

EVOLUTIONARY BIOLOGY

Postweaning maternal care increases male chimpanzee reproductive success

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Humans are unusual among animals for continuing to provision and care for their offspring until adulthood. This “prolonged dependency” is considered key for the evolution of other notable human traits, such as large brains, complex societies, and extended postreproductive lifespans. Prolonged dependency must therefore have evolved under conditions in which reproductive success is gained with parental investment and diminished with early parental loss. We tested this idea using data from wild chimpanzees, which have similarly extended immature years as humans and prolonged mother-offspring associations. Males who lost their mothers after weaning but before maturity began reproducing later and had lower average reproductive success. Thus, persistent mother-immature son associations seem vital for enhancing male reproductive success, although mothers barely provision sons after weaning. We posit that these associations lead to social gains, crucial for successful reproduction in complex social societies, and offer insights into the evolution of prolonged dependency.

INTRODUCTION

Among mammals, humans and great apes share an unusually extended immature phase spanning more than a decade between weaning and sexual maturity (1, 2). In humans, continuous provisioning (1–3) of food to weaned immatures throughout the extended period before attaining sexual maturity is thought to have profoundly shaped the evolution of humans by enabling extensive brain growth and affording immatures the social opportunities to learn complex foraging skills (1, 3). As with most mammals, in humans and great apes, mothers invest most in offspring care, primarily through lactation and carrying, and later potentially through agonistic support. We therefore posit that for selection to have favored postweaning maternal investment, immature offspring with living mothers should later have higher reproductive success relative to orphans, thereby providing an evolutionary mechanism for mothers to continue investing in immature offspring. However, the rarity of cross-generational data in long-lived species, including humans (4), makes it difficult to examine whether and how extensive postweaning parental investment affects the reproductive success of offspring. Here, we examine this topic using data from a closely related great ape, the chimpanzee.

Although few mammals provide or facilitate acquisition of food for weaned offspring (5, 6), maternal loss during the postweaning immature period affects offspring survival or development in some species with shorter life histories and smaller brain to body size ratios than apes. For example, maternal loss before sexual maturity (2 to 3 years) in red deer (*Cervus elaphus*) results in sons with smaller antlers and daughters giving birth later than those whose mothers remain alive (6). In baboons (*Papio cynocephalus*), maternal loss before sexual maturity (4 years) results in reduced offspring survival (7). Similar survival gains provided by mothers have also been demonstrated in two long-lived species with relatively large brain to body size ratios, orcas (*Orcinus orca*) and chimpanzees (*Pan troglodytes*)

(8, 9). These findings suggest that even in the absence of provisioning, mothers provide key benefits that aid offspring survival. Likely benefits are support against predators and conspecifics, information transfer, or acquisition of foraging patterns (7, 10).

In long-lived species, determining the impact of maternal loss upon later reproductive outcomes, a direct test of fitness, is problematic, as cross-generational data take decades to acquire. In humans, an additional problem is that sociocultural factors can be influential, such as those that provide buffering effects for orphans via “alloparental” care [e.g., (1, 4, 11)]. Hence, studies have examined the impact of maternal loss on survival, a less direct measure of fitness. In humans, motherless children under 2 years old have significantly reduced chances of survival compared to those with mothers. After weaning, in the societies tested, there is little effect of maternal loss on survival, likely due to the impact of effective alloparental care after weaning (11).

Looking to one of our closest living relatives, recent studies examining maternal loss in the postweaning immature phase in wild chimpanzees also reveal reduced survival (9). This is especially the case for sons (12), where maternal loss after aged 10 years continues to affect sons’ but not daughters’ survival. In addition, maternal loss slows growth during development in both sexes (13) and delays sexual maturity and first reproduction of daughters (14). Chimpanzees require a similar number of years to reach sexual maturity as humans (1), and both species maintain a flexible fission-fusion community structure so not all community members remain together every day (15). Nonetheless, chimpanzee offspring tend to travel, nest, and forage alongside their mothers until sexual maturity. After that point, sons, as well as daughters who do not emigrate, may continue to associate with their mothers at high rates compared to association rates with other female group members (16). Because of female-biased dispersal, typically, the only adult kin of mature females are their own male offspring. Chimpanzees have a polyandrous mating system, with no or limited paternal care (17, 18). Competition among males for reproduction is intense in chimpanzees (19–21), and while the presence of mothers may facilitate adult and adolescent son’s paternity success in closely related bonobos, mother presence has limited effects in the chimpanzee communities studied thus far (22).

