrasexual association among females does not appear to incur substantial energetic costs in terms of feeding competition (Nurmi, Hohmann, Goldstone, Deschner, & Schülke, 2018). These studies collectively support the notion that feeding competition among female bonobos is reduced when compared to that among female chimpanzees.

In accordance with the ERAH, weight and age data from captive individuals demonstrate that female bonobos attain higher and earlier peak velocities in body weight growth than female chimpanzees (Leigh & Shea, 1996). This accelerated growth relates to dispersal patterns; while females of both species disperse from their natal communities, female bonobos do so considerably earlier (6–10 years of age in bonobos; Furuichi, 1989; Sakamaki et al., 2015; 11–13 years of age in chimpanzees; Emery Thompson, 2013). Furthermore, among captive populations, the onset of puberty, as marked by pronounced

increases in circulating testosterone, occurs approximately 3 years earlier in female bonobos than in female chimpanzees (Behringer, Deschner, Murtagh, Stevens, & Hohmann, 2014). It is currently unclear whether these differences in the timing of female maturation correspond to variation in age at first birth—a critical life history milestone marking the end of the immature period and the diversion of energy from growth to reproduction (Charnov & Berrigan, 1993; Stearns, 1992)—because such data on wild individuals of known age are absent for bonobos and rare for chimpanzees (reviewed in Walker, Walker, Goodall, & Pusey, 2018). However, existing data based on captive individuals and age estimates of wild individuals show that first birth occurs at similar or earlier ages in female bonobos when compared to female chimpanzees (De Lathouwers & Van Elsacker, 2005; Kuroda, 1989; Walker et al., 2018). Furthermore, Han, Andrés, Marques-Bonet, and Kuhlwilm (2019) recently compared the genomes of the two *Pan* species and found that bonobos are enriched in genes related to the age at menarche in humans, indicating that selection has acted differentially upon the timing of reproductive maturation between *Pan* females. These genotypic and phenotypic differences suggest that female bonobos have evolved faster—or female chimpanzees slower—behavioral, physiologic, somatic, and reproductive maturation in a manner that is consistent with the ERAH.

Despite this evidence for faster maturation in female bonobos, some studies suggest that infant and juvenile behavioral maturation occurs more slowly in bonobos than in chimpanzees, particularly in terms of the attainment of independence from mothers and the development of social skills (reviewed in Gruber & Clay, 2016; Kuroda, 1989). Specifically, Kuroda (1989) presented qualitative data suggesting that wild infant chimpanzees increase spatial proximity from their mothers, transition from riding to independent travel, begin to ingest solid foods, and begin to socialize with individuals other than their own mothers at earlier ages than do infant bonobos. This evidence for delayed behavioral maturation in bonobos relative to chimpanzees appears inconsistent with the ERAH, as well as with empirical data suggesting faster reproductive maturation in bonobos. Results from additional comparisons, however, support some but not all of the results found by Kuroda (1989): in a quantitative comparison of captive populations, De Lathouwers and Van Elsacker (2006) found that chimpanzees under 5 years of age spent more time at distances greater than 5 m from their mothers and ceased suckling earlier than age-matched bonobos, but the species did not differ in the amount of time that immatures spent in contact with their mothers or time spent engaged in social play, and bonobos groomed conspecifics more than did chimpanzees. Similarly, in a quantitative comparison of wild populations, Koops, Furuichi, and Hashimoto (2015) found that bonobos under 8 years of age spent more time within 2 m of their mothers than did age-matched chimpanzees, but like De Lathouwers and Van Elsacker (2006), they did not find species differences in the total amount of time engaged in social play.

It is unclear why bonobos should attain independence from their mothers and develop social skills slower than chimpanzees. Potential explanations require a consideration of additional sources of immature mortality risk, which may influence maturation independent of risks

related to feeding ecology. Furuichi et al. (1998) showed that infant mortality is higher in chimpanzees than in bonobos and suggested that an important driver of this difference may relate to species differences in infanticide: both intra- and intercommunity infanticide occur across chimpanzee subspecies but do not appear to occur among bonobos (Hohmann, Vigilant, Mundry, Behringer, & Surbeck, 2019). Infanticide pressure may thus act to accelerate maturation in infant chimpanzees if more developed infants are less prone to infanticide. Various sources of evidence suggest that primate infants wean earlier when infanticide pressure is high (Colmenares & Gomendio, 1988; Fairbanks & McGuire, 1987; Saj & Sicotte, 2005; Watts, 2010; Zhao, Tan, & Pan, 2008). Most recently, Bădescu et al. (2016) showed that infanticide risk, rather than predation risk or risk associated with feeding competition, resulted in faster infant development among ursine colobus (*Colobus vellerosus*).

