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PAPER



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Systematic mapping of developmental milestones in wild chimpanzees

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Abstract

Postnatal development is protracted relative to lifespan in many primates, including modern humans (*Homo sapiens*), facilitating the acquisition of key motor, communication and social skills that can maximize fitness later in life. Nevertheless, it remains unclear what evolutionary drivers led to extended immature periods. While the developmental milestone literature is well established in humans, insight we can gain from one-species models is limited. By comparing the timing of reliable developmental milestones in a closely related species, the chimpanzee (*Pan troglodytes*), we can gain further understanding of the evolution of such an extended developmental phase. To date, few studies have specifically attempted to estimate developmental milestones in a manner comparable to the human literature, and existing studies lack sufficient sample sizes to estimate which milestones are more plastic with higher inter-individual variation in the timing of their emergence. Here, we describe the emergence of gross motor, fine motor, social interaction and communication traits from a longitudinal sample of 19 wild chimpanzee infants (8 females and 11 males), Taï National Park, Côte d'Ivoire. Gross motor traits emerged at a mean of 4 months, communication traits at 12 months, social interaction traits at 14 months and fine motor traits at 15 months, with later emerging milestones demonstrating greater inter-individual variation in the timing of the emergence. This pattern of milestone emergence is broadly comparable to observations in humans, suggesting selection for a prolonged infantile phase and that sustained skills development has a deep evolutionary history, with implications for theories on primate brain development.

KEYWORDS

communication, fine and gross motor, life-history theory, ontogeny, *Pan troglodytes*, social

1 | INTRODUCTION

Postnatal development is a principal component of mammalian life history (Charnov, 1991; Charnov & Berrigan, 1993; Purvis & Harvey, 1995). Many species are not born with the traits necessary

for adulthood and must acquire these during early life. Classic life-history theory states that longer maturation can decrease age-specific survival (Stearns, 1992). A predominant theory to explain the evolution of delayed maturation in the primate lineage is that sustained brain and somatic growth may require an extended time

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to mature (Barton & Capellini, 2011; León et al., 2008). A trade-off between juvenile mortality risk and the necessary time taken to develop adult traits likely shape overall fitness and the evolution of species as a whole. Some species have slower postnatal development and reach maturity later than others, with much variation in development found within orders. For example in primates such as black-and-white ruffed lemurs (*Varecia variegata*), females reach sexual maturity after 5.2 months, compared to humans (*Homo sapiens*) with an average of 16.5 years (Harvey & Clutton-Brock, 1985). This translates into 2% and 24% of the respective species' lifespan, supporting a quantitative difference in the length of the immature period (Hakeem, Sandoval, Jones, & Allman, 1996).

In contrast to other mammals of similar size, large primate species develop at around 10 times slower rates with an unusually long immature period (Case, 1978; Joffe, 1997; Jones, 2011; Walker, Burger, Wagner, & Von Rueden, 2006). Humans have an exceptionally long developmental period relative to body size and lifespan (Harvey & Clutton-Brock, 1985). It is hypothesized that the extended ontogeny in humans compared to other primates reflects the time needed for the relatively large brain to develop and to invest in years of learning to acquire skills required for survival in adult life, both being linked to an exceptionally long lifespan (i.e. life-history brain development hypothesis (Garwicz, Christensson, & Psouni, 2009; Harvey & Clutton-Brock, 1985; Kaplan, Hill, Lancaster, & Hurtado, 2000)). In line with this, it has been predicted that humans develop at a slower pace than other primates (Hawkes et al., 2017; but see Bard, Brent, Lester, Worobey, & Suomi, 2011). However, it remains unclear to what extent our long developmental period is driven by underlying constraints such as brain size growth (i.e. prenatal maternal constraints such as the obstetrical dilemma hypothesis Rosenberg & Trevathan, 1995; Washburn, 1960) or the metabolic dilemma hypothesis (Dunsworth, Warrener, Deacon, Ellison, & Pontzer, 2012), or by a necessity to acquire relevant skills for adult survival (e.g. the delayed benefits hypothesis, Powell, Barton, & Street, 2019).

It is not possible to test between the aforementioned hypotheses until there is detailed data available on the development of both behaviour and brain across several primate species. We use three methods used in other comparative studies for comparing developmental milestone emergence across species: (a) absolute ages (Finlay & Darlington, 1995), (b) ages corrected for species' average age at first reproduction (Boesch, Bombjaková, Meier, & Mundry, 2019) and (c) ages corrected for species' modal adult lifespan (i.e. modal old-age mortality; Helton, 2008; Horiuchi, Ouellette, Cheung, & Robine, 2013). Measures of absolute age allow for direct comparison with brain maturation milestones, whereas measures that account for variation in life history allow for a correction factor for milestone emergence relative to life history. To give the best comparative assessment across humans and chimpanzees, we use all three approaches, as each carries advantages and disadvantages (Table 1).

A step towards shedding light on the underlying drivers of extended developmental periods is to compare developmental

Research Highlights

- Patterns of milestone emergence in wild chimpanzees are broadly comparable to observations in the human literature.
- As in humans, chimpanzee gross motor traits emerge on average before communication, social interaction and fine motor traits.
- Later emerging milestones demonstrate greater inter-individual variation in the timing of the emergence.

milestones in behaviour that are expected to reflect brain maturation, such as of traits relating to motor and sociocognitive development (e.g. Brauer, Anwender, Perani, & Friederici, 2013; Marrus et al., 2018; Wiesmann, Schreiber, Singer, Steinbeis, & Friederici, 2017). In human psychology and medicine, developmental milestones are defined as 'a set of behaviours, skills or abilities that are demonstrated by specified ages during infancy and early childhood in typical development' (Beighley & Matson, 2013) and provide a framework for observing and monitoring an infant's developmental progress with respect to the norm over time. A breadth of studies has determined developmental milestones human infants reach (Flensburg-Madsen & Mortensen, 2018; Gladstone et al., 2010; Siegler, DeLoache, & Eisenberg, 2014; WHO Multicentre Growth Reference Study Group, 2019), including key motor traits such as walking, social traits (e.g. playing with others) and communication traits (e.g. saying the first word). Systematic mapping of these milestones in non-human primate species is a topical field of research in developmental science.