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We examined the impact of maternal loss upon the reproductive careers of chimpanzee sons using a dataset including demography and paternity assignments across three communities of the Tai National Park, Ivory Coast, spanning, on average, 16.7 years (range, 5 to 27 years) per community. Our data include 48 paternity assignments from 12 and 11 males who were or were not “orphaned” by the mother’s death before the son reached social independence—aged 12 years in this population (23). We did not assess the impact of maternal loss on the reproductive careers of daughters, as they typically disperse at sexual maturity, making assessment of their reproductive success extremely difficult. This population of chimpanzees exhibits considerable reproductive skew, wherein alpha males sire more offspring than any other male, with little variation between other males (20, 21). Thus, arguably the best assessment for male quality across the reproductive lifetime is alpha tenure rather than maximum or mean dominance rank, which assume a more linear distribution of paternities. If maternal loss reduces competitive ability, then we expect orphans to experience less time as alpha males. We further predict that maternal loss increases the age at first siring, effectively affecting the number of reproductive years available to each male. Last, we expect that maternal loss results in lower observed reproductive success as measured by the number of offspring sired per conception opportunity.

Because high rates of mortality occur within the first years of life in chimpanzees (24) and noninvasive genetic sampling of younger infants is extremely challenging, we could only estimate siring of viable offspring, that is, those surviving to ≥ 2 years of age ($n = 48$ assigned paternities). These represent more than 95% of all offspring surviving to 2 years during the study period. We corrected for the number of conception opportunities of viable offspring that each male was exposed to after sexual maturity and included those with ≥ 4 reproductive years. Sexual maturity is taken as the minimum known siring age for this population (10 years). Note that this is earlier than sons’ social independence from mothers (12 years). In this sample, only two paternities were attributed to males younger than 12 years, and neither were orphans.

RESULTS

Impact of maternal loss on competitive ability

First, to determine whether maternal loss specifically affects their sons’ quality over their reproductive lifetime, we tested whether orphans experience shorter alpha tenure relative to non-orphans (model 1). Here, we fitted a linear model using a Gaussian error structure with identity link function, with orphan status as the test predictor. Alpha tenure is the years spent holding the alpha position across each males’ reproductive years (means \pm SD, 1.75 ± 2.49 years; dataset S1). Those who never became alpha ($n = 11$) were marked as zero. We included a measure of male-male competition, the average number of sexually mature males in the community per conception during individuals’ lifetime (aged 10 years until death or to current age), as a control variable. We also included the number of reproductive years per male as a control variable, as this is expected to affect alpha tenure in this high mortality population (24).

Maternal loss tended to negatively affect alpha tenure ($P = 0.068$), with orphans’ alpha tenure length less than half that of sons who did not experience maternal loss before aged 12 years (full-null model comparison likelihood ratio test, $F_{3,19} = 3.718$, $P = 0.068$; Fig. 1A and Table 1). The Tai chimpanzee population has relatively high

reproductive skew (21) with alpha males siring between 38 and 67% of offspring, when there are less than 10 males in a community (20), as is the case in this dataset. Each other male sires $<20\%$ of offspring (20, 25). However, to control for other possible influences of dominance, we repeated the model exchanging alpha tenure for average dominance rank across reproductive lifetime, including tenure of each rank. The full versus null model comparison was nonsignificant (likelihood ratio test, $F_{3,19} = 0.026$, $P = 0.872$).

Age at first sire

We next asked whether chimpanzee male orphans sire their first offspring at a later age compared with non-orphans (model 2). To do this, we fitted a linear model with Gaussian error structure, with orphan status as the test predictor, and once again, controlling for male dominance rank as a measure of quality. Here, maximum dominance rank attained until first siring was used rather than alpha tenure from model 1, as most males sired their first offspring before attaining the alpha position. We also controlled for male-male competition, here, the average number of adult males in the community per conception from aged 10 years until death or current age. Orphaned males sired their first offspring, on average, 3 years later (means \pm SD, 16.32 ± 2.00 years) than non-orphans (12.93 ± 1.63 years) (full-null model comparison likelihood ratio test, $F_{3,19} = 15.454$, $P = 0.0008$; Fig. 1B and Table 1).