Furthermore, Gruber and Clay (2016) note that the existing evidence for slower behavioral maturation during infancy and juvenility in bonobos could be explained by the Self-Domestication Hypothesis. First proposed by Wrangham and Pilbeam (2001), and later formalized as the Self-Domestication Hypothesis (SDH) by Hare, Wobber, and Wrangham (2012), this hypothesis posits that greater resource availability and reduced feeding competition among female bonobos reduce the costs of grouping, facilitating the larger, mixed-sex foraging parties that characterize bonobos. These authors argue that this increased gregariousness selected for a reduction in the intensity of male aggression, which then resulted in a “domestication syndrome,” a suite of traits that appears to co-occur in some domesticates relative to their wild counterparts after being selected for tameness (reviewed in Hare et al., 2012). This domestication syndrome is composed of traits in adults that resemble those of juveniles, such as exaggerated socio-sexual behavior, high levels of social tolerance, and underdeveloped inhibitory skills. One possibility is that the presence of such juvenilized traits in adult bonobos is due in part to delays in the attainment of independence from mothers and social skill development during immaturity; however, the SDH does not make explicit predictions regarding the precise developmental mechanisms involved in generating juvenilized traits during adulthood.

Here, we aim to contribute additional insights into the existing body of research on comparative development in *Pan* by focusing on female behavioral maturation in wild infants and juveniles. Infancy (Altmann, 1980; Hinde, 1971; Lonsdorf, 2017; Lonsdorf et al., 2014) and juvenility (Fairbanks, 1993; Joffe, 1997; Meredith, 2013; Watts & Pusey, 1993) in primates are critical periods during which individuals develop behavioral skills that likely influence adult survival, and the timing of this skill development is related to species-specific patterns of adult socioecology (van Noordwijk & van Schaik, 2005). Therefore, characterizing variation in the timing of early behavioral development between *Pan* females and understanding how this relates to putative differences in feeding ecology and reproductive maturation will help to elucidate the factors leading to their starkly different behavioral phenotypes during adulthood. While the existing data presented above indicate variation in the pace of maturation between infants

and juveniles of the two *Pan* species, neither the direction of temporal asynchrony nor the extent of differentiation across different behaviors shows a consistent pattern. These inconsistent results may reflect true behavioral plasticity between populations, different methodological parameters, and/or the use of relatively small samples sizes. We utilize what is to our knowledge the largest data set on infants and juveniles from wild populations of either species to test the competing predictions that (a) female bonobos undergo faster behavioral maturation than age-matched female chimpanzees, as would be expected based on the ERAH or (b) female chimpanzees undergo faster behavioral maturation due to species differences in infanticide risk and/or self-domestication in bonobos. We compare females from birth until the average age of dispersal reported for bonobos (8 years) and consolidate all previously evaluated metrics regarding infant and juvenile behavioral maturation into a single quantitative study. Thus, our study provides a novel and direct comparison to further evaluate the extent to which behavioral development varies between the two species, as well as between different populations within species.

2 | MATERIALS AND METHODS

2.1 | Study site and subjects

Data on wild bonobos were collected at LuiKotale, Democratic Republic of the Congo, on the Bompusa West community (formerly called the Bompusa community) and the Bompusa East community, from July 2015 through June 2018. All bonobos are habituated to human observers and individually recognizable, and we only included immatures of known age. During the study period, the Bompusa West community included up to 19 mature (>12 years) females, 8 mature males, and 27 immatures (<12 years). The Bompusa East community included up to 13 mature females, 5 mature males, and 19 immatures. Data on wild chimpanzees were collected on the Kasekela community at Gombe National Park, Tanzania from January 1976 through November 2016. All chimpanzees were habituated to human observers and individually recognizable and all infants and juveniles included in this study are of known age. During the study period, the community included up to 25 mature females, 14 mature males, and 29 immatures.