Most studies on early chimpanzee development to date come from a captive setting (e.g. Bard et al., 2014; Gardner & Gardner, 1989; Kimura, 1987; Poti & Spinozzi, 1994; Tomasello, George, Kruger, Jeffrey, & Evans, 1985), which, although informative, examine the emergence of behaviours in an environment unreflective of the ecological setting in which developmental trajectories evolved. For example it has been estimated that teeth and female sex skin mature several years earlier in captive chimpanzees compared to those in the wild (Coe, Connolly, Kraemer, & Levine, 1979; Smith & Boesch, 2011; Zihlman, Bolter, & Boesch, 2007), highlighting the differences in development that can arise in varying settings. In the wild, developmental data from the first years of life are sparse; classic studies having focused on a limited number of behaviours across few individuals (Boesch & Boesch-Achermann, 2000; Lonsdorf, Eberly, & Pusey, 2004; Plooi, 1984; Pontzer & Wrangham, 2006; Van Lawick-Goodall, 1968). Overall, a systematic map of when behavioural traits emerge in natural conditions is still lacking in our closest living relatives. Expanding on early life samples from wild populations enables us to assess key developmental milestones. Once established, milestones can approximate species' norms, from which inter-individual variation in the emergence of behavioural traits can be determined, and hence the impact of factors on variation, such

TABLE 1 Advantages and disadvantages of different methods to compare the emergence of development milestones across species

Developmental method	Advantages	Disadvantages	Humans (pre-industrial societies)	Chimpanzees (wild populations)
Absolute age	Direct comparison of developmental milestones between species ¹	Species' differences in developmental milestones may be due to different pace of brain maturation and life history ^{2,4}		
Age standardized by first reproduction	Species' differences in developmental milestones due to different pace of brain maturation and life history may be accounted for ²	In female chimpanzees, exact birth dates are hard to obtain as most emigrate from natal communities before first reproduction ⁵ In humans, cultural and social constraints may cause divergence between age at sexual maturity and age at first reproduction ^{6,7}	19 years (women) ⁸	16 years (known emigrated females) ⁹
Age standardized by modal adult lifespan (excluding immature, pathological or human-induced mortality)	Species' differences in developmental milestones due to different pace of brain maturation and life history may be accounted for ³	In many human societies dates of birth are not systematically recorded—ages, especially for older individuals, are rarely known ⁸ In chimpanzees, dates of birth of oldest individuals remain estimates, even in field sites with >40 years of records ⁵	70 years ^{10,11}	45 years ⁵

Note: References: (1) Finlay & Darlington, 1995; (2) Boesch, Bombjaková, et al., 2019; (3) Helton, 2008; (4) Clancy, Darlington, & Finlay, 2001; (5) Wittig & Boesch, 2019a; (6) Gillespie et al., 2013; (7) Rindfuss & St. John, 1983; (8) Walker, Gurven, et al., 2006; (9) Walker et al., 2018; (10) Gurven & Kaplan, 2007; (11) Lahdenperä, Lummaa, Helle, Tremblay, & Russell, 2004.

as rearing conditions, maternal effects and socioecology (Bard & Leavens, 2014, 2017; Fröhlich, Müller, Zeiträg, Wittig, & Pika, 2017; Markham, Lonsdorf, Pusey, & Murray, 2015).

The aim of this study was to perform a systematic investigation of the development of a broad repertoire of behavioural traits found in wild chimpanzees. By comparing these data to existing human milestones, and in the future to developmental milestones in other primates, one can eventually gain insight into fundamental evolutionary drivers of prolonged developmental periods. This evolutionary approach is an alternative to the classic psychological one. Specifically, we predict that, as life-history theory posits a more analogous maturation scheme of brain and behaviour, due to a similar socioecology and phylogenetic proximity, developmental milestones should be reached in a similar progression in chimpanzees and humans (Bard et al., 2011). We test these predictions comparing chimpanzee data with published human data.

Additionally, if extended development is about acquiring complex skills, we expect these to emerge later than simple skills in both species (Shettleworth, 2009; Taylor, Elliffe, Hunt, & Gray, 2010). We define behaviours as complex if they involve a combination of different types of behaviours and require more than one decision and action in a rapid order or simultaneously (American Psychological Association, 2019). For instance we class attentive looking as less complex than tool use, which involves multiple actions such as selecting and/or manufacturing and employing the correct environmental object to reach a goal, such as extracting food successfully (Shumaker, Walkup, Beck, & Burghardt, 2011). We also expect these later emerging behaviours to exhibit more inter-individual variation and plasticity due to variation in experience and underlying cognitive differences. Substantial differences in captive versus wild studies

already suggest considerable environmental influence on a few selected developmental milestones in chimpanzees (Coe et al., 1979; Smith & Boesch, 2011; Zihlman et al., 2007). Before this can be fully examined, a comprehensive mapping of developmental milestones is required, as has been done in human development.