Impact of maternal loss on reproductive success

Third, to test whether postweaning maternal loss affects the number of offspring males sire when adult, we used the same dataset as in model 1 and fitted a general linear model with Poisson error structure and log link function, including orphan status as the test predictor (model 3). We also included alpha male tenure as a control predictor for male quality. Again, as in model 1, alpha tenure is likely to better account for reproductive skew than other dominance measures. Siring potential is likely to decrease with increased male-male competition. Therefore, to account for potential male-male competition, we included the inverted average number of males as an offset term. By including the inverted number, we account for an expected negative effect of the number of males on siring potential. Siring probabilities are also expected to increase with increased conception opportunities, and hence, conception opportunities across each male’s reproductive lifetime are included in the model as an offset term. The dataset included $n = 23$ males, $n = 48$ offspring with assigned paternities, and $n = 21$ mothers of adult sons (dataset S1; table S1 shows the distributions of model variables).

We found that orphans ($n = 12$ males and $n = 11$ mothers) had, on average, half as many offspring per conception opportunity ($n = 12$ offspring) as other males ($n = 11$ non-orphans, $n = 10$ mothers, and $n = 36$ offspring) (full-null model comparison likelihood ratio test, $\chi^2 = 5.871$, $df = 1$, $P = 0.015$; means \pm SD, orphan = 0.08 ± 0.12 and non-orphan = 0.2 ± 0.14 offspring/conception opportunity; Fig. 1C and Table 1). Males who held the alpha position for longer also had more offspring ($P = 0.013$; Table 1 and Fig. 1D). Fifty-two percent of males became alpha and sired 87.5% of the viable offspring. The 48% of males who never became alpha sired only 12.5% of the offspring, suggesting the potential for strong reproductive skew in this dataset. To control for other possible influences of dominance, we repeated the model exchanging alpha tenure for average dominance rank across each male’s reproductive lifetime, which did not change the results (table S2).

