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Maternal Behavior by Birth Order in Wild Chimpanzees (*Pan troglodytes*)

Increased Investment by First-Time Mothers

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Parental investment theory predicts that maternal resources are finite and allocated among offspring based on factors including maternal age and condition, and offspring sex and parity. Among humans, firstborn children are often considered to have an advantage and receive greater investment than their younger siblings. However, conflicting evidence for this “firstborn advantage” between modern and hunter-gatherer societies raises questions about the evolutionary history of differential parental investment and birth order. In contrast to humans, most nonhuman primate firstborns belong to young, inexperienced mothers and exhibit higher mortality than laterborns. In this study, we investigated differences in maternal investment and offspring outcomes based on birth order (firstborn vs. laterborn) among wild chimpanzees (*Pan troglodyte schweinfurthii*). During the critical first year of life, primiparous mothers nursed, groomed, and played with their infants more than did multiparous mothers. Furthermore, this pattern of increased investment in firstborns appeared to be compensatory, as probability of survival did not differ by birth order. Our study did not find evidence for a firstborn advantage as observed in modern humans but does suggest that unlike many other primates, differences in maternal behavior help afford chimpanzee firstborns an equal chance of survival.

Conditions experienced during early development can have lasting fitness consequences (Lindstrom 1999). In most mam-

mals, early experiences are primarily mediated by the mother (Fairbanks 1996; Maestriperi 2009). According to parental investment theory, maternal resources are finite, and a mother will invest in herself and her offspring in a manner that maximizes her reproductive success (Clutton-Brock 1991; Trivers 1972). In general, primate mothers invest a substantial amount of time and energy in a few, high-quality offspring. How these resources are allocated, however, depends on a number of variables, including maternal age and condition, and offspring age, sex, and parity (Clutton-Brock 1991; Daly and Wilson 1995; Trivers 1974; Trivers and Willard 1973).

Human firstborns are often considered to be at an advantage when compared to laterborns. Studies report higher intelligent quotients among firstborn children (e.g., Kristensen and Bjerkedal 2007) who may benefit from spending part of their dependency not competing with siblings for resources. Firstborns also traditionally receive more schooling and inherit more land and wealth (Hrdy and Judge 1993). Additionally, American parents invest more “quality time” in their firstborn child (Price 2008) and engage in more affiliative behaviors with their firstborn infant (Jacobs and Moss 1976). Theoretically, even if parents divide resources equally among offspring at any given time, the cumulative distribution favors the firstborn (Hertwig et al. 2002).

The evidence for a human firstborn advantage is prevalent in stratified societies characterized by nuclear families and inheritable material wealth. However, some argue that this right-of-birth is not present among hunter-gatherers due to the absence of divisible material wealth and a communal rearing environment where children do not fall into birth-order specific social niches (Draper and Hames 2000). In support of this argument, a study of the Ju/'hoan (!Kung) revealed a positive relationship between higher birth order and “achievement” defined as fertility and reproductive success (Draper and Hames 2000). However, despite cultural differences, firstborn humans may still theoretically receive greater parental investment, particularly when resources are limited. Firstborns are closer to reproductive maturity at any given time than their younger siblings and thus a “safer investment” (Jeon 2008).

Conflicting evidence in humans based on cultural differences raises questions concerning the evolutionary history of parental investment by birth order and the origins of a firstborn advantage. In contrast to humans, research suggests that nonhuman primate firstborns are at a disadvantage. First-time mothers are typically less skilled than experienced mothers (Fairbanks 1996; Nguyen et al. 2012) and tend to be more protective and less rejecting (Fairbanks 1988, 1996; Gomendio 1989; Holley and Simpson 1981). These differences in maternal behavior in turn correspond to later offspring independence and increased anxiety in stressful situations (Bardi and Huffman 2002; Fairbanks 1996; Schino et al. 2001).