Hence, we investigated data on behavioural traits as part of a long-term project in the Taï National Park, Côte d'Ivoire. A total of 19 individuals were included in this study from whom we have behavioural data from the first month after birth. We collected data on the emergence of different motor (gross and fine), social and communication traits during the first 5 years of life and defined developmental milestones based on this data. We calculated three standard developmental measures to compare milestone emergence patterns of chimpanzees with human children: absolute age at emergence, ages corrected for age at first reproduction and corrected for modal adult lifespan. To our knowledge, this study provides a first systematic description of the emergence of the behavioural repertoire in wild chimpanzees across a wide array of motor and sociocommunicative traits.

2 | MATERIALS AND METHODS

2.1 | Study site and population

We collected behavioural data during 1989–1995 in the North group of the habituated western chimpanzee community (*Pan troglodytes verus*) inhabiting the west of the Taï National Park (5°45'N, 7°07'W), Côte d'Ivoire (Boesch & Boesch-Achermann, 2000; Wittig, 2018). This community has been studied since 1979 on various aspects of life history, intra- and inter-group dynamics, tool use, etc. (Boesch &

Boesch-Achermann, 2000; Boesch, Wittig, et al., 2019). Habituation of the community was achieved by 1984.

2.2 | Data collection

The early-life data set is based on an ethogram developed by C. Boesch to be compatible with the one used by J. Goodall on the Gombe chimpanzees in 1994 (see Table S1). We collected behavioural data during all-day focal follows of infants, using instantaneous scan sampling (Altmann, 1974). All the data were collected on a standardized data sheet by G. Nohon Kohou, who was trained and supervised by C. Boesch. G. Nohon Kohou collected data on the minute, interrupted by a 10-min break once per hour, between maximum 6:00 a.m. and 7:00 p.m. The full data set comprised 19 chimpanzee infants (N females = 8, N males = 11), for whom we have behavioural data from the first month after birth (Table 2). We knew the exact birth date for the majority of infants; for two individuals (Ovide and Pollux) this information was available at the monthly level. In both of these latter individuals, the first observation day was before the 15th of the month, thus we used the first day of the month in which they were born as an estimated birth date and calculated their ages accordingly (Estienne, Cohen, Wittig, & Boesch, 2019). Overall, we investigated the first occurrence of the different behavioural traits in data ranging from the first month after birth until an average of 3 years (± 2.0 SD, range = 0.03–5.9; Figure S1).

We collected a total of 759 observation days (mean per individual = 40, range = 1–98) and 3,459 observation hours (M = 182, range = 4–454) at an average frequency of once per month, though the frequency for older individuals was slightly lower.

2.3 | Data analysis

We utilized the R environment, version 3.5.1 (R Core Team, 2018), to collate and analyse the data. We collated the first emergence of motor, social and communication traits (for an operational definition of each trait see Table S1). We define the first emergence of a trait as the first time we observed the trait while following an individual, and thus cannot exclude that it occurred earlier while we were not present. We minimized estimation error with the aim of following each individual from the first month after birth regularly (i.e. once per month). Sample sizes differed per trait as some traits were not observed in all individuals (see Table S2). We compiled averages, \pm SD and ranges and present boxplots for each trait (Figure 1; Table S2). We split motor traits into gross and fine motor traits, with the former involving coordination of vision (i.e. eye movement) and large body parts such as arms and legs, such as sitting and walking, and the latter involving smaller, more precise movements occurring in the hands, fingers, feet and toes, such as object manipulation

Subject	Sex	Mother	Age (months)		Days	Duration (hr)
			Minimum	Maximum		
Aphro	F	Agathe	0.16	11.31	12	64.22
Bagheera	F	Belle	0.99	19.56	11	56.80
Dorry	F	Dilly	0.36	57.90	49	195.70
Fédora	F	Fossey	0.20	21.83	20	105.70
Foutou	F	Fanny	0.43	24.39	25	71.52
Mognié	F	Mystère	0.79	62.27	64	274.62
Piment	F	Poupée	0.69	43.99	47	211.03
Vanille	F	Vénus	0.43	69.83	57	236.52
Baloo	M	Bijou	0.72	24.95	36	152.03
Bambou	M	Bijou	0.76	24.82	56	311.60
Cacao	M	Castor	0.07	27.09	18	79.43
Congo	M	Castor	0.46	12.95	7	37.70
Don Quichotte	M	Xérès	0.72	17.82	17	88.40
Gargantua	M	Goma	0.20	55.07	80	378.58
Hector	M	Héra	0.00	58.65	66	304.23
Lefkas	M	Loukoum	0.16	67.66	98	454.13
Ovide ^a	M	Ondine	0.36	0.36	1	3.77
Papot	M	Perla	0.36	70.72	91	412.52
Pollux ^a	M	Castor	0.43	5.98	4	20.88

TABLE 2 Details of the individual subjects used in this study with associated sample sizes. Sex (M/F), name of the Mother, Age (exact or estimated^a) in months across which observations occurred (Minimum–Maximum), Days: the number of focal observation days and total 'Duration' in hours of observational data are reported for each subject

^aWe used the first day of the birth month as an estimated birth date and calculated ages accordingly