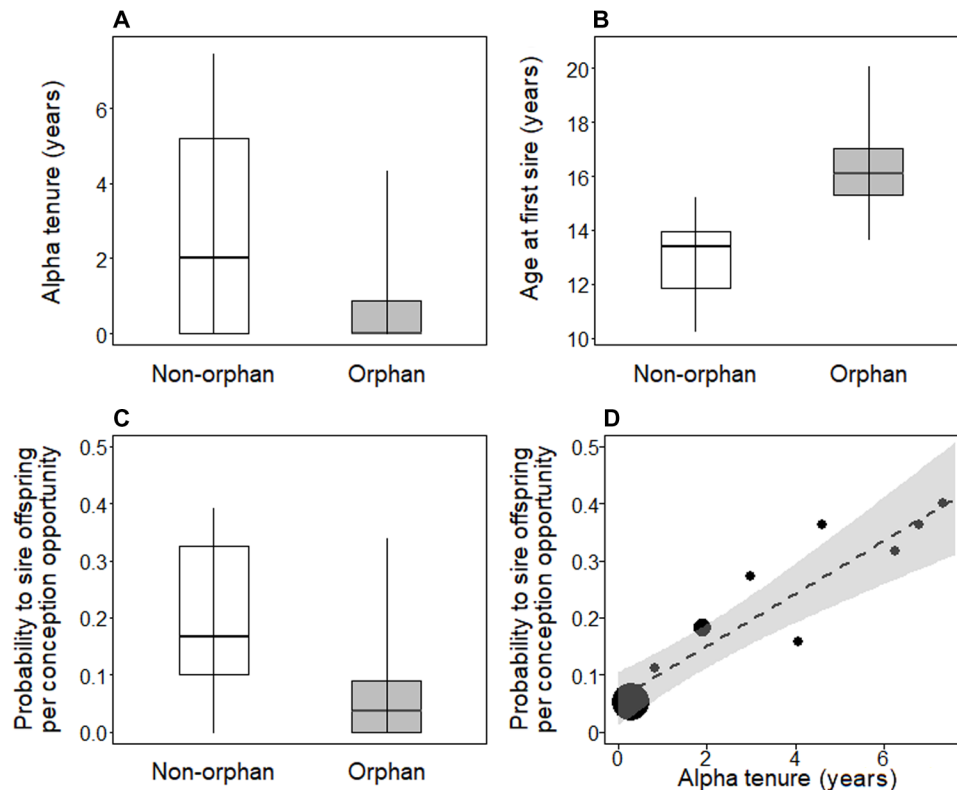


Fig. 1. The impact of maternal loss on male chimpanzees' reproductive careers. Impact of maternal loss on (A) alpha tenure, (B) age at first sire, and (C) likelihood of siring offspring. (D) Impact of alpha tenure on likelihood of siring offspring. Boxes show the median, 25th, and 75th percentiles, and whiskers are interquartile range $\times 1.5$. (D) Model line (dashed) and 95% confidence intervals (gray), and larger points denote larger number of observations.

Last, if prolonged maternal investment affects the quality and reproductive success of sons, then we expect age at maternal death to negatively correlate with alpha tenure and positively correlate with reproductive success. However, as the dataset was too small for reliable statistical inference of these effects, we tentatively show the predicted correlations in a supplementary figure (fig. S1).

DISCUSSION

Our results show that, in a species in which males experience considerable competition over mates, males whose mothers die when they are weaned immatures are subsequently less competitive than non-orphaned males in producing offspring. Specifically, orphaned sons lose out on alpha tenure, sire their first offspring at a later age, and have fewer offspring that survived to age 2 years during their reproductive years. Our combined measure of reproductive success demonstrates that either orphan males lose out on siring or that their offspring are less likely to survive to 2 years. Either way, we conclude that mothers continue to provide key benefits to sons throughout the prolonged postweaning immature phase, at least until sexual maturity at aged 12 years. It seems that these maternal benefits contribute both to sons' competitive ability as an adult and to sons' reproductive success.

Alpha tenure—the number of years each son maintained the alpha position—had a moderate positive effect on reproductive success, with doubling of tenure length increasing reproductive success by $>50\%$. Maternal loss negatively affected alpha tenure,

with orphans typically having less than half the alpha tenure length of non-orphans. A recent study in the same population showed that chimpanzees orphaned after weaning lose out on growth during development (13). Together, these results demonstrate that, although direct provisioning of food by mothers is rare, mothers' presence contributes to sons' growth during development and competitive ability as adults.

Maternal loss had an additional negative impact on reproductive success that was independent of alpha tenure (model 3). We posit that mothers may not only contribute to sons' competitive ability but a mothers' presence may also provide other kinds of benefits, which contribute to sons' fitness. In chimpanzees, given that subordinates do sire some offspring, and at higher rates in populations with more males than Tai (specifically Ngogo as well as Gombe and Sonso populations) (21), it is considered that attaining dominance is not the only reproductive strategy (and may explain why the number of males had little impact on reproductive success or alpha tenure). A potential alternative male strategy is building long-term relationships with females, which has been shown to increase the likelihood of gaining copulations with that female or of siring her offspring (16, 26, 27). Maintaining long-term affiliative relationships may require certain social skills, which are thought to vary across individuals (7, 28), and may be negatively affected by early maternal loss (7).

Thus, maternal presence may benefit weaned immature sons in several ways. First, mothers may provide indirect nutritional benefits. As ripe fruit specialists, chimpanzees experience contest competition

Table 1. Models testing the impact of maternal loss on male chimpanzee alpha tenure, age at first siring and reproductive success. Bold, $P < 0.05$; italic, $P < 0.01$. Reference category of factors is in parenthesis. Asterisk (*) indicates test predictor. Full versus null model comparisons: (1) Gaussian: $F_{3,19} = 3.718$, $P = 0.068$; (2) Gaussian: $df = 1$, $F_{3,19} = 15.454$, $P = 0.0008$; and (3) Poisson: $df = 1$, $\chi^2 = 5.871$, $P = 0.015$. Offset terms: average number of males present per conception and number of conceptions resulting in viable births across reproductive years per male. Z transformed: all continuous predictor variables. Effect sizes = R^2 .