At both sites, detailed behavioral data are collected systematically during focal follows of a single mother and its dependent offspring using 1-min point samples. At Gombe, a given focal follow focuses on a mother and its two youngest dependent immatures simultaneously and ranges from several hours to a full day, while at LuiKotale, follows are on a mother and one of its dependent immatures at a time and are conducted for 1 hr. These differences are due to practical constraints associated with observation conditions at LuiKotale that make it difficult to consistently follow two immatures simultaneously for extended durations. However, the behavioral ethogram in place at LuiKotale was designed to be comparable to that at Gombe in order to ensure consistency in comparative analyses. Behavioral data include activity, the identity of social partners, and proximity between the mother and its dependent immatures. Focal subjects were chosen

randomly to the extent that was possible, but nonrandom, practical constraints frequently resulted in biased observation hours toward more easily observable individuals. Therefore, focal subjects were often chosen to balance observation hours across individuals.

2.2 | Behavioral data

To compare behavioral maturation, we pooled focal follow data on each immature female into 1-year age classes. We included all females that were less than 8 years of age for which we had collected at least 10 hr of good observations for a given age class (Table 1). Good observations included those 1-min point samples in which the activity of the female can be determined, as opposed to bad observations in which the activity could not be determined due to poor visibility. We did not include individuals that died prior to reaching 1 year of age or those that were orphaned prior to reaching 8 years of age as these individuals may exhibit atypical developmental patterns. In total, our sample included 17 unique immature female bonobos, 30 unique immature female chimpanzees, 14 unique bonobo mothers, and 22 unique chimpanzee mothers. Following Lonsdorf et al. (2014), we utilized the proxies described below to measure (1) the attainment of independence from mothers and (2) the development of social skills.

1. We measured the attainment of independence from mothers by characterizing the extent to which immature females (a) break contact and (b) move away from their mothers, (c) depend on their mothers for transportation, and obtain nutrition from their (d) mothers, and (e) on their own:
 - a. *Maternal Contact*—Immature is in physical contact with its mother.
 - b. *Distance > 5 m from Mother*—Immature is at a distance greater than 5 m from its mother
 - c. *Ride on Mother*—The immature is riding ventrally, that is, being transported as it clings to its mother's belly, gripping hair between flexed fingers and toes, or riding dorsally, that is, being transported as it lays or sits on its mother's back.
 - d. *Suckle*—Immature's mouth is in contact with its mother's nipple.
 - e. *Eat*—Ingestion of solid food.

TABLE 1 Sample size

Age class (years)	Bonobo	Chimpanzee
0–1	2 34	19 1,191
1–2	5 73	18 915
2–3	3 63	15 798
3–4	6 79	15 532
4–5	5 83	14 562
5–6	5 69	13 658
6–7	5 72	14 541
7–8	2 26	10 298
	Total hours = 499	Total hours = 5,495

Note: Number of individuals | Observation hours.

2. We measured the development of social skills by characterizing the extent to which immatures engaged in (a) social play and (b) social grooming with peers:
 - a. *Social Play*—Nonaggressive interaction between two or more individuals that include one or more of the following: tickling, wrestling, chasing, kicking, rubbing, thrusting, biting, or pulling. May incorporate an object (e.g., tugging of sticks back and forth).
 - b. *Social Grooming*—Parting of another individual's hair with hands, fingers, and/or lips and removal of debris or ectoparasites.

All metrics, except *Ride on Mother*, were calculated as the number of point samples that the female was engaged in the behavior of interest during the given age class, divided by the total number of good observations collected on that female during the given age class. For *Social Play* and *Social Grooming*, we followed Kuroda (1989) and De Lathouwers and Van Elsacker (2006) in that we did not consider interactions between immatures and their mothers given our primary interest in the development of social skills with peers in the broader social milieu, that is, with those individuals outside of the mother-offspring dyad. Thus, we removed point samples in which the play or groom partner was the immature female's mother from the numerators of *Social Play* and *Social Grooming* analyses. For *Ride on Mother*, we calculated the number of point samples that the female spent riding on its mother as described above for the other behaviors; however, to control for potential between-species differences in maternal travel time, we took the number of point samples that females spent riding and divided it by its mother's total number of point samples spent traveling. This generated a relative riding index for each female that is weighted by its mother's total travel time.