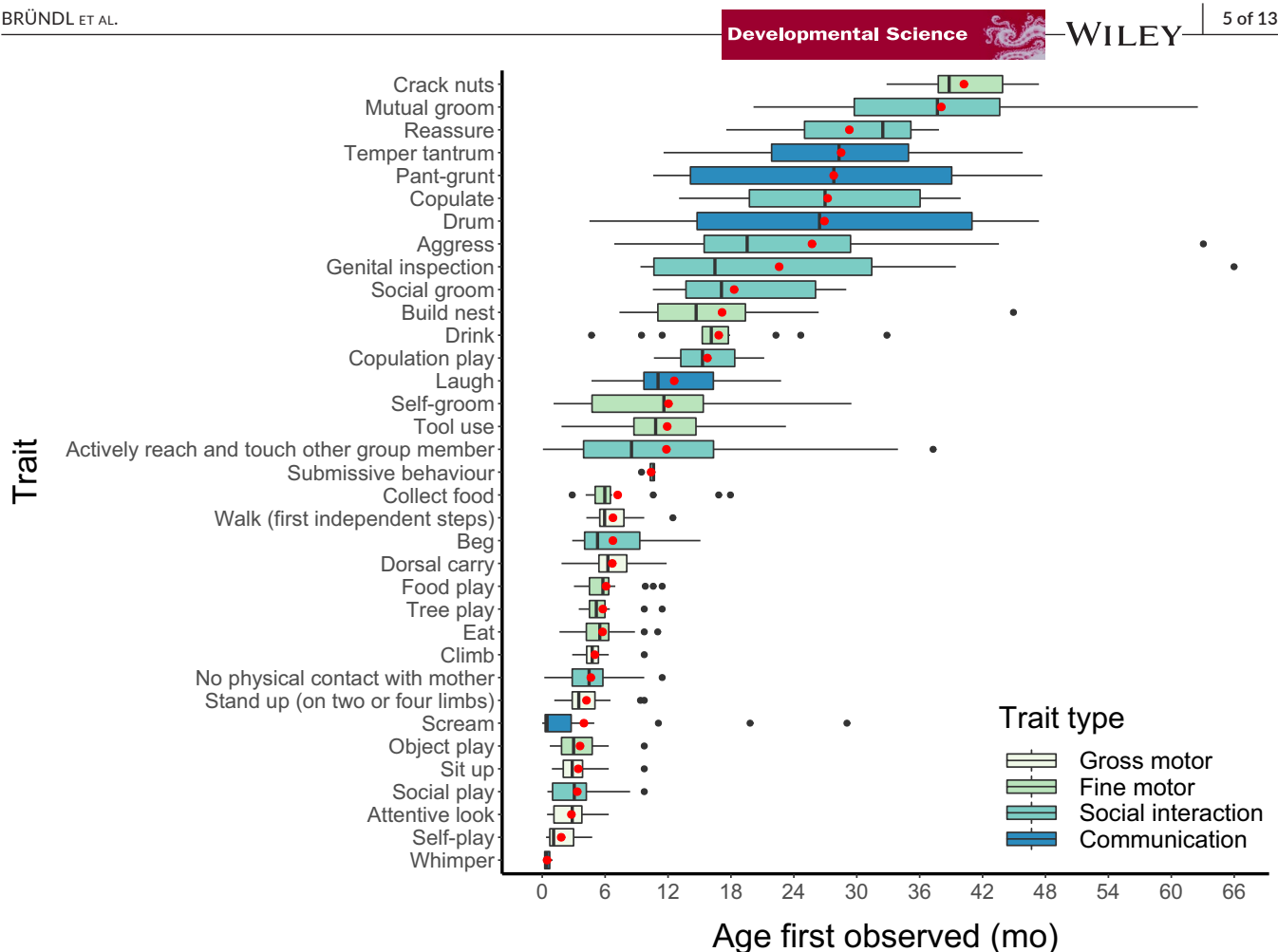


FIGURE 1 Developmental milestones of motor, social interaction and communication traits. Boxplots represent the first observed occurrence (in months) of each behavioural trait, including the interquartile range, median, minimum and maximum range and outliers. Red points represent the means per behavioural trait. Traits are sorted by ascending mean

and tool use (Krapp & Wilson, 2005). Then, we compiled and compared 10 functionally overlapping motor milestones with those found in humans (Table 3). For the statistical comparison of these motor milestones, we ran a paired samples Wilcoxon signed-rank test (the data were non-normally distributed). We compared our data to the mean first emergence of other studies performed on wild chimpanzee populations (Figure 2). The studies were selected on the criteria that we could extract first emergence of comparable behavioural traits as in our study. In particular, we included studies with continuous data from the first year of life, not clustered into age groups.

Lastly, we compare our data to the data from human studies (Figure 3). Comparing development between humans and chimpanzees is not unproblematic (see Table 1). For instance lifespan in the absence of medical intervention during life remain estimates in both species: in many human societies dates of birth are not systematically recorded, hence actual ages, especially for older individuals, are rarely known (Walker, Gurven, et al., 2006). Chimpanzees are long-lived primates so that even in field sites with >40 years of records, dates of birth of the oldest individuals remain estimates (Wittig & Boesch, 2019a). Likewise,

corrected for other life-history traits such as age at sexual maturity can be hard to directly measure, often requiring a proxy measure of age of first reproduction (see Boesch, Bombjaková, et al., 2019). Whilst this can be relatively accurately determined for male chimpanzees using genetic paternity testing, most female chimpanzees emigrate from their natal communities before first reproduction, hence ages of reproductive females in habituated communities are usually estimates (Wittig & Boesch, 2019b). From a limited sample size of females that emigrated from one habituated community into another habituated community, exact birth dates are known, allowing calculation of age at first reproduction, as 16 years (Walker, Walker, Goodall, & Pusey, 2018). In humans, cultural and social constraints may cause a divergence between age at sexual maturity and age at first reproduction for both women and men (Gillespie, Russell, & Lummaa, 2013; Rindfuss & St. John, 1983). To compensate for these shortcomings, we present all three measures of developmental milestone emergence: absolute age of emergence of developmental milestones, and milestones corrected with estimates of age at first reproduction and modal adult lifespan (i.e. old-age mortality; see Horiuchi et al., 2013).