Term	Estimate	SE	CI	F	P	R ²
1. Alpha tenure						
Intercept	2.461	0.505	2.121, 2.829	–	–	–
Orphan (yes)*	–1.355	0.702	–1.707 to –1.033	3.718	0.068	0.163
Reproductive years	1.547	0.362	1.191 to 1.718	18.240	0.0004	0.489
Average males per conception	–0.572	0.360	–0.797 to 0.374	2.519	0.128	0.117
2. Age at first siring						
Intercept	13.435	1.205	12.292 to 13.849	–	–	–
Orphan (yes)*	3.041	0.773	2.763 to 3.448	15.453	0.0008	0.448
Maximum dominance	0.725	0.399	0.519 to 0.904	3.287	0.085	0.147
Average males per conception	–0.051	0.176	–0.127 to 0.065	0.085	0.772	0.004
Term	Estimate	SE	CI	χ^2	P	
3. Number of offspring						
Intercept	–0.010	0.234	–0.133 to 0.237	–	–	–
Orphan (yes)*	–0.863	0.367	–1.103 to –0.718	5.872	0.015	0.297
Alpha tenure	0.337	0.138	0.239 to 0.400	6.133	0.013	0.329

due to the ephemeral patchy nature of ripe fruit (29, 30). Thus, mothers may contribute to their weaned offspring's nutritional status through providing agonistic support at food patches and, in addition, by reducing predation risk (31, 32). As weaned offspring typically travel with their mothers, mothers likely also assist in finding patchy, ephemeral foods. As well as individual learning opportunities, mothers may provide food-related social learning opportunities either directly from themselves (33) or indirectly by facilitating their sons' close association with other group members [e.g., (34)]. These social learning opportunities could include better nutrition obtained from learning extractive foraging techniques on nutrient-rich foods (33, 35) and acquisition of hunting skills (36–39). Mothers also sometimes directly share energy-rich, difficult-to-access foods and the tools required for extractive foraging with their offspring, such as nuts, honey, and insects (33, 35), although this is not considered to be at a frequency to constitute provisioning (1, 2).

Second, mothers may provide social benefits, such as through social buffering in the face of exposure to stressors. Social buffering can limit the risk of chronic hypothalamic-pituitary-adrenal (HPA) axis function (23, 40), hence having a positive impact on health and survival (28). Mothers, for example, continue to groom offspring through the immature years into adulthood, where grooming kin is associated with the release of a neuropeptide, oxytocin (Fig. 2) (41). Oxytocin is thought to down-regulate HPA axis function, potentially reducing detrimental effects from repeated exposure to stressors (40). Little discussed in previous studies, social benefits may also accrue through social learning opportunities that facilitate adult social life, either through acquiring skills needed for the building and maintaining of social bonds or for using complex social and coop-

eration skills required to out-compete out-group members (23, 42) and in-group conspecifics (19, 21, 43, 44). This could be particularly pertinent in highly territorial, fission-fusion social systems, such as chimpanzees. Successful adult male chimpanzees need to not only navigate the social complexities of securing coalition partners to outcompete in-group rivals (19, 44) but also maintain territorial defense by cooperating with the same individuals with whom they compete intensely over mating opportunities (23, 45, 46). Research in humans and rodents show that the extent of maternal nurturing received may affect offspring's later adult social skills (47, 48). Thus, a broader take on the benefits accrued from prolonged maternal investment in species with extended immature periods to include social benefits may be justified in chimpanzees and other species.

In other long-lived species with prolonged immature periods, adult sons may continue to gain benefits from their mothers' presence. In orcas, living mothers continue to influence their adult son's survival, potentially due to maternal knowledge of ephemeral food sources (8). In primates, for sons, mothers' presence at the time of siring increases the reproductive success of sexually mature male muriquis (*Brachyteles arachnoides*) (49) and bonobos (*Pan paniscus*) but not of chimpanzees (22). In each case, the reported influence is during adolescence or adulthood, whereby mothers who maintain bonds with their sons gain indirect fitness benefits in the form of grandoffspring. In species where females are the philopatric rather than the dispersing sex, coresidence and social bond maintenance of adult daughters with mothers is well known to provide direct and indirect benefits to both mothers and daughters, by increasing the survival of each other and of their offspring (50–52). In addition, in



Fig. 2. Mother, Sumatra, grooming her 9 year old son, Solibra. Photograph by L.S.

female baboons, maternal loss in the juvenile period is known to affect later survival (7). Here, we show specifically that the mother's presence during immature periods provides reproductive benefits to sons, apparently at least in part by enhancing their ability to out-compete other males in siring offspring. Additional studies with larger datasets could determine, first, if sons orphaned at younger ages experience greater deficits and, second, if orphans adopted by others, as can occur in chimpanzees (53), experience fewer deficits.