Primiparous nonhuman primate mothers are also typically young and still investing in their own somatic growth and

maturation (Bercovitch et al. 1998; Setchell et al. 2002). Even across human societies, adverse pregnancy outcomes are greater in mothers under 15 years of age who are not yet developmentally mature (Kramer and Lancaster 2010). The period of maternal investment may lengthen accordingly in order to reduce daily costs. Indeed, the interbirth interval (IBI) following the first birth is almost always longer than subsequent IBIs (e.g., gorillas: Robbins et al. 2006; chimpanzees: Jones et al. 2010; rhesus macaques: Gomendio 1989). Not surprisingly, firstborn savannah baboon offspring weigh less than laterborns (Altmann and Alberts 2005), mandrill infants of young mothers grow at a slower rate (Setchell et al. 2001), and young marmoset and rhesus mothers weigh less, produce less milk, and have smaller infants (Hinde et al. 2009; Tardif et al. 2001).

While marginal condition may favor a longer period of investment in firstborns, the increase often fails to compensate sufficiently. A recent review of primate literature found that 15 of 21 studies reported a negative relationship between birth order or young maternal age and offspring survival (Pusey 2012). Notably, this research is lacking in wild great apes, with the exception of a study of mountain gorillas in which first-born mortality was not significantly different than that of secondborns (Robbins et al. 2006).

Here, we examine how maternal behavior and offspring survival vary by birth order (firstborn vs. laterborn) among the wild chimpanzees (*P. troglodyte schweinfurthii*) of Gombe National Park, Tanzania. Previous work in chimpanzees demonstrated a longer IBI after the firstborn than after laterborns (Jones et al. 2010), but it is unclear if this is compensatory or biased investment. Like humans, chimpanzees live in multi-male, multi-female fission-fusion societies where temporary subgroups vary in size and composition (Goodall 1986; Nishida 1968). Males are the more gregarious sex, while female East African chimpanzees spend between 40% and 70% of their time alone with dependent offspring in overlapping core areas (Gombe: Murray et al. 2007; Williams et al. 2002; Wrangham and Smuts 1980; see Miller et al. [2014] for more discussion). High female dominance rank correlates with higher reproductive success (Pusey et al. 1997), which is likely due to differential space use and access to food (Emery Thompson et al. 2007; Kahlenberg et al. 2008; Murray et al. 2007). Female chimpanzees ascend the hierarchy with age (Murray et al. 2006); thus primiparous mothers are low ranking and likely outcompeted by older, higher-ranking multiparous females for access to high-quality resources.

The mother-infant relationship is primary in chimpanzees, and individuals are dependent upon their mothers for an extended period (Goodall 1967, 1986). Offspring are typically weaned between the ages of 3 and 5 (Clark 1977; Pusey 1983; Van de Rijt-Plooi and Plooi 1987; unpublished data); however, juveniles travel with their mother until adolescence (Pusey 1990). Here, we focused on three maternal behaviors: nursing, grooming, and playing. While work in other primates has examined nursing (e.g., Gomendio 1989), little is known

about other prosocial maternal behaviors despite their prevalence later in life. Grooming is the most common affiliative and stress-reducing behavior in primates (Aureli et al. 1999; Goosen 1981; Gust et al. 1993). Although grooming also serves a hygienic function (Akinyi et al. 2013), it is an integral aspect of chimpanzee social life (Goodall 1986). Social play is also considered important to young primates, and higher rates of social playing among Gombe chimpanzee infants is correlated with earlier spatial independence and age at first mating attempt (Heintz 2013).

We predict that levels of nursing will be higher in first-time mothers given that they are younger and lower in rank. At Gombe, female chimpanzees increase in mass until ~21 years of age (Pusey et al. 2005). The average age at first birth in this community is 15.5 years (unpublished data); thus first-time mothers are typically smaller and still investing in their own growth. These conflicting demands of maturation and lactation may influence milk quality or yield and favor more nursing (reviewed in Hinde and Milligan 2011) and may also constrain the frequency of less critical maternal behaviors, including grooming and playing. We further examine how birth order relates to offspring survival. Higher survival would suggest that firstborn chimpanzees carry an advantage similar to that found among some humans.