TABLE 3 Characteristics of the emergence of comparable behavioural traits for chimpanzees and humans, including the mean first day of emergence and standard deviation (SD). Operational definitions for chimpanzee traits can be found in Table S2 (advanced tool use in chimpanzees refers to nut cracking) and for human traits can be found in Table S3

Trait	Species				Reference
	Chimpanzee		Human		
	M	SD	M	SD	
Attentive look	2.78	1.92	2.00	NA	1
Sit up	3.43	2.21	6.00	1.10	2
Object play	3.60	2.40	3.50	NA	3
Stand up	4.22	2.49	11.00	1.90	2
Climb	5.01	1.49	21.10	5.20	4
Eat	5.75	2.52	8.87	2.58	5
Walk	6.75	2.26	12.10	1.80	2
Tool use	11.92	5.92	15.00	NA	5
Laugh	12.59	5.37	4.00	NA	6
Drink	16.83	6.73	17.50	4.60	4
Advanced tool use	40.22	4.72	48.00	NA	7

Note: Corresponding references from the human literature are: (1) Fantz, 1964; (2) Onis, 2006; (3) Williams, 2003; (4) Flensburg-Madsen & Mortensen, 2018; (5) Carruth et al., 2004; (6) Sroufe & Wunsch, 1972; (7) Boesch, Bombjaková, et al., 2019.

3 | RESULTS

Gross motor traits, involving coordination of large body parts such as arms and legs, were the first to develop with a mean emergence of 4 months (± 2.8 SD, range = 0.4–6.7). Traits such as sit up ($M = 3.4$ months ± 2.2 SD, range = 0.9–9.7), stand up ($M = 4.2$ months ± 2.5 SD, range = 1.2–9.7) and walk ($M = 6.7$ months ± 2.3 SD, range = 4.2–9.7) followed a head-to-toe order in emergence pattern. We found that fine motor traits generally emerged later, mostly after the first 6 months ($M = 15$ months ± 7.4 SD, range = 3.6–40.2). For example we found that, object play, where infants play with objects such as leaves, shrubs or lianas, emerged at 4 months (± 2.4 SD, range = 0.7–9.7) compared to more complex traits such as cracking nuts, which emerged at 3.3 years, that is an average 40 months (± 4.7 SD, range = 32.8–47.4).

We observed social interaction traits emerge at a mean of 14 months (± 7.2 SD, range = 3.3–38.1). We first observed touching other group members and mutual grooming, that is reciprocal grooming between the infant and another member of the group, at respective 12 months (± 11.8 SD, range = 0.1–37.3) and 38 months (± 12.7 SD, range = 20.2–62.5). Communication traits had a mean emergence of 12 months (± 6.4 SD, range = 0.5–28.5), though there was much variation between traits. For example we found that whimpering emerged immediately after birth ($M = 0.5$ months ± 0.3 SD, range = 0.1–1.0), whereas more complex, socially directed

vocalizations such as pant-grunting ($M = 27.8$ months ± 13.9 SD, range = 10.6–47.7) emerged later.

We found more variation around the mean for later emerging and more complex traits such as social grooming ($SD = 6.7$) and tool use ($SD = 5.9$), compared to gross motor traits, for instance sitting up ($SD = 2.2$). When comparing our results with other studies performed on wild chimpanzee and pre-industrial human populations, we found considerable overlap in the timing of emergence of traits (Figures 2 and 3; Table 3). For the later emerging traits, more variation between chimpanzee studies was found. However, we estimated similarly large levels of variation for these later traits within our study as between studies.

4 | DISCUSSION

This study systematically presents the first occurrence of a wide array of behavioural traits in wild chimpanzees, traits which emerge across the first years of life. We found that gross motor traits were the first to emerge at an average of 4 months with the majority of gross motor traits observed during the first six postnatal months (Figure 1). Communication traits emerged at an average of 12 months, social interaction traits at 14 months and fine motor traits at 15 months. Variation in the emergence of behavioural traits increased with later developing, more 'complex' traits (Figure 1).

Our results reveal that although gross motor milestones generally emerge earlier in chimpanzees than in humans, this is not necessarily the case for fine motor, social and communication milestones, at least across the first 5 years of life. The patterns were similar across the three comparative measures of milestone emergence (absolute age, ages standardized by age at first reproduction and lifespan) (see Table 1; Figure 3). For instance we found a similar head-to-toe sequence of gross motor emergence as seen in humans (Bard & Leavens, 2014; Gesell & Ames, 1940; Woollacott, Debu, & Mowatt, 1987) (Figure 3), which also mirrors emergence patterns found in smaller sample sizes of other wild chimpanzee studies (Figure 2). We observed fine motor traits emerge later than gross motor traits (Figure 1). It is harder to directly compare fine motor traits between chimpanzees and humans as many traits are functionally different. That said, some fine motor traits are of comparable nature (Figure 3). For example object play emerges at around 4 months in chimpanzees and humans (Williams, 2003). Object play may mark the transition from gross to fine motor skills and the development of fine hand motor control such as reaching-grasping, which may indicate maturation of cortical motor areas (Ferrari, Bonini, & Fogassi, 2009; Ferrari, Paukner, Ruggiero, et al., 2009). Our current ethogram does not let us distinguish between these more subtle differences in motor abilities, though we plan further, detailed investigation on this in chimpanzees.