2.3 | Statistical analyses

We conducted all analyses in R version 3.5.2 (R Core Team, 2018) using the lme4 version 1.1-19 (Bates, Mächler, Bolker, & Walker, 2014), lmerTest version 3.1-0 (Kuznetsova, Brockhoff, & Christensen, 2017), car version 3.0-2 (Fox et al., 2012), and emmeans version 1.3.1 (Lenth, 2018) packages. To compare behavioral maturation between females of the two species, we fit a linear mixed model (LMM) to each metric using the lmer function in the lme4 package. For each model, our response variable was the arcsine square root transformed proportion of time engaged in the behavior of interest, and our fixed predictor variables included species and 1-year age class. We also included hours of observation as a fixed predictor to control for the fact that females were followed for different amounts of time. Female identity was included as a random effect because the same female could be represented in multiple age classes. We evaluated assumptions of normality and homogeneity of variance visually using diagnostic residual plots. To determine the significance ($\alpha = .05$) of fixed effects, including the interaction between species and age class, we conducted F tests using the ANOVA function in the car package (Kenward–Roger degrees of freedom approximation, Type III sum of

squares). If this interaction was not significant, we removed it and refit the model using species and age class as independent fixed effect predictors (Kenward–Roger degrees of freedom approximation, Type II sum of squares). If the interaction between species and age class was significant, we conducted Tukey's pairwise post hoc comparisons between species within each age class.

3 | RESULTS

The only model in which the interaction between species and age class had a significant effect was for *Distance > 5 m from Mother* ($F_{7,123.78} = 2.370$, $p = .026$). Our post hoc analysis revealed that female bonobos spent more time at distances greater than 5 m from their mothers during the 3–8 age classes, and that the species did not differ during the 0–3 age classes (Table 2; Figure 1). Observation hours did not have a significant effect ($F_{1,123.36} = 0.446$, $p = .505$). We included parameter estimates for all models in Table S1.

The only model in which species had a significant effect was for *Ride on Mother* ($F_{1,57.00} = 6.088$, $p = .017$); female bonobos rode on their mothers relatively more than did female chimpanzees (Figure 2).

TABLE 2 Tukey's pairwise post hoc comparisons for *Distance > 5 m from Mother*

Age class	Estimate	SE	df	t	p
0–1	−0.014	0.082	122	−0.167	.868
1–2	0.073	0.057	110	1.270	.207
2–3	0.083	0.067	130	1.237	.218
3–4	0.145	0.053	118	2.744	.007
4–5	0.193	0.057	122	3.410	<.001
5–6	0.220	0.062	128	3.572	<.001
6–7	0.208	0.058	112	3.570	<.001
7–8	0.415	0.084	125	4.959	<.001

Note: Significance ($p < .05$) is indicated in bold. Comparison direction is bonobo minus chimpanzee.

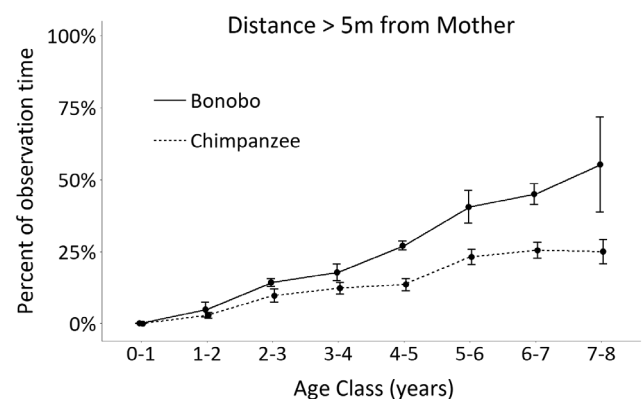


FIGURE 1 Mean $\pm$ SE percentage of observation time that infant and juvenile females spent at a distance greater than 5 m from their mothers

Age class also had a significant effect in the model for *Ride on Mother* ($F_{7,120.37} = 167.736$, $p < .001$), with relative riding time decreasing with age in both species, while observation hours did not have a significant effect ($F_{1,139.01} = 0.042$, $p = .838$).