Material and Methods

Study Site

Gombe National Park is a small (35 km²) park located in western Tanzania that currently contains three chimpanzee communities. Here, we focused on the central Kasekela community, which has been studied continuously since 1960. During the study period, the community ranged in size from 38 to 64 individuals with 7–14 adult males, 12–26 adult females (adult ≥12 years), and 16–26 subadults.

Maternal Behavior by Birth Order

Behavioral Data. Data included in this study were collected from 1988 to 2012 as part of a long-term study of mother-infant behavior. Each observation day, research staff followed a focal mother, infant, and youngest sibling and recorded their behavior(s), relevant social partner, and distance between family members at 1-minute instantaneous point samples (Altmann 1974; Goodall 1986). Key behavioral events, such as aggression, were also recorded *ad libitum*. The target duration for mother-infant follows varied over the course of the study from 6 hours to 12 hours; however, some follows are shorter and durations unequal due to search times and losing sight of the focal. We focused on mother-infant pairs who were well sampled in a given year of the infant's life. We included all pairs with a minimum of four follows at least five hours in length per year (table 1). We examined maternal behavior toward infants in age classes 0–1, 1–2, and 2–3 years. After age 3 years mothers often begin to cycle; thus maternal behavior is potentially confounded with future reproductive

Table 1. Summary of observation time by birth order and age class

Age class	Birth order	Number of mother-infant pairs	Mean hours followed	SD hours followed
0–1	Firstborn	6	55.53	36.31
	Laterborn	12	58.58	23.66
1–2	Firstborn	6	63.19	31.66
	Laterborn	12	50.35	25.21
2–3	Firstborn	3	74.70	47.60
	Laterborn	13	55.17	13.63

effort. Since not all mother-infant pairs were well sampled at multiple ages, pairs included in each age class differed. For behavioral analyses, three mothers lost their actual firstborn within the first month of life and the subsequent surviving infant was considered her firstborn. These three mothers had limited maternal experience and were within the age range of primiparous mothers at the time of their subsequent surviving infant's birth. Maternal age at the birth of infants included in behavioral analyses ranged from 11.9 to 20.2 years (mean \pm SD: 15.5 \pm 2.8) for primiparous mothers and from 15.7 to 44.3 years (mean \pm SD: 29.4 \pm 8.4) for multiparous mothers. Maternal age was based on known births or estimated based on comparison of appearance to known-aged individuals (Goodall 1986).

Behavioral Metrics. We examined three types of mother-infant behavioral interactions: nursing, grooming, and playing. These behaviors were measured as the daily proportion of a follow spent engaged in that behavior. Minutes where the mother or infant behavior was unknown were excluded.

Behavioral Analyses. To investigate differences in the amount of time mothers spent interacting with their offspring, we fit separate generalized linear mixed models (GLMMs) for each age class with the proportion of each follow spent engaging in a behavior as the response variable and firstborn status (yes/no) as a fixed explanatory variable. To examine whether differences in maternal grooming and playing corresponded to differences in overall levels of infant social interactions, we also ran separate GLMMs with the proportion of each follow an infant spent engaged in social play or being groomed by any individual as the response variable. To account for behavioral differences associated with infant development over the course of the year, all GLMMs included infant age in days as a fixed factor. Infant ID nested within mother ID was included as a random effect to control for individual differences. Because the response variables were proportions and highly skewed, we dichotomized each behavioral variable (e.g., minutes the mother was playing with her infant vs. minutes not playing with her infant) and fit GLMMs using a binomial error distribution and a logit link function. An additional observation-level random effect was added to correct for overdispersion (Bates et al. 2011). Because some maternal behavior may differ toward infants of

different sexes, we also ran models including infant sex as a fixed effect. However, this factor was consistently nonsignificant and was not included in our final models. Also, because the firstborn sample at age class 2–3 consisted of all males, we ran this age class in two separate models: one including only male laterborns and another including both male and female laterborns. The results were similar, and we present results including both sexes.