Other fine motor traits, such as simple tool use, emerge at similar times in chimpanzees (12 months) and children (15 months; Carruth, Ziegler, Gordon, & Hendricks, 2004). Successful, more advanced

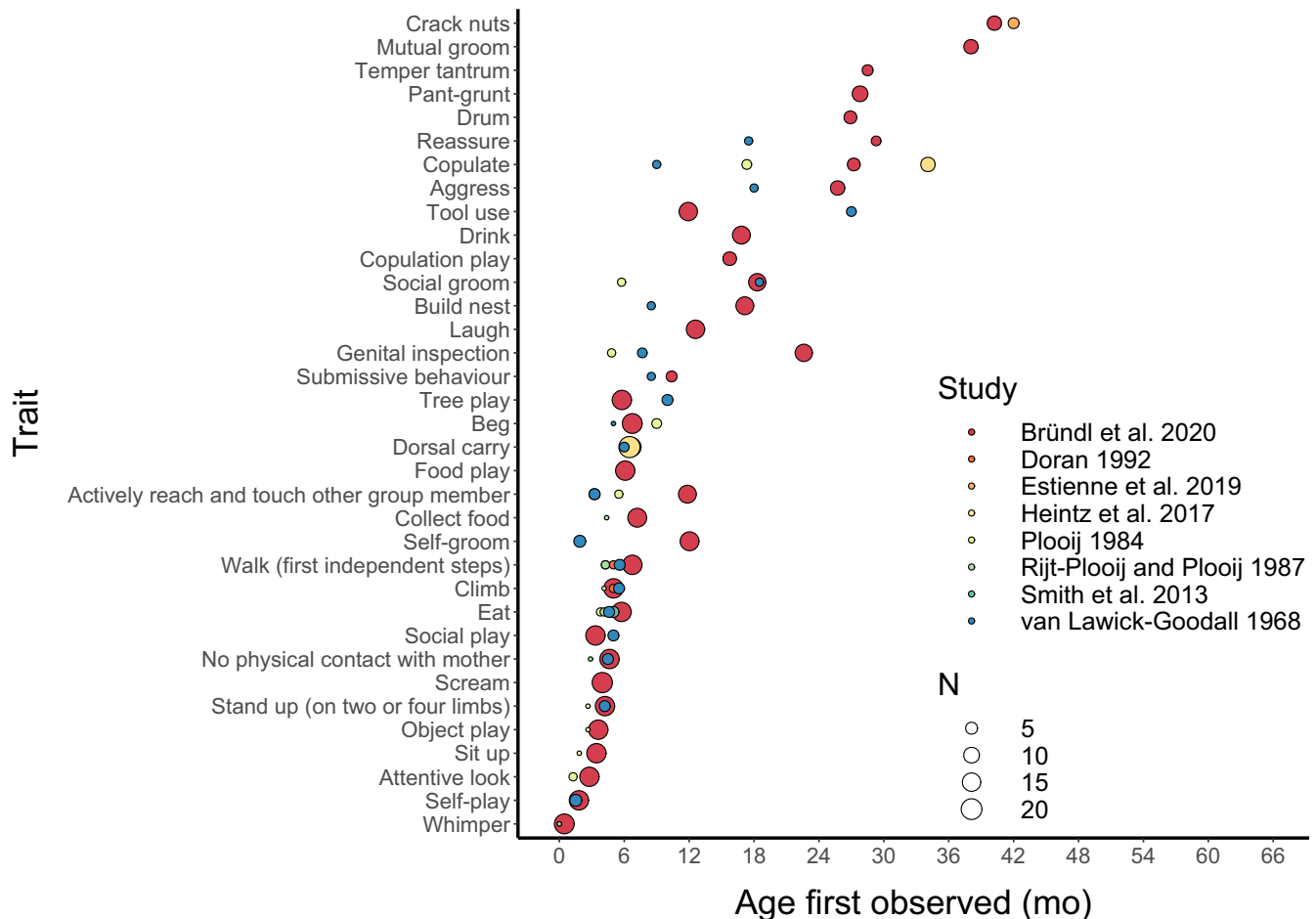


FIGURE 2 Comparison of developmental milestones of the first observed occurrence (in months) of motor, social interaction and communication traits between different studies of wild chimpanzee populations (References: Doran, 1992; Estienne et al., 2019; Heintz, Murray, Markham, Pusey, & Lonsdorf, 2017; Plooij, 1984; Rijt-Plooij & Plooij, 1987; Smith et al., 2013; Van Lawick-Goodall, 1968). Points represent means per behavioural trait with point size being proportional to sample size. Traits are sorted by ascending mean

tool use, that is cracking nuts, emerge at 3.4 years in chimpanzees. This timeframe is in accordance with previous studies investigating tool use in the wild (e.g. Boesch, Bombjaková, et al., 2019; Estienne et al., 2019). Again, we see overlap in tool use emergence patterns with humans; for example children from the Mbendjele forager society, Republic of Congo, show interest and emerging skills in tool use to crack nuts under the age of five, indicating similar levels of cognitive development affecting nut cracking as in chimpanzees (Figure 3; Boesch, Bombjaková, et al., 2019). In the traditional, indigenous Parakanã people of Brazil girls as early as 4 years start manufacturing palm leave baskets (Gosso, Otta, Ribeiro, & Bussab, 2005). However, in chimpanzees as in humans, tool use may start in infancy, but efficiency levels are still lower than in adults. Estienne et al. (2019) found, for example that chimpanzee tool use does not reach a plateau of success until after 8 years of age (in support see Boesch, Wittig, et al., 2019; Matsuzawa, 1994). This similar slow timeframe in reaching developmental milestones in chimpanzees and humans suggests that this reflects a similarly long brain development and skills acquisition period in both species, though this should be investigated on a large scale.