Species did not have a significant effect in the models for *Maternal Contact* ($F_{1,57.00} = 0.030$, $p = .862$), *Eat* ($F_{1,72.86} = 3.910$, $p = .052$), *Suckle* ($F_{1,60.41} = 0.001$, $p = .978$), *Social Play* ($F_{1,60.51} = 1.030$, $p = .314$), or *Social Grooming* ($F_{1,60.19} = 0.613$, $p = .437$). Age class had a significant effect in the models for *Maternal Contact* ($F_{7,118.35} = 171.23$, $p < .001$), *Eat* ($F_{7,129.67} = 66.013$, $p < .001$), *Suckle* ($F_{7,122.66} = 31.983$, $p < .001$), *Social Play* ($F_{7,122.75} = 10.817$, $p < .001$), and *Social Grooming* ($F_{7,122.48} = 13.299$, $p < .001$). Time spent in contact with mothers, suckling, and social play decreased with age, while time spent eating and social grooming increased with age in both species (Figure 3). Observation hours had a significant effect in the model for *Maternal Contact* ($F_{1,139.88} = 4.425$, $p = .037$), but not for *Eat* ($F_{1,89.00} = 2.371$, $p = .127$), *Suckle* ($F_{1,137.143} = 0.724$, $p = .396$), *Social Play* ($F_{1,136.89} = 0.264$, $p = .608$), or *Social Grooming* ($F_{1,137.64} = 2.810$, $p = .096$).

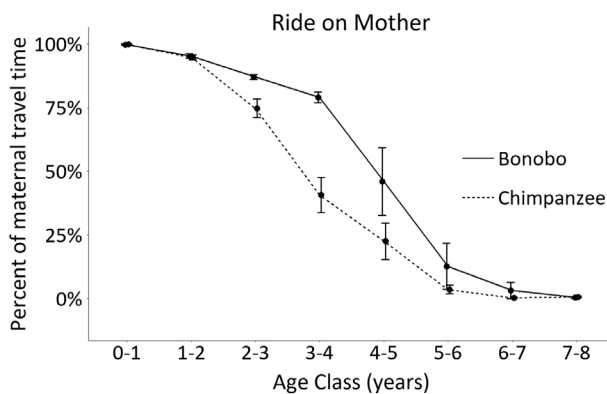


FIGURE 2 Mean $\pm$ SE percentage of maternal travel time that infant and juvenile females spent riding on their mothers