Across species, we see that mothers' presence after weaning affects survival, competitive abilities, and reproductive success. What remains unclear and needs to be addressed in future studies is by what mechanisms mothers' presence enhances reproductive success of her offspring and how much active investment and care is involved. Of particular interest in socially complex species that gain fitness through building long-term relationships (50–52) is how much mothers contribute to learning of social skills required to maintain these relationships.

We acknowledge the possibility that differences in reproductive success were driven by hereditary factors rather than maternal loss. For example, mothers who survive longer may do so, because they are better quality, and the genes responsible may produce better quality sons who gain higher reproductive success than rivals. This potential confound is common to studies of this type (22) and is difficult to address with the genomic and genealogical data available from slow life-history wild animals. Although hereditary factors may play a role in driving the patterns we observe, we argue that the particular structure of chimpanzee society featuring male philopatry and life-long associations between males and mothers makes our inference regarding the importance of the prolonged mother and offspring relationship highly plausible.

The maternal effects we observe are in contrast to a recent meta-analysis demonstrating the different contributions of maternal and heritable effects across 64 species including short-lived vertebrates and invertebrates. The meta-analysis showed that, on average, maternal effects accounted for 10% and heritability for 20% of phenotypic variation (54). Unlike in this study, the impact of maternal effects was not elevated for species that provided maternal care after egg laying or parturition compared to those that did not [but see (55)]. Thus, the strong effects of postweaning maternal

investment reported in this study—and other studies on long-lived species (8, 9, 12)—are more pronounced than the maternal effects reported for the shorter-lived mammals in (54) and are greater than the heritable and maternal effects combined in the meta-analysis (55). This strongly suggests that maternal care in long-lived species with prolonged immature ontogeny may differ in kind from that provided by shorter-lived mammal and non-mammal species.

In summary, we provide evidence that prolonged association of mothers with their immature sons provides substantial reproductive benefits, despite evidence of only limited direct postweaning provisioning of food. In anthropology, a central hypothesis for explaining rapid encephalization in the hominid lineage, as well as human's prolonged juvenile dependency, is related to extended parental provisioning of food for years beyond weaning (1, 2). Our closest living relatives, the other great apes including chimpanzees, already show selection for rapid encephalization and prolonged juvenile dependency since the split from the catarrhine/old world monkey clade. These traits may then have been shared with the common ancestor of the great apes including humans and may be best explained by the social benefits of maternal investment described here, which we call the social benefits hypothesis. The addition of extensive food provisioning, potentially facilitated by alloparenting, may then explain the more extreme juvenile dependence and encephalization seen in humans, as suggested by the prolonged juvenile dependency hypothesis.

While further research is needed to ascertain exactly what chimpanzee mothers provide their sons with, we posit that benefits likely include both indirect nutritional gains and social benefits. In terms of social benefits, we expect that offspring are more likely to receive these benefits from mothers than from other community members. We expect social benefits to include, first, social buffering, which is known to be effective in stress reduction and, second, effective social learning of social skills required for navigating the complexities of chimpanzee adult social life. We expect both to affect reproductive success. We posit that the socioecological environment in which chimpanzees have evolved makes mother-offspring association throughout the extended immature period influential in producing males that can accrue high paternity success. Chimpanzees and humans share notable similarities in traits such as life history (similarly extended immature period), social structure (fission-fusion societies), and socioecological factors that lead both species to express highly territorial behavior, requiring group-level cooperation to defend territories. We suggest that these similarities make chimpanzees a good model species for examining the evolution of prolonged immature dependency, for which chimpanzee mother-offspring associations may constitute a precursor.