Sociocommunicative milestones are not readily comparable in humans and chimpanzees. Tentatively, we find no initial indication that chimpanzee communication and social milestones emerge earlier than in humans. For communication traits, we found that whimpering emerged immediately after birth which is comparable to infant crying in humans (Zeskind, 1985). Laughing is seen from 4 months in humans (Sroufe & Wunsch, 1972) versus 12.6 months in chimpanzees, that is 0.5% and 2.3% of the respective species' lifespan. This is despite play, the context in which laughter is emitted, emerging much earlier in chimpanzees at 3 months (Figure 1). More complex, socially directed vocalizations such as pant-grunts, which in chimpanzees are used as expressions of submission directed towards dominant individuals, emerge at 2.3 years (Laporte & Zuberbühler, 2011). In humans, first words are uttered at the end of the first year (Capute et al., 1986), although it is not straight forward to relate human words to chimpanzee vocalizations. For social interaction traits, we can compare reassurance of group members by infant chimpanzees, emerging at an average of 2.4 years, whereas comforting behaviours by human infants are observed as early as 13 months (Dunfield, Kuhlmeier, O'Connell, & Kelley, 2011; Zahn-Waxler, Radke-Yarrow,

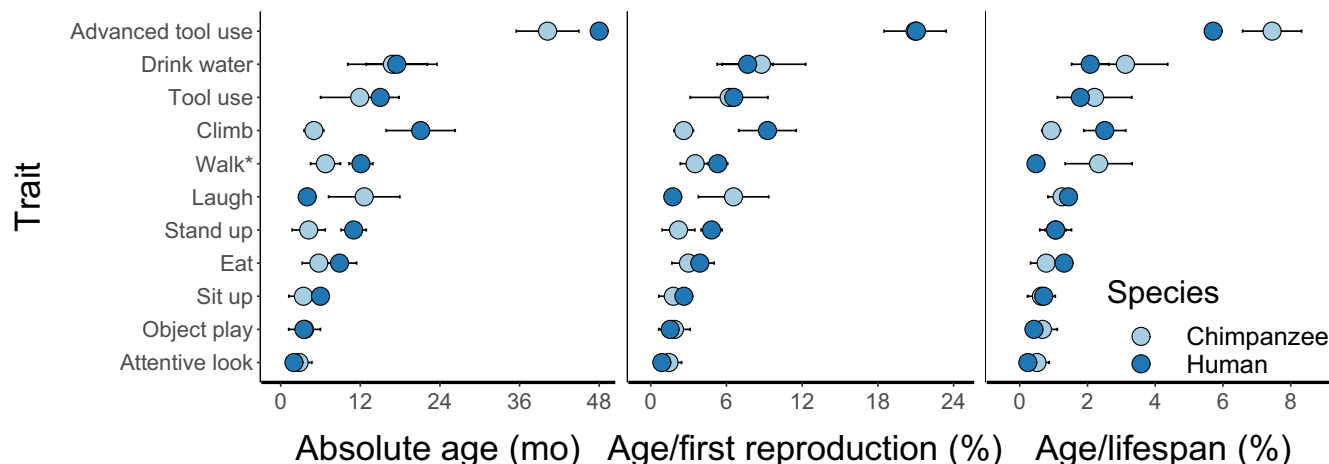


FIGURE 3 Comparison of developmental milestones of the first observed occurrence of traits between wild chimpanzees and humans. (a) Points represent mean first, absolute age of emergence (in months) and lines represent standard deviation (SD); (b) points represent mean first, relative age of emergence standardized as % of age at first reproduction and lines represent SD (standardized as % of age at first reproduction); (c) points represent mean first, relative age of emergence standardized as % of modal adult lifespan and lines represent SD (standardized as % of modal adult lifespan). Operational definitions for chimpanzee traits can be found in Table S2 (advanced tool use in chimpanzees refers to nut cracking) and for human traits can be found in Table S3. Traits are sorted by ascending mean. *First independent steps. Corresponding references from the human literature are: attentive look: Fantz, 1964; sit up, stand up, walk: Onís, 2006; object play: Williams, 2003; climb, drink: Flensburg-Madsen & Mortensen, 2018; eat, tool use: Carruth et al., 2004; laugh: Sroufe & Wunsch, 1972; advanced tool use: Boesch, Bombjaková, et al., 2019

Wagner, & Chapman, 1992). This translates into 5.6% and 1.5% of the respective chimpanzee and human lifespan.

One key species difference is that human infants are weaned at an earlier age than chimpanzees, at an average 2.5 years earlier, and that in turn, the inter-birth interval is shortened by around 2 years in humans (Kaplan et al., 2000). One hypothesis for these differences in the inter-birth interval is the evolution of extensive alloparenting in humans (Hawkes et al., 2017; Hrdy, 2005, 2011; Isler & van Schaik, 2012; Richerson et al., 2016), which is comparatively absent in chimpanzees (Bădescu, Watts, Katzenberg, & Sellen, 2016). This species difference in alloparenting may, in turn, be associated with species differences in reliance on social interactions and vocal communication during development (Matsuzawa, 2006), whereby human infants develop social and communication skills rapidly relative to other milestones in order to advertise their needs beyond their mother-offspring dyad to non-maternal group members (Zuberbühler, 2011). Conversely, it has also been suggested that there may be selection pressures for rapid vocal and social development in chimpanzees. For example interaction efforts by young chimpanzees may lower infanticide risk, with more socially communicative infants receiving less aggression from group members (Laporte & Zuberbühler, 2011). Given that these two ideas are somewhat conflicting and social and communicative traits are often not readily comparable between the species with current data sets, this prevents us from setting up clear comparative predictions on the development of these traits. By aligning data collection protocols across species, comparisons of social and communication milestones across more primate species with different social systems, levels of alloparental care and development pressures are likely to be informative. Building a comprehensive evolutionary framework to predict

variation in developmental progression across primates that can be related to life-history variation is needed.