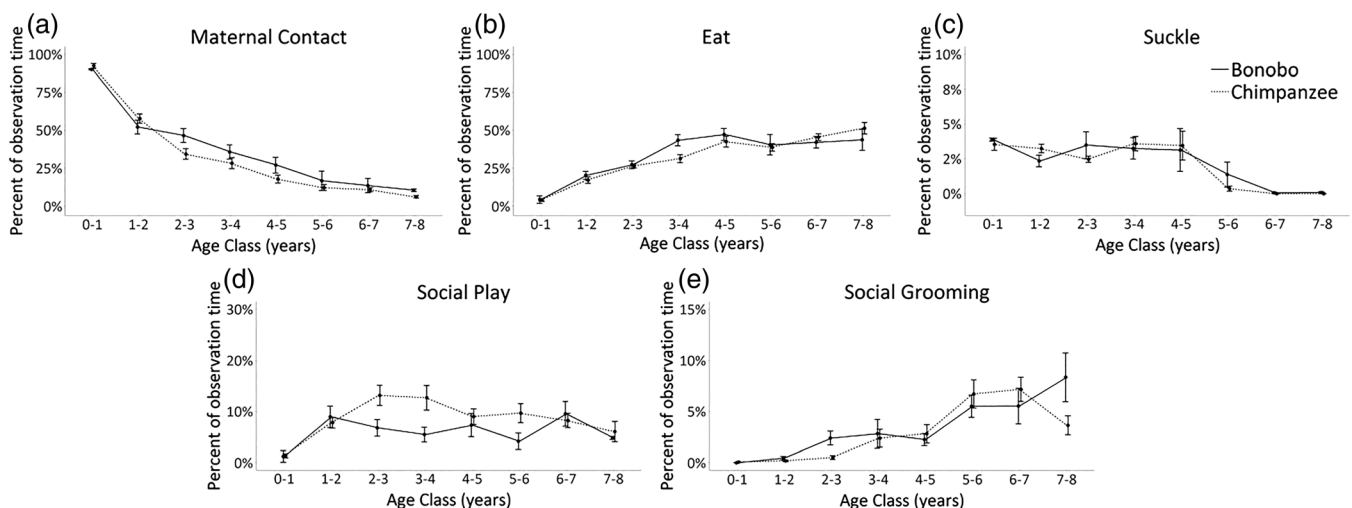


FIGURE 3 Mean $\pm$ SE percentage of observation time that infant and juvenile females spent (a) in contact with their mothers, (b) eating, (c) suckling, (d) engaged in social play, and (e) engaged in social grooming

Because we found a significant effect of species in the model for *Ride on Mother*, and because offspring are in contact with their mothers when riding, species differences in *Ride on Mother* may confound patterns of *Maternal Contact*. Therefore, we reran *Maternal Contact* after removing all point samples in which immature females were riding on their mothers. The pattern of significance was the same as before we removed *Ride on Mother* point samples: species did not have a significant effect ($F_{1,50.37} = 0.186$, $p = .668$), age class had a significant effect ($F_{7,105.45} = 100.617$, $p < .001$), with contact time decreasing with age, and observation hours had a significant effect ($F_{1,118.57} = 9.433$, $p = .003$). We included parameter estimates for both *Maternal Contact* analyses in Table S1.

4 | DISCUSSION

Our aim in this study was to compare the timing of infant and juvenile behavioral maturation between female bonobos and chimpanzees in order to explore potential effects of ecological risk, infanticide risk, and self-domestication. We were particularly interested in the attainment of independence from mothers and the development of social skills. Contrary to previous studies that have reported that immature bonobos exhibit delays in these aspects of maturation (De Lathouwers & Van Elsacker, 2006; Koops et al., 2015; Kuroda, 1989), we found that female bonobos spent more time at distances greater than 5 m from their mothers between the ages of 3–8 years. Although Fröhlich et al. (2016) recently showed that infant bonobos from LuiKotale spent more time in closer proximity to their mothers than did infant chimpanzees in their study on mother–infant gestural communication, they intentionally restricted their analyses to video footage of mother–infant social interactions that included communicative behavior. Their analyses thus represent a subset of total activity budgets. Furthermore, the LuiKotale bonobos included in their study did not exceed 50 months of age, while

the difference in proximity that we found in our study regards females between the ages of 36–96 months. We also found that female bonobos spent a greater proportion of travel time riding on their mothers; although previous studies did not compare riding behavior, this result is in accordance with indications that bonobos exhibit delays in the attainment of independence from their mothers. We did not find differences in the time that females spent in contact with their mothers or engaged in suckling, eating, social play, or social grooming.

Our results indicate broad similarities between infant and juvenile females of the two species in the metrics and populations considered herein. This suggests that the pace of behavioral maturation is relatively conserved among *Pan* females during infancy and juvenility and that risks associated with feeding ecology and infanticide have limited impact on interspecific variation in the speed with which these traits develop. However, we emphasize that comparisons with additional populations of both species are required in order to confirm whether these are species-level patterns. Our results are intriguing in this sense, though, given that Gombe represents a relatively seasonal environment (Pusey, Oehlert, Williams, & Goodall, 2005) with relatively high rates of infanticide (Wilson et al., 2014) when compared to other chimpanzee populations, indicating that the maturational similarities that we found are not likely to be artifacts of similar local ecologies. Our results also indicate that the domestication syndrome in bonobos arises through variation in developmental mechanisms that are largely independent of the metrics evaluated in this study.