Offspring Outcomes and Birth Order

Firstborn Survival. To test for differential survival by birth order we analyzed demographic data from 133 individuals ($N_{\text{firstborn}} = 37$, $N_{\text{laterborn}} = 96$) born in 1964 or later whose parity and sex were known and whose birthdates were known within 90 days. Individuals were considered dead only if strong evidence existed, such as observed poor health (Strier et al. 2010). Individuals who disappeared (and could have joined other communities) and individuals alive as of December 31, 2012, were right-censored. We used mixed-effects Cox models with birth order (firstborns compared to laterborns) and offspring sex (males compared to females) as fixed explanatory variables and mother ID as a random factor (Therneau and Grambsch 2000). We examined separate models for survival to age 1 year (critical first year of life when mortality is high), 5 years (approximate weaning), and 12 years (adulthood).

All analyses were conducted in R (version 3.0.1; R Development Core Team 2013) using the lme4 package for GLMMs (Bates et al. 2011) and the coxme package for mixed-effects Cox models (Therneau 2011).

Results

Maternal Behaviors

During the first year of life, primiparous mothers nursed, groomed, and played with their infants more than multiparous mothers (table 2; fig. 1). There were no significant differences between primiparous and multiparous mothers in age class 1–2 (mean proportion \pm SE: nursing: firstborn, 0.030 \pm 0.002, laterborn, 0.030 \pm 0.002; grooming: firstborn, 0.029 \pm 0.003, laterborn, 0.027 \pm 0.003; playing: firstborn, 0.013 \pm 0.003, laterborn, 0.018 \pm 0.003; table 2) or age class 2–3 (mean proportion \pm SE: nursing: firstborn, 0.029 \pm 0.003, laterborn, 0.024 \pm 0.002; grooming: firstborn, 0.028 \pm 0.005, laterborn, 0.031 \pm 0.003; playing: firstborn, 0.013 \pm 0.006, laterborn, 0.006 \pm 0.001; table 2).

Offspring Behaviors

There were no significant differences between firstborns and laterborns in the total amount of playing with any individual (mean proportion \pm SE: age class 0–1: firstborn, 0.035 \pm 0.009, laterborn, 0.019 \pm 0.003; age class 1–2: firstborn, 0.108 \pm 0.013, laterborn, 0.121 \pm 0.009; age class 2–3: firstborn, 0.118 \pm 0.019, laterborn, 0.122 \pm 0.011. GLMM estimate \pm SE: age class 0–1: 0.743 \pm 0.602, $z = 1.234$, $P =$

Table 2. Parameter estimates of GLMMs with average proportion of time spent engaged in a maternal behavior as the response variable

Infant age class	Response variable	Fixed factor	Estimate	SE	Z	P
0-1	Nursing	Intercept	-3.914	.189	-20.672	<.001
		Firstborn	.678	.258	2.624	.009
		Age	.0004	.001	.602	.547
	Playing	Intercept	-11.088	1.111	-9.972	<.001
		Firstborn	1.771	.783	2.263	.024
		Age	.010	.004	2.399	.016
	Grooming	Intercept	-5.498	.249	-22.096	<.001
		Firstborn	.669	.263	2.546	.011
		Age	.005	.001	5.359	<.001
1-2	Nursing	Intercept	-4.033	.264	-15.265	<.001
		Firstborn	.024	.190	.129	.898
		Age	.001	.0004	1.475	.140
	Playing	Intercept	-3.930	.910	-4.318	<.001
		Firstborn	-.423	.628	-.673	.501
		Age	-.003	.002	-1.709	.087
	Grooming	Intercept	-3.682	.462	-7.964	<.001
		Firstborn	.190	.189	.987	.324
		Age	-.001	.001	-.842	.400
2-3	Nursing	Intercept	-2.691	.515	-5.229	<.001
		Firstborn	.064	.403	.158	.875
		Age	-.001	.001	-2.511	.012
	Playing	Intercept	-5.443	2.754	-1.977	.048
		Firstborn	.888	.822	1.081	.280
		Age	-.003	.003	-.899	.329
	Grooming	Intercept	-.915	.761	-1.202	.229
		Firstborn	-.185	.221	-.835	.404
		Age	-.003	.001	-3.895	<.001

Note. Age is the infant's age in days. Significance of fixed effects was determined using Wald tests. $P < .05$ is indicated in bold. GLMM, generalized linear mixed model; SE, standard error.