Our results illustrate that comparisons of the emergence of developmental milestones between species can be informative. However, gaps in determining the emergence of developmental milestones remain. For example more subtle, very early mother-infant communication exchanges have been observed in humans and other primate species, which may also exist in wild chimpanzee infants, warranting further study (Ferrari, Paukner, Ionica, & Suomi, 2009). Tomasello and Carpenter (2007) have also argued that shared intentionality, that is 'collaborative interactions in which participants share psychological states with one another', is a primarily human characteristic, with human infants as young as 1-year-old being highly motivated to share their knowledge with group members. In contrast, intentionality in chimpanzees has largely been demonstrated in adults (Crockford, Wittig, Mundry, & Zuberbühler, 2012; Crockford, Wittig, & Zuberbühler, 2015; Hobaiter & Byrne, 2014; Schel, Townsend, Machanda, Zuberbühler, & Slocombe, 2013), and it is not yet known when this complex form of social cognition develops in the species. However, overall our findings are in line with the delayed benefits hypothesis, which posits that extended development is necessary for acquiring adult skills, with these skills being linked to increases in overall survival and fitness, and therefore leading to the selection of similar life histories in humans and chimpanzees (Charnov & Berrigan, 1993; Jones, 2011; Powell et al., 2019; Stearns, 1992).

We also observed increasing inter-individual variation in the emergence of later and more complex traits compared to earlier traits (Figure 1). This pattern matches other studies from the human developmental literature (Siegler, 2006; Siegler et al., 2014; Vereijken, 2010). Both species live in complex ecological and social

settings and rely heavily on fine motor and socially directed traits for survival, especially as adults. For instance individuals in both species have to manipulate their environment (e.g. use tools) to acquire high-nutrient foods (Boesch, 2012; Boesch & Boesch-Achermann, 2000). They also need to cooperate with non-kin group members to defend their territory (Samuni, Mielke, Preis, Crockford, & Wittig, 2019; Samuni et al., 2017), these being the same individuals they compete with at the within-group level over food and mates (Wittig & Boesch, 2003). Whilst early-emerging traits may be under strong genetic control, later emerging traits may be more prone to environmental influence. Relevant socioecological factors may include exposure to ecological stressors (Tung, Archie, Altmann, & Alberts, 2016; Wessling et al., 2018) or maternal effects (Bard, 1994; Bogart, Bennett, Schapiro, Reamer, & Hopkins, 2014; Murray et al., 2018). In humans, for instance variation in reaching developmental milestones may be caused by a genetic predisposition, general health or other environmental factors, such as maternal investment (Bateson et al., 2004). A study in the Taï chimpanzee population recently showed that offspring of low-ranking mothers and those whose mothers die post weaning experience lower growth than those of high-ranking mothers or mothers who stay alive (Samuni et al., 2020). Whether maternal effects also impact on motor and sociocommunicative milestones remains to be investigated in chimpanzees (Lee et al., 2019), but is known to be influential in humans (Fraley, Roisman, Booth-LaForce, Owen, & Holland, 2013). The fact that both species have more inter-individual variation in the timing of later milestones highlights a shared element of developmental plasticity important for a long-lived species.

5 | CONCLUSIONS

Overall, we found that developmental milestones continue to emerge at least across the first 5 years of chimpanzee life. We found *no* general bias of earlier development compared to humans, supporting the delayed benefits hypothesis (Charnov & Berrigan, 1993; Jones, 2011; Powell et al., 2019; Stearns, 1992). Particularly, more complex traits such as fine motor, social interaction and communication traits generally emerged later than gross motor milestones with considerable variation between individuals. Based on our results we hypothesize, that development in motor cortex areas involving gross motor movement might be faster in chimpanzees, but that development in fine-motor and social cognition brain areas parallel development found in humans. Our results support the life-history brain development hypothesis (Garwicz et al., 2009; Harvey & Clutton-Brock, 1985; Kaplan et al., 2000), suggesting that chimpanzees sustain a similarly slow brain development as humans, at least during the first 5 years of life. A further test of this key hypothesis in human evolution would be to examine development across an array of primate species. Species with more rapid brain maturation should meet motor and sociocognitive milestones earlier than species with slower brain maturation. Our results demonstrate the value in comparative developmental studies

in understanding life history, especially by focusing on early development, and on a range of behavioural and sociocommunicative traits to estimate population and species level norms and differences in development across primates (Bard & Leavens, 2014). Our data are helpful in forming hypotheses about brain maturation in primate species and also provides a comparative machine for evaluating norms versus inter-individual differences in development, which is relevant for assessing causes of within-species variation in reaching development milestones, such as maternal or genetic effects. It remains a challenge to directly compare developmental milestones in humans and other animals such as chimpanzees but given similar underlying functions, this is a fruitful avenue for future research into the evolution of life histories. Finally, we recommend greater consideration of species comparisons in attempts to understand the evolutionary drivers of developmental trajectories.

ETHICS STATEMENT

Permissions to conduct the research were granted by the Ministries of Research and Environment of Côte d'Ivoire and the Office Ivoirien des Parcs et Réserves. Methods were approved by the 'Ethikrat der Max-Planck-Gesellschaft'.

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CONFLICT OF INTEREST

We have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

ACB, CB, RMW and CC conceived the study, GNK collected the data, ACB compiled the data and conducted the analyses, and ACB wrote the paper with important contributions from PT, CB, RMW and CC. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in 'figshare' at <https://doi.org/10.6084/m9.figshare.12280268.v1>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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