MATERIALS AND METHODS

Behavioral data

Data were collected at the Taï National Park, Côte d'Ivoire (5°45'N, 7°7'W) (56) on three different chimpanzee communities (north, south, and east). Systematic observation including collection of demography data covers the following periods (57) for each community: north: 1982 to present, mean adult (≥ 12) group size = 18.894, SD = 12.562, range size = 9.25 to 16.24 km²; south: 1993 to present, mean adult (≥ 12) group size = 22.962, SD = 4.586, range size = 15.49 to 36.59 km²; east: 2000 to present, mean adult

(≥ 12) group size = 19.95, SD = 3.103, range size = 20.6 to 34.45 km². For the spatial location of each territory, see (58). Behavioral data included nest-to-nest focal follows (59) of individuals of the different social groups on a daily basis by trained local assistants and researchers, providing a continuous record of births, deaths, dominance rank, and alpha male tenure length. We applied a likelihood-based adaptation of the Elo rating approach (60–62), standardized to a range between 0 and 1, to assess males' dominance relationships within each group using submissive unidirectional pant grunt vocalizations (63). To standardize dominance rank across periods with varying numbers of males, we converted ranks to a proportion between 0 and 1, depending on the number of males at any given time. This is necessary because the number of males varied across years, and thus, the same rank (R) held a different significance in different years (e.g., the sixth ranking male is the lowest ranking when the group consists of six males but is midranking when the group consists of 12 males). Thus, we standardized R to the number of sexually mature males aged ≥ 10 years in the hierarchy (nm) using the following formula: $(nm - R)/(nm - 1)$ (64).

Parentage analysis using microsatellite genotyping of DNA obtained from noninvasive samples has been carried out on members of these study groups since 1999. The current dataset includes 259 individuals with an average of 83% complete genotypes at 19 loci. Briefly, ~100-mg samples of feces were extracted using either the QIAamp DNA Mini Stool Kit (QIAGEN) or the GeneMATRIX Stool DNA Purification Kit (Roboklon) as instructed. Aliquots were first amplified at all 19 loci simultaneously and then subsequently reamplified using fluorescently labeled primers as detailed in (65). Resultant genotypes were compared using the "identity analysis" function of CERVUS (66) to confirm identities, and the "parentage analysis" function was used to confirm maternities and assign paternities, using confidence assessments of 80 and 95%. Each of the paternity assignments received a high likelihood, and other potential sires were excluded by two or more mismatches. Parentage analyses revealed fathers and confirmed mothers for adult males for north group from 1990, south group from 1999, and east group from 2012.

We limited the dataset to males who survived at least four reproductive years, taken from the age of the youngest siring age known for this population (10 years old) until 14 years of age, and for whom we have a near-complete siring history (i.e., were at least 10 years old when fecal sample collection and paternity analysis were established such that >90% of offspring reaching 2 years old had assigned paternities). Last, we limited siring to viable offspring, those who survived ≥ 2 years of age. This gave us a sample across groups of $n = 23$ sexually mature males (≥ 10 years old) with known mothers ($n = 21$) and a near-complete siring history of offspring that survived to ≥ 2 years (with 95% of paternities known across the study period). $n = 12$ of these were orphans, defined as the mother dying before the sons reached social independence from their mothers, when males in this population associate and travel more with the adult males than with their mothers (12 years old) (37, 62). These orphans, who reached the minimum age of 14 years, lost their mothers between the ages of 4 and 12 years old (dataset S1), where weaning occurs between 4 and 5 years old (9, 31). Thus, the sample of orphans represents maternal loss during the postweaning period. This sample included $n = 48$ offspring with genetically identified fathers.

Statistical analysis

We conducted a series of models to assess the impact of maternal loss on male reproductive success.

First, to determine whether maternal loss affected alpha tenure, we fitted a linear model with orphan status (y/n) as the test predictor, using a Gaussian error structure and an identity link function. To control for the impact of the number of sexually mature males in the group influencing the likelihood of achieving alpha position, we included the average number of males present across conceptions that lead to viable offspring. To control for number of reproductive years until death or current age, we included the number of reproductive years per male as a control variable. We reran the model switching alpha tenure for average dominance rank, such that we calculated the average dominance rank across each males' reproductive lifetime while considering the duration each male held each dominance position [if a male held a position a for x duration, b for y duration, and c for z duration, then we calculated the average dominance rank as follows: $(a * x + b * y + c * z)/(x + y + z)$].

We fitted all models in R (version 3.5.3) (67), using the functions *glm* and *lm* of the R package "lme4" (68). For all models, we conducted appropriate checks on collinearity with all variables with variance inflation factor (< 3), model stability, and model assumptions. We verified the assumptions of normally distributed and homogeneous residuals by visual inspection of Q-Qplots and residuals plotted against fitted values. These evaluations did not reveal obvious deviations from model assumptions.