The earlier increase in distance from mothers is consistent with the earlier dispersal and puberty of female bonobos and partially supports our hypothesis that female bonobos undergo faster behavioral maturation. This is despite two of our female bonobo subjects having dispersed during the study at approximately 6.5 and 7.5 years of age, removing individuals from our analysis that presumably developed most quickly. However, it is possible that species differences in time spent away from mothers reflects variation in risks of male aggression rather than differences in the attainment of independence from mothers. Supporting this notion is the finding by Otali and Gilchrist (2006) that infant chimpanzees in the Kanyawara population move further from their mothers when in parties with fewer males, suggesting that mothers and/or infants are sensitive to the threat of male aggression. Although male bonobos can also be aggressive toward immatures, this aggression has never been shown to be lethal as can be the case in chimpanzees (Hohmann, Ortmann, Remer, & Fruth, 2019).

Regardless of the cause of this difference in spatial proximity to mothers, future research should compare the nature of female social interactions during immaturity to evaluate its potential functional significance. Pusey (1990) noted that immature female chimpanzees at Gombe remained in close association with their mothers until first estrous, which occurred at approximately 10 years of age during the study. Similarly, Stumpf, Emery Thompson, Muller, and Wrangham (2009) showed that immature female chimpanzees at Kanyawara exhibited a steep decline in association with their mothers in the year preceding dispersal, which occurred at an average age of 12.6 years during the study. Both Pusey (1990) and Stumpf et al. (2009) found

that the decreasing association between immature females and their mothers was accompanied by an increase in association between immature females and other group members, particularly adult males. Variation in social interactions between immature females of each species may relate to putative differences in dispersal strategies and requires further investigation.

Our finding that female bonobos rode on their mothers later into development than did female chimpanzees lends support to previous studies that have found that bonobos mature more slowly during infancy and juvenility. However, given that this is the only evidence for slower maturation that we found in bonobos, we cannot rule out alternative explanations that pertain specifically to this behavior. One possibility is that this difference reflects variation in maternal investment as it pertains to carrying offspring rather than differences in the pace of behavioral maturation. Evidence suggests that the energetic costs of independent travel by offspring may exceed the costs of maternal transport (Young & Shapiro, 2018), and given that birthweight in bonobos is lower than in chimpanzees (Leigh & Shea, 1996), female bonobos may reduce energetic costs by carrying offspring. Supporting this are anecdotal reports from Wamba (Furuichi et al., 1998) and LuiKotale (Lee, personal observation) in which bonobo mothers carried their two youngest dependent offspring simultaneously. Simultaneous offspring carrying is rarely observed in our chimpanzee study population (Lonsdorf, Murray, personal observation) and to our knowledge has not been reported elsewhere. Bonobo mothers may thus be more tolerant of their offspring and/or less energetically constrained in terms of carrying. Another explanation for this difference in riding could relate to species-differences in substrate-use. For example, Doran (1993) proposed that bonobos engage in more arboreal travel than chimpanzees (but see Ramos, 2014) and LuiKotale bonobos also frequently travel in extremely swampy terrain to forage on aquatic vegetation (Hohmann, Ortmann, et al., 2019). These travel patterns may necessitate more riding in bonobos than in chimpanzees. Future research should evaluate species-differences in substrate use and maternal tolerance and energetics as they relate to carrying and locomotor behavior.

Our study indicates a conservation of maturational pathways between female bonobos and chimpanzees for the metrics and age classes considered herein. Although distance from mothers and riding differed between species, we propose viable explanations that do not invoke differences in rates of maturation and thus require further study (e.g., threat of male aggression, substrate use). This suggests that the onset of independence from mothers and social skills in *Pan* may be critical prerequisites for normal growth and development such that there is relatively little room for variation in their timing. In this sense, the evolution of *Pan* females is constrained and variation between adults of the two species are likely due to other components of development. Therefore, future studies should investigate additional aspects of female behavior during juvenility, particularly those relating to sociosexuality and aggression, as these are known to vary substantially between adult females of the two *Pan* species (reviewed in Gruber & Clay, 2016). For example, unlike female chimpanzees, female bonobos across study sites frequently win agonistic contests against males in

both dyadic and coalitionary contexts (Nurmi et al., 2018; Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016). Additionally, more populations of both species must be compared in order to clarify the extent of within and between species variation in female behavioral maturation given documented subspecific variation in adult female chimpanzee sociality (Lehmann & Boesch, 2009; Wakefield, 2013).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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