.217; age class 1-2: -0.326 ± 0.307 , $z = -1.051$, $P = .293$; age class 2-3: -0.027 ± 0.789 , $z = -0.034$, $P = .973$) or total grooming received at any age; however there was a tendency for firstborns to receive more grooming during the first year of life (mean proportion \pm SE: age class 0-1: firstborn 0.034 ± 0.005 , laterborn 0.029 ± 0.003 ; age class 1-2: firstborn 0.030 ± 0.003 , laterborn 0.039 ± 0.004 ; age class 2-3: firstborn 0.029 ± 0.005 , laterborn 0.043 ± 0.004 . GLMM: age class 0-1: 0.499 ± 0.265 , $z = 1.881$, $P = .060$; age class 1-2: -0.103 ± 0.211 , $z = -0.490$, $P = .624$; age class 2-3: -0.359 ± 0.345 , $z = -1.041$, $P = .298$).

Offspring Survival

There was no difference by firstborn status in survival to age 1 year (birth order: $\beta = -0.319$, hazard ratio = 0.727, $z = -0.66$, $P = .51$; sex: $\beta = 0.168$, hazard ratio = 1.183, $z = 0.40$, $P = .69$), 5 years (birth order: $\beta = 0.093$, hazard ratio = 1.098, $z = 0.29$, $P = .77$; sex: $\beta = 0.120$, hazard ratio = 1.128, $z = 0.41$, $P = .68$), or 12 years (birth order: $\beta = -0.071$, hazard ratio = 0.932, $z = -0.24$, $P = .81$; sex: $\beta = 0.153$, hazard ratio = 1.165, $z = 0.57$, $P = .57$).

Discussion

Primiparous mothers nursed, groomed, and played with their infants more than multiparous mothers in the first year of the infant's life. That maternal behavior differed in the first year is not surprising as mortality rates are highest during this period (Bronikowski et al. 2011; Goodall 1986; Hill et al. 2001), and infants spend the first 4-6 months in almost constant contact with their mothers (Goodall 1986). Isolation studies in macaques also suggest that the first 6-12 months of life are critical for proper socialization (Harlow and Novak 1973). Despite the observed increased investment in firstborns