For the Poisson model, we checked for overdispersion, which did not reveal any issue, being < 1 . We log-transformed the response variable of alpha tenure (model 1) to better approximate a normal distribution. We analyzed the statistical significance of models using full-null comparisons and a likelihood ratio test for the Poisson model and with F tests for the Gaussian models. We measured the significance of each single term by comparing reduced models to the full model using the *drop1* function in R (69). Model stability tests revealed no influential identities.

Second, to determine whether chimpanzee male orphans sire their first offspring at a later age compared with non-orphans, we fitted a linear model using a Gaussian error structure and an identity link function. We tested the age at first sire as the response variable with orphan (y/n) as the test predictor. To account for male quality and potential male-male competition, we added the control predictors of maximum dominance rank reached by the age at first sire and the average number of males present across conceptions that led to viable offspring from age 10 years until age of first sire, respectively. Given that chimpanzees had sired their first offspring before they became alpha, we used maximum dominance rank rather than alpha tenure in this analysis.

Third, to test whether postweaning maternal loss affects the number of viable offspring males sire when adult, we fitted a general linear model using a Poisson error structure and log link function. We tested the response variable, the number of offspring sired, against the categorical test predictor, orphan (y/n). To control for variation in male quality across each male's reproductive lifetime, we added the control predictor that we expected to best reflect their lifetime dominance rank history: alpha male tenure length (in years). Those who never became alpha were marked as zero. Siring potential is likely to decrease with increased male-male competition. Therefore, to account for potential male-male competition, we

included the log of the inverted average number of males present for each conception during each male's reproductive lifetime as an offset term. In addition, as siring probabilities are expected to increase with increased conception opportunities, we accounted for the conception opportunities using the number of conceptions that led to viable offspring (2 years old) across each male's reproductive years by adding an offset term of the log of total number of births that reached 2 years of age during each males' reproductive years. By this, we simultaneously considered both the length of reproductive age and conception opportunities per male. Last, we reran the model switching alpha tenure for average dominance rank, such that we calculated the average dominance rank across each males' reproductive lifetime while considering the duration each male held each dominance position [if a male held a position a for x duration, b for y duration and c for z duration, then we calculated the average dominance rank as follows: $(a^*x + b^*y + c^*z)/(x + y + z)$; table S2]. To determine effect sizes, for the Gaussian models, we calculated R^2 from the residuals' sum of squares (RSS) using the drop1 output and used the following formula: (RSS predictor A – RSS intercept)/RSS predictor A. For Poisson models, we calculated the log likelihood of the full model and reduced models, with the model missing one predictor at a time.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/38/eaaz5746/DC1>

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Acknowledgments: We thank the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique and the Ministère de Eaux et Forêts in Côte d'Ivoire and the Office Ivoirien des Parcs et Réserves for permitting the study. We are grateful to the Centre Suisse de Recherches Scientifiques en Côte d'Ivoire and the staff members of the Tai Chimpanzee Project for support. We are grateful to R. Mundry for statistical support and A. Nicklisch, V. Staedele, and C. Rowney for lab work. We thank K. Langergraber for valuable comments reading an early version of this manuscript. **Funding:** This study was funded by the Max Planck Society under the Evolution of Brain Connectome Project and the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 679787) awarded to C.C. **Ethics statement:** All methods were noninvasive and were approved by Ethics Committee of the Max Planck Society (4 August 2014) and the European Research Council. **Author contributions:** C.C. and R.M.W. conceived the study and compiled data from long-term Tai Chimpanzee Project database, including data from L.S. Genetic analyses were conducted by L.V. C.C. and L.S. compiled the data, conducted the behavioral analyses, and devised the figures. C.C. wrote the paper with important contributions from L.S., L.V., and R.M.W. All authors gave final approval for publication and agree to be held accountable for the work performed therein. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability statement:** All data needed to evaluate the conclusions in the paper are present in the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 13 December 2019

Accepted 28 July 2020

Published 18 September 2020

10.1126/sciadv.aaz5746

Citation: C. Crockford, L. Samuni, L. Vigilant, R. M. Wittig, Postweaning maternal care increases male chimpanzee reproductive success. *Sci. Adv.* **6**, eaaz5746 (2020).

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Sci Adv **6** (38), eaaz5746.

DOI: 10.1126/sciadv.aaz5746

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