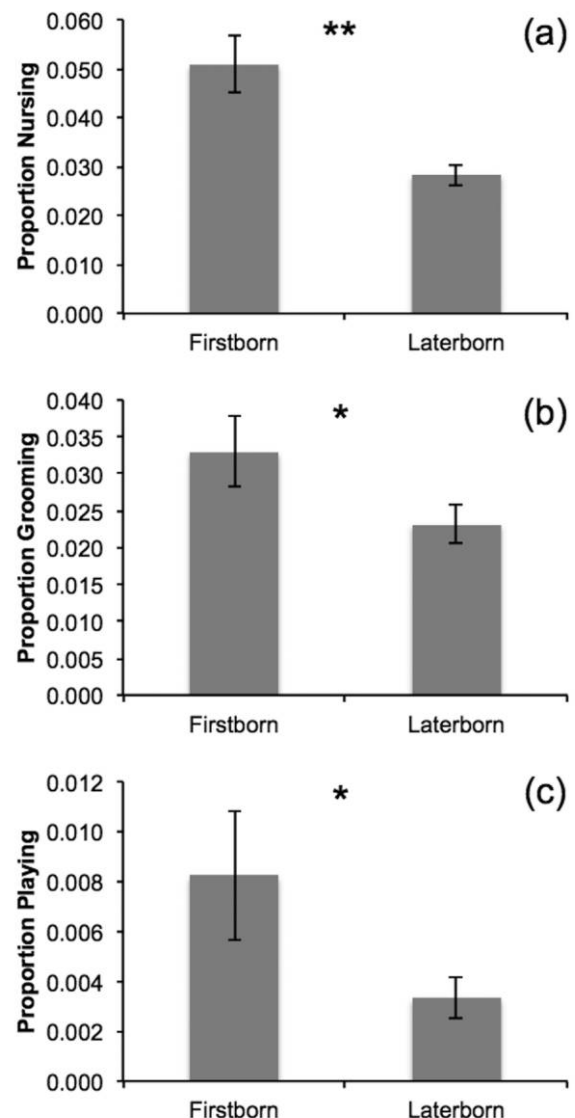


Figure 1. Mothers' proportion (mean \pm SE) of time spent (a) nursing, (b) grooming, and (c) playing with their infant by birth order at age class 0-1 years. $N_{\text{firstborn}} = 6$; $N_{\text{laterborn}} = 12$. (* $P < .05$, ** $P < .01$).

by chimpanzee mothers, we did not find differences in survival. Firstborns and laterborns were equally likely to survive; thus, by spending more time in maternal behavior than multiparous mothers, primiparous females appear to be compensating for their presumed poor condition and inexperience rather than enhancing firstborn success.

Whether the greater time spent nursing corresponds to greater nutritional investment in firstborns is uncertain since the amount and composition of the milk transferred is unknown. Firstborns may nurse more to compensate for lower milk quality or yield (Hinde and Milligan 2011); thus the nutritional investment in firstborns and laterborns may be the same. It is also possible that firstborns nurse more to compensate for their smaller size or poor condition. Regardless of nutritional investment, the longer IBIs following first births (Jones et al. 2010) represent a greater investment of maternal time in firstborns.

Most intriguingly, first-time mothers spent a greater proportion of time interacting with their infants. This difference may be partially explained by the targeted investment hypothesis, which posits that primiparous mothers are not experienced enough to allocate their time efficiently; thus more attention is not necessarily beneficial (Cameron et al. 2000; Fairbanks 1996; Nguyen et al. 2012). However, another important consideration is that firstborns lack an older sibling to interact with. Since chimpanzee juveniles remain behaviorally dependent on their mothers after the birth of the next infant, the majority of laterborns have a readily available social partner. Interestingly, our results indicate that firstborns engaged in overall social play as much as laterborns, but they tended to receive more overall grooming in the first year of life. Brent et al. (1997) found that wild chimpanzee infants without siblings engaged in social interactions as often as infants with siblings and suggested that all infants seek a given level of social interaction. In that study, infants without siblings interacted more with others but not with their mothers; however, those analyses focused on older infants and did not differentiate firstborns from laterborns whose siblings had died. Our results suggest that the early social requirements for firstborns, at least for play behavior, are met by mother-infant interactions, rather than interactions with others.

How mother-infant interactions are influenced by the presence of older siblings remains an open question in wild chimpanzees. It is possible that mothers interact more with their firstborn infant because there is no older offspring competing for attention. Indeed, this is cited as a possible source of the firstborn advantage in modern humans (Lindert 1977). The observed increased grooming by the mother to the point that firstborns tend to receive more grooming overall is likely explained by this lack of distraction. Regardless of whether mothers specifically interact more with firstborns, or the increased attention is a by-product of having only one dependent, our results indicate that firstborn chimpanzees receive more maternal interaction than laterborns; however, this difference does not translate into differential survival.

Wild chimpanzees have both higher mortality and lower fertility than human hunter-gatherers (Emery Thompson 2013; Hill et al. 2001; Kaplan et al. 2000). When considered in concert with the absence of male provisioning and direct paternal care, maternal investment in each infant is likely even more critical to reproductive success in chimpanzees than in humans. Although primiparous chimpanzee mothers face the detrimental effects of young age, low rank, and inexperience, our results indicate that differences in their behavior help overcome these challenges. Offspring of primiparous mothers are as likely to survive as those of multiparous mothers. While we did not find evidence for the firstborn advantage in chimpanzees that is observed in modern human societies, chimpanzee firstborns also do not appear to be at the same disadvantage as many other firstborn primates. Our results suggest that in chimpanzees, differences in maternal behavior toward firstborns are compensatory and help afford firstborns an equal opportunity to survive. In humans, certain societal conditions, such as inherited material wealth, may intensify this investment beyond compensation to the point of a firstborn advantage